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A test of food web hypotheses by exploring time series of fish, zooplankton and phytoplankton in an oligo-mesotrophic lake

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Abstract

The strength of trophic cascades in the pelagic area of lakes at low productivity has been discussed intensively, but predictions of trophic coupling differ strongly. Many studies suggest that trophic cascades are weak in oligotrophic lakes, but some models discussed that trophic interactions might be strong at low nutrient concentration. Here, we used time series over 9 (phytoplankton and zooplankton) or 6 (fish) years from the oligo-mesotrophic Lake Stechlin (Germany) to explore correlative relationships between biomasses of these trophic levels. The fourth trophic level of piscivorous fish was almost absent in the pelagic area. The biomass of planktivorous coregonid fishes was not at all correlated to total zooplankton biomass, which was dominated by calanoid copepods. However, there was a strong negative correlation of adult coregonid biomass to the proportion of *Daphnia* in zooplankton, and a strong positive correlation of adult fish to proportion of calanoid copepods. Zooplankton and phytoplankton biomasses were not correlated except for a significantly negative correlation between *Daphnia* biomass and biomass of Cyanobacteria. Overall, our results suggest that planktivorous fish may modify the zooplankton structure, but not the zooplankton biomass, in lakes of low productivity. However, this top-down effect by fish does not cascade further down to the phytoplankton biomass or community structure, confirming earlier hypotheses that trophic cascades are weak in oligotrophic lakes.
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Introduction

The strength of top-down interactions in the pelagic area of lakes has been discussed intensively, both from the perspective of basic research (e.g., Brooks and Dodson, 1965; Carpenter et al., 1985; Brett and Goldman, 1996) and with respect to the application as a management tool to improve lake water quality (i.e., biomanipulation; Shapiro et al., 1975; DeMelo et al., 1992; Mehner et al., 2002). Hypotheses on the correspondence between the strength of pelagic trophic cascades and the trophic state of lakes can be grouped into three distinct concepts. The first concept assumes that trophic cascades are strongest at intermediate

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productivity, and weaker at both oligotrophic and eutrophic states. According to the intermediate trophic state hypothesis, Carney (1990) and Elser and Goldman (1991) suggested that the grazing by herbivorous zooplankton (mainly *Daphnia*) on phytoplankton is maximised at mesotrophic conditions. This hypothesis has been supported by empirical analyses in 466 temperate lakes where the *Daphnia* proportion of total zooplankton biomass showed a unimodal curve, peaking at intermediate levels of total phosphorus concentration (Jeppesen et al., 2003). Similarly, the food chain theory suggested that an efficient control of planktivorous fishes by abundant populations of piscivorous predators occurs only at mesotrophic conditions (Persson et al., 1992). Consequently, only at intermediate productivity was phytoplankton expected to be efficiently controlled by zooplankton grazing. At oligotrophic states, the low overall productivity of the system prevents the establishment of a fourth trophic level (Persson et al., 1992).

The top-down:bottom-up hypothesis predicted that the strength of trophic cascades is a negative function of enrichment because of the increasing importance of inedible algae along the nutrient gradient such that phytoplankton control by zooplankton grazing was expected to be strong only in oligotrophic lakes (McQueen et al., 1986). The third hypothesis (referred to as nutrient enrichment) stated in contrast that the grazing effect of zooplankton on phytoplankton is a positive function of nutrient enrichment (Sarnelle, 1992), and that the effects of zooplankton on phytoplankton would be low in oligotrophic lakes because of an overall low zooplankton biomass in which inefficient grazers like copepods dominate (Elser and Goldman, 1991). A weak trophic cascade at low productivity was corroborated by empirical studies which failed to detect a significant influence of fish on zooplankton and phytoplankton biomasses in Canadian oligo-mesotrophic lakes (Currie et al., 1999; Bertolo et al., 2005).

Accordingly, the intermediate trophic state hypothesis, the food chain hypothesis and the nutrient enrichment hypothesis predict weak trophic cascades in oligotrophic lakes, whereas the top-down:bottom-up hypothesis suggests stronger pelagic interactions at low productivity. Therefore, we tested these hypotheses by analysing the inter-annual variability of phytoplankton, zooplankton and fish biomasses in the deep, oligo-mesotrophic Lake Stechlin (Germany). In this lake, the dominant planktivorous fish species were coregonids, namely vendace (*Coregonus albula*) and the lake-endemic *Coregonus fontanae* (Schulz and Freyhof, 2003; Schulz et al., 2006). Vendace populations are especially suitable for such analyses since they show population cycles with strongly differing abundances between subsequent years due to negative inter-cohort interactions and differential recruitment rates (Hamrin

and Persson, 1986; Helminen and Sarvala, 1997). Accordingly, we expected that the fluctuating fish populations may induce a trophic cascade differing in strength between the years such that negative correlations of time series between trophic levels would mainly reflect real interactions in the pelagic area of Lake Stechlin.

Material and methods

Lake description

Lake Stechlin is situated about 100 km north of Berlin (Germany). It has a surface area of 4.25 km^2 and mean and maximum depths of 22.3 and 69 m, respectively. According to long-term (1998–2006) annual averages of total phosphorus concentrations (grand mean over nine years $= 11$ mg m^{-3}, range 10–14 mg m^{-3}) and chlorophyll-*a* concentrations (grand mean over nine years $= 3$ mg m^{-3}, range 2–4 mg m^{-3}), the lake can be considered as oligotrophic to weakly mesotrophic (Koschel et al., 2002; Koschel and Adams, 2003).

According to earlier analyses of trophic variables with high spatial and temporal resolution in Lake Stechlin (Mehner et al., 2005), horizontal variability between the lake basins is low such that samples taken at the deepest location of the lake reliably reflect biomass and assemblage composition of the entire pelagic area. However, there was a strong seasonal effect on variability of samplings (Mehner et al. 2005). Accordingly, we used annual averages of phytoplankton and zooplankton to integrate over the entire season. Fish samples were taken in June since both young-of-the-year vendace and the recruited 1+ vendace and Fontane cisco are reliably recorded as pelagic targets by hydroacoustics during this month (Mehner and Schulz, 2002; Mehner et al., 2007).

Phytoplankton sampling and analyses

Phytoplankton sampling and analyses were conducted according to Padisák et al. (2003). Samples from 10 depths evenly distributed within the 0–25 m layer were taken at the sampling site located at the maximum depth of the lake. Phytoplankton composition and biomass were then estimated from integrated samples. Sampling frequency varied between weekly and monthly, with more frequent sampling during the vegetation period. Phytoplankton species were identified using the most up-to-date phycological manuals and literature. The phytoplankton species were grouped into the larger systematic groups (divisions) Cyanobacteria, Chlorophyta, Cryptophyta, Dinophyta and Heterokontophyta. The two most important classes of Heterokontophyta in

Stechlin, the classes Chrysophyceae and Bacillariophyceae, were grouped separately. The phytoplankton species which do not belong to these systematic categories were grouped as 'other phytoplankton'. A minimum of 400 settling units per species (cells, filaments or colonies) were counted in each Lugol-fixed sample, giving a counting accuracy of $\pm 10\%$ for total phytoplankton (Lund et al., 1958). Phytoplankton biomass was estimated by geometrical approximations using the computerised plankton counter Opticount (Hepperle and Schmidt-Halewicz, 2000). For each systematic group the monthly and annual means were calculated. Additionally, autotrophic picoplankton was also counted in parallel samples with epifluorescence technique as described in Padisák et al. (1997). All values were expressed as g fresh weight (fwt) m^{-2}, scaled to the mean depth (22.3 m) of Lake Stechlin.

Zooplankton sampling and analyses

Crustacean plankton was collected by vertical tows from 0–22 m (mean depth) and 22–65 m, respectively, using a cone-shaped closing net (mesh size 90 µm, opening 27 cm^2; length 1.2 m, Hydrobios, Kiel, Germany) at the deepest location of the lake (NE basin). From April to October, the lake was sampled biweekly. For the rest of the year monthly samples were taken. Samples were preserved in a 4% sugar-formaldehyde solution. A sub-sample containing at least 100 individuals of the dominating species or group was counted using an inverted microscope at 60-fold magnification. Mean length was estimated by measuring 30–40 individuals. Biomass of the crustaceans was calculated using published length–weight relationships (Bottrell et al., 1976; Kasprzak, 1984). Dry weight (dw) and carbon (c) were converted into fresh weight (fwt) following Winberg et al. (1971) (dw = c∗2, fwt = dw∗5). Taxa were identified according to Flößner (1972, 2000), Lieder (1996), Einsle (1993) and Kiefer and Fryer (1978).

Zooplankton were categorised into six groups, namely daphnids (*Daphnia cucullata*, *D. hyalina*, *Daphnia hyalina x cucullata*), *small cladocerans* (*Bosmina coregoni*, *Bosmina longirostris*, *Alonella* sp., *Ceriodaphnia quadrangula*, *Alona* sp., *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Polyphemus pediculus*), calanoid copepods (*Eudiaptomus gracilis*, *Eurytemora lacustris*, *Heterocope appendiculata*), cyclopoid copepods (*Thermocyclops oithonoides*, *Mesocyclops leuckarti*, *Diacyclops bicuspidatus*, *Acanthocyclops* sp., *Paracyclops fimbriatus*), juvenile copepods (copepodit and nauplii stages) and invertebrate predatory zooplankton (*Leptodora kindtii*, *Bythotrephes longimanus*).

Conversion of invertebrate abundance into biomass was done by assuming a fixed biomass for *Leptodora kindtii* and *Bythotrephes longimanus* of about 500 µg fwt (see formula in Mehner et al., 1995), since length measurements were not available.

Zooplankton biomass was calculated as areal value over the total water column (g fresh weight (fwt) m^{-2}) summed from epilimnetic and hypolimnetic biomasses. To allow for comparison with phytoplankton and fish biomasses obtained from differing depth ranges, this value was finally scaled to the mean depth of the lake (22.3 m; i.e., multiplied by $22.3/65 = 0.34$). Group-specific annual average biomasses were calculated from the individual samples.

Fish sampling and analyses

Fish biomass was estimated by hydroacoustic methods. Night-time surveys were conducted every June in the years from 2000 through 2006 except for 2004. Since vendace larvae hatch in April, the juveniles are of sufficient size to be identified by hydroacoustics in June (Mehner and Schulz, 2002). Accordingly, annual surveys in June are expected to record appropriately the inter-annual differences in fish population biomass due to variable fish recruitment. On-axis calibrations of the hydroacoustic systems were performed at least once per year by a standard copper sphere of 23.0 mm diameter (reference target strength (TS) = −40.4 dB at 1490 m s^{-1} sound speed). Each annual survey covered five transects about 1 km long, all with a maximum depth of least 45 m, in the central and north basins of Lake Stechlin (for location of transects, see Mehner et al., 2007). We used either a SIMRAD EY-500 120 kHz split-beam transceiver with $4° \times 10°$ elliptical transducer (years 2000–2002) or a SIMRAD EY-60 120 kHz split-beam transceiver with $7° \times 7°$ circular transducer since 2003. Pulse duration was 0.1 or 0.3 ms (EY-500) or 256 µs (EY-60), and pulse interval varied between 0.1 and 0.4 s.

Data analysis was performed by the Sonar 5Pro software, version 5.9.5 (Balk and Lindem, 2005). Upper echo thresholds for file conversion were set to −80 dB (volumetric backscattering strength, S_v) and −75 dB (TS). Single echo detection (SED) was based on 0.8–1.2 relative pulse widths, a one-way beam compensation of 3 dB, and a maximum phase deviation of 0.8. The recorded file of each transect was split into 13 separate 5 m thick depth layers, starting outside of the near-field range of the transducer at 1 m water depth (1–6, 6–11 m,…, 61–66 m). These layers were separately analyzed to prevent biased estimates of total fish densities due to inhomogeneity in vertical distribution (see Mehner et al., 2005).

TS of echoes were converted into vendace total lengths (TLs) by

$$\text{TS (d}B) = 25.5 \log_{10} \text{TL (cm)} - 70.9$$

(Mehner, 2006). Estimates were limited to the potential length range of vendace (2–25 cm TL, identical to a TS

range between -60 and -36 dB). Areal fish abundances (ind. m^{-2}) per 5-m thick layer were converted into areal biomasses (g fresh weight (fwt) m^{-2}) by

$$fwt(g) = 0.00507 \, TL \, (cm)^{3.089}$$

(Mehner and Schulz, 2002). Finally, areal biomasses were summed over all vertical layers per transect, and an average areal fish abundance for Lake Stechlin was calculated from the five transects per survey. According to the frequency distribution of single targets, total biomass was split into biomass of fish <10 cm TL (i.e., mainly juvenile fish, TS <-45 dB) and biomass of fish >10 cm (i.e., mainly adult fish TS $\geqslant-45$ dB). Echoes stronger than -36 dB, i.e. >25 cm TL, were considered predatory fish (presumably perch, *Perca fluviatilis*, Anwand et al., 2003). Average depth of the five transects was 40 m. To allow for direct comparison with zooplankton and phytoplankton biomasses, all areal fish biomasses were multiplied by 0.56 to scale the data to 22.3 m mean depth of Lake Stechlin.

Statistical analyses

All time series (single groups of phytoplankton, zooplankton and fish biomasses) were tested for serial autocorrelation. There was no autocorrelation at annual lags -1, -2 or -3 years except for a weak negative correlation for calanoid copepod biomasses between the current and the previous years (lag -1 year, $r = -0.59$, Box–Ljung statistics $= 4.36$, $p = 0.037$). Accordingly, pairwise linear correlation coefficients (Pearson's r) were calculated between all time series, with particular emphasis on negative interactions between single groups from different trophic levels which would indicate the existence of a pelagic trophic cascade. We did not correct the significance level from $\alpha = 0.05$ to a lower, table-wide value by a sequential Bonferroni procedure according to recent discussions that the chance of many weakly significant correlations being spurious is extremely improbable (Moran, 2003). If we found weakly significant negative interactions between biomasses of fish and certain zooplankton groups, we tested in addition whether fish biomass and zooplankton assemblage structure (group proportions of total crustacean biomass) were negatively correlated. All calculations were performed by SPSS 9.0 (SPSS Inc. 1999, Chicago, IL, USA).

Results

Phytoplankton composition was dominated by Cyanobacteria only in 1998. From 1999 onwards, there was an increasing proportion of Bacillariophyceae in the phytoplankton such that this group dominated the total phytoplankton biomass by 48–61% in the years 2000–2006. Except for 1998 and 1999, Cyanobacteria, Chrysophyceae and Cryptophyta had intermediate biomasses, whereas Chlorophyta, Dinophyta and others (Euglenophyta, Xanthophyceae) contributed only marginally to total phytoplankton biomass (Fig. 1a). The total annual average phytoplankton biomass ranged between 8.47 (year 1999) and 18.87 (year 2006) g fwt m^{-2} (Fig. 1a).

Zooplankton biomass was clearly dominated by calanoid copepods (41–68% of total zooplankton biomass), with *Eudiaptomus gracilis* contributing strongest to biomass among all zooplankton species. *Daphnia* and small cladocerans (mainly *Bosmina longirostris*) contributed with 5–12% each to overall zooplankton biomass (Fig. 1b). The proportion of *Leptodora* and *Bythotrephes* was less than 1% all over the years (Fig. 1b). The annual average total zooplankton biomass varied between 1.19 (2006) and 3.66 (2002) g fwt m^{-2} (Fig. 1b).

The fish biomass varied 3.4-fold between 2.02 and 6.81 g fwt m^{-2} between 2000 and 2006 (Fig. 1c). Biomass of fish <10 cm length was lower than that of adult fish in almost all years, but exceptionally low proportions were recorded in 2005 (12.1%) and 2006 (8.0%) (Fig. 1c). Only very few echoes were detected which represented piscivorous predators (i.e., fish >25 cm TL). Their annual contribution to the total number of echoes per survey was very low and ranged between 0 and 0.8% (Fig. 1c). Accordingly, conversion of predator abundance into biomass would have been based on uncertain length–frequency distributions due to low number of detections, and was thus avoided. Instead, the numerical proportions of predatory fishes were graphically displayed (Fig. 1c).

Time series of single groups of phytoplankton, zooplankton and fish biomasses were only occasionally significantly correlated (Table 1). There were a number of positive correlations between single phytoplankton groups, such as Dinophyta and Bacillariophyceae, or between single zooplankton groups, such as juvenile and calanoid copepods (Table 1). A top-down effect by fish on lower trophic levels was indicated by the weakly significant negative correlations between fish >10 cm biomass and *Daphnia* biomass ($r = -0.73$, $n = 6$, $p = 0.108$; Fig. 2a), and between *Daphnia* biomass and Cyanobacteria biomass ($r = -0.76$, $n = 9$, $p = 0.017$; Fig. 2e). In contrast, fish <10 cm and juvenile copepods were weakly positively correlated ($r = 0.72$, $n = 6$, $p = 0.111$; Fig. 2b), and cyclopoid copepods and Chrysophyceae were significantly positively correlated ($r = 0.86$, $n = 9$, $p = 0.003$; Fig. 2f). However, there was a strong top-down effect of fish on zooplankton assemblage structure. The biomass of fish >10 cm was significantly negatively correlated to *Daphnia* proportion of total crustacean biomass ($r = -0.89$, $n = 6$,
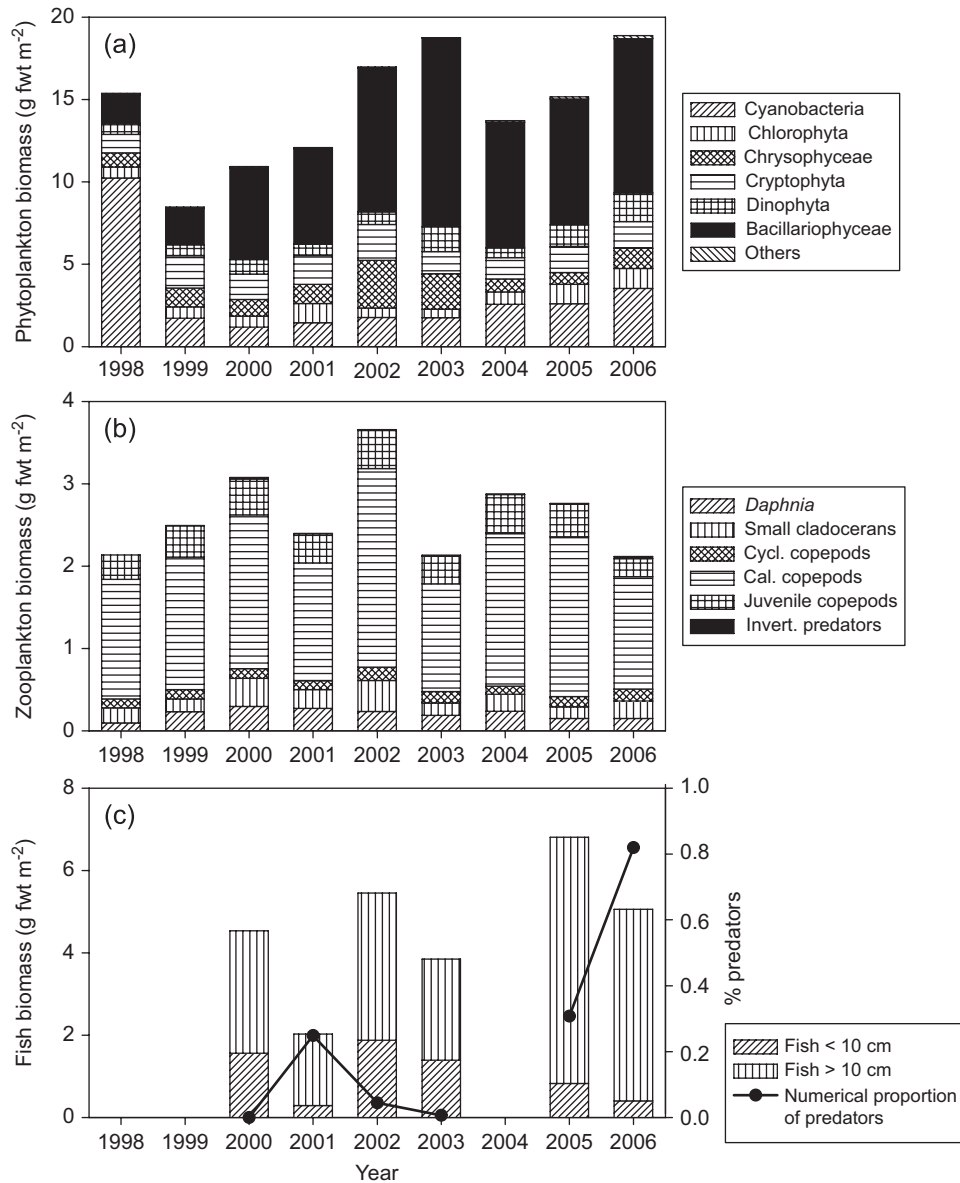
Fig. 1. Annual average areal biomasses (g fresh weight (fwt) m^{-2}, scaled to 22.3 m mean depth) of seven groups of phytoplankton (a), six groups of zooplankton (b), and two groups of fish biomass or numerical proportion of piscivorous fish (c) in Lake Stechlin between 1998 and 2006. Fish biomasses are missing in 1998, 1999 and 2004.

$p = 0.016$; Fig. 2c), whereas the proportion of calanoid copepods significantly positively correlated with fish > 10 cm biomass ($r = 0.92$, $n = 6$, $p = 0.009$; Fig. 2d).

Discussion

The time series of phytoplankton, zooplankton and fish biomasses in the oligo-mesotrophic Lake Stechlin accumulated over the last 9 years gave little evidence for the existence of a strong pelagic trophic cascade. Despite a more than three-fold inter-annual variability in

biomass of the planktivorous coregonids, the drastic changes at the top of the food web did not result in synchronous changes at either the zooplankton or the phytoplankton biomass levels. Furthermore, the fourth trophic level of piscivorous predators was almost absent such that the biomass of coregonid fishes was likewise not top-down controlled. A few weak correlations indicated that *Daphnia* biomasses tended to be higher in years with lower adult fish biomasses. Similarly, Cyanobacteria biomass was higher in years with low *Daphnia* biomasses. These negative interactions would reflect a control of larger cladocerans by fish feeding, which in turn facilitates the population

Table 1. Linear correlations (Pearson's r) between time series of phytoplankton (1998–2006), zooplankton (1998–2006) and fish biomasses (2000–2006, 2004 missing) in Lake Stechlin (all values are annual averages in g fwt m^{-2})

	Cyanobacteria	Chlorophyta	Chrysophyta	Cryptophyta	Dinophyta	Bacillariophyta	Other phytoplankton	*Daphnia*	Small cladocerans	Cyclopoid copepods	Calanoid copepods	Juvenile copepods	Invertebr. predators	Fish <10 cm	Fish >10 cm
Cyanobacteria		−0.067	−0.297	−0.577	−0.118	−0.476	0.212	**−0.763**	−0.240	−0.225	−0.287	−0.459	−0.201	−0.493	0.729
Chlorophyta	0.863		−0.478	0.064	0.346	0.072	**0.716**	−0.188	−0.283	−0.175	−0.238	−0.418	0.083	**−0.917**	0.418
Chrysophyta	0.438	0.193		0.521	0.136	0.508	−0.551	0.176	0.462	**0.858**	0.349	0.178	0.151	0.647	−0.310
Cryptophyta	0.104	0.870	0.150		−0.129	0.038	−0.071	0.450	0.443	0.463	0.512	0.286	−0.006	0.251	0.017
Dinophyta	0.762	0.361	0.727	0.742		**0.685**	0.298	−0.419	−0.303	0.522	−0.346	−0.585	0.564	−0.270	0.483
Bacillariophyta	0.195	0.855	0.162	0.923	**0.042**		−0.064	0.046	0.063	0.634	0.079	0.005	0.502	0.193	0.129
Other phytoplankton	0.583	**0.030**	0.124	0.856	0.436	0.869		−0.337	−0.067	−0.134	0.007	−0.348	0.416	−0.538	0.713
Daphnia	**0.017**	0.628	0.651	0.224	0.262	0.906	0.375		0.582	−0.063	0.347	0.646	0.106	0.342	−0.718
Small cladocerans	0.533	0.461	0.210	0.232	0.428	0.872	0.864	0.100		0.423	0.632	0.465	0.382	0.568	−0.288
Cycl. copepods	0.561	0.652	**0.003**	0.209	0.149	0.067	0.731	0.872	0.256		0.309	−0.084	0.449	0.571	0.131
Cal. copepods	0.454	0.537	0.358	0.159	0.362	0.840	0.987	0.361	0.068	0.418		**0.797**	−0.049	0.649	0.314
Juvenile copepods	0.214	0.263	0.647	0.455	0.098	0.989	0.358	0.060	0.207	0.830	**0.010**		−0.266	0.714	−0.116
Invertebr. predators	0.604	0.832	0.699	0.988	0.114	0.169	0.265	0.786	0.310	0.225	0.900	0.489		0.052	0.111
Fish <10 cm	0.320	**0.010**	0.165	0.631	0.604	0.714	0.271	0.507	0.240	0.236	0.163	0.111	0.922		−0.106
Fish >10 cm	0.100	0.410	0.551	0.975	0.331	0.807	0.112	0.108	0.580	0.805	0.545	0.827	0.835	0.842	

The biomasses of trophic levels are split into several groups. Correlation coefficients are given above the diagonal, whereas significance levels are given below the diagonal. Significant ($p < 0.05$) correlations are indicated in bold.
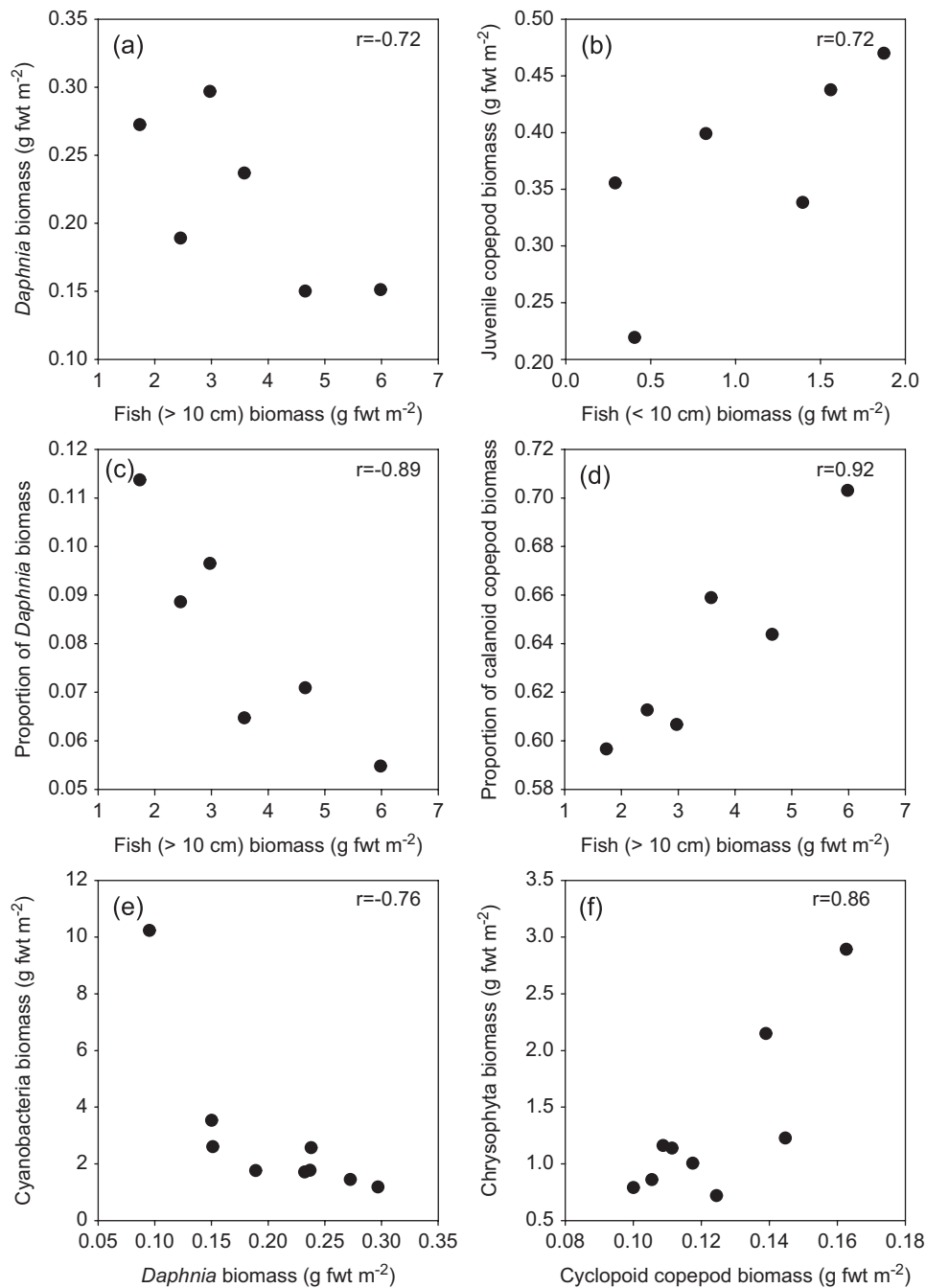
Fig. 2. Scatter plots and Pearson's correlation coefficients between annual biomasses (g fwt m^{-2}) of fish > 10 cm and *Daphnia* (a), fish < 10 cm and juvenile copepods (b), fish > 10 cm and *Daphnia* proportion of crustacean biomass (c), fish > 10 cm and calanoid copepod proportion of crustacean biomass (d), *Daphnia* and Cyanobacteria biomasses (e), and cyclopoid copepod and chrysophyta biomasses (f).

development of blue–green algae. The negative trend between fish and *Daphnia* and the positive trend between fish and calanoid copepods became much more pronounced if proportions of these groups of total crustacean biomass were considered instead. This underlines that the adult coregonids in Lake Stechlin seem to control the zooplankton assemblage structure, but exerted little predation effect on total zooplankton biomasses. Furthermore, since almost all correlations between biomasses of zooplankton and phytoplankton groups were weak, it is suggested that inter-annual differences in pelagic fish density had no cascading influence on the phytoplankton in Lake Stechlin.

Vendace are primarily zooplanktivorous fish (Naesje et al., 1991; Bohn and Amundsen, 2001). In empirical studies it was demonstrated that the feeding by vendace and the related whitefish (*Coregonus* spp.) populations modified abundances and species structures of zooplankton communities or single zooplankton groups (Helminen and Sarvala, 1997; Eckmann et al., 2002). Accordingly, a strong impact of predation by vendace and Fontane cisco on the zooplankton in Lake Stechlin was expected. In Lake Stechlin, the diet of the coregonids consisted mainly of cladocerans (*Bosmina* and *Daphnia*) and predatory zooplankton (*Leptodora* and *Bythotrephes*), whereas copepods were of minor importance (Schulz et al., 2003). Accordingly, biomasses of fish and cladocerans were expected to correlate negatively, whereas the biomass of copepods should be varying independently of fish biomass. Earlier work in Lake Stechlin has estimated that the trophic transfer efficiency between zooplankton and fish was only about 6%, indicating that a top-down control of zooplankton production by fish feeding was rather unlikely (Schulz et al., 2004). Comparative studies in Canadian and Faroese oligotrophic lakes at TP-ranges similar to Lake Stechlin found no negative response of zooplankton biomass to fish predation, but this lack of correlation was mainly attributable to the overall low biomass of truly pelagic planktivorous fish (Bertolo et al., 2005; Amsinck et al., 2006). Our results and these studies would suggest that the control of zooplankton biomass by fish feeding in low-productivity lakes is indeed negligible.

Based on analyses from another 29 lakes of low productivity in Canada (TP-range 5.5–27 mg m^{-3}), Currie et al. (1999) found likewise no correlative evidence that variance in plankton abundance among lakes was related to variation in fish communities. However, they detected an effect of fish on the size structure of zooplankton. When piscivores were present, cladocerans were larger (Currie et al., 1999). The most comprehensive study, covering 466 temperate and Artic lakes over three magnitudes of TP-concentrations, indicated that fish abundance and lake productivity modified zooplankton assemblage structure (Jeppesen et al., 2003). The proportion of *Daphnia* in zooplankton assemblages was unimodally related to TP concentrations, peaking at about 90 mg m^{-3} in lakes deeper than 6 m (Jeppesen et al., 2003). In both low-productivity and high-productivity systems, the *Daphnia* proportions were lower. If the analysis was limited to low-productivity lakes, *Daphnia* proportion and catch per unit effort (CPUE) of fish in gillnets correlated negatively, and *Daphnia* were almost absent in all lakes where fish CPUE exceeded a certain threshold (Jeppesen et al., 2003). This analysis indicates that predation by abundant zooplanktivorous fish in oligo- to mesotrophic lakes rather modified the zooplankton structure than

declined the absolute biomass of total zooplankton or single groups. This conclusion was supported by the time series from Lake Stechlin.

However, the negative correlation between fish and *Daphnia* did not cascade further down to phytoplankton. Except for the fact that Cyanobacteria biomass showed an opposite trend to *Daphnia* biomasses over the years, most of the phytoplankton seemed to be unaffected by changes in zooplankton biomass or assemblage structure. Zooplankton in Lake Stechlin was dominated by calanoid copepods, mainly *Eudiaptomus gracilis* and *Eurytemora lacustris* (Kasprzak et al., 2005; Helland et al., 2007). The dominance of calanoid copepods is typical for low-productivity lakes, whereas the proportions of *Daphnia* and cyclopoid copepods increase with increasing chlorophyll-*a* concentrations (Kasprzak and Koschel, 2000). Earlier studies suggested that herbivorous calanoid copepods can exert little influence on phytoplankton biomasses due to their low overall biomasses, slow growth and low metabolic rates (summarised by Sommer and Stibor, 2002). More recent results from mesocosm experiments in a mesotrophic lake revealed that copepods suppressed large phytoplankton, whereas cladocerans suppressed small phytoplankton (Sommer et al., 2001). However, even by grouping the phytoplankton data into small, mainly edible (Chlorophyta, Bacillariophyceae, Cryptophyta, Chrysophyceae) and large, mainly non-edible taxa (Cyanobacteria, Dinophyta), correlation strength did not change. Only *Daphnia* was still significantly negatively correlated to the non-edible phytoplankton due to the dominance of Cyanobacteria in this group. However, picoplanktonic Cyanobacteria such as *Cyanobium* were frequent in Lake Stechlin and their depth distribution range partially overlapped with that of daphnids (Kasprzak and Schwabe, 1987; Padisák et al., 1997). Accordingly, it may be assumed that a reason for the negative correlation between *Daphnia* and cyanobacteria can be found in the fact that picoplanktonic cyanobacteria were heavily grazed by the cladocerans.

The only weak negative correlations between pelagic trophic levels in Lake Stechlin do not support the top-down:bottom-up hypothesis, which predicts that alterations of zooplankton grazing will have the greatest effects in low-nutrient lakes (McQueen et al., 1986). In contrast, our results support the intermediate trophic state, the food chain and the nutrient enrichment hypotheses suggesting that a pelagic trophic cascade is weak in lakes at low productivity (Elser and Goldman, 1991; Persson et al., 1992; Sarnelle, 1992). The low impact of zooplankton on phytoplankton in oligotrophic lakes was explained by the dominance of copepods and the lower nutrient regeneration rates at low phosphorus concentrations (Carney, 1990). A weak trophic cascade at low productivity is also a confirmation of the food chain theory (Persson et al., 1992).

These authors suggested that a strong top-down influence on phytoplankton can be expected only when the food web consists of an even number of trophic levels (two or four). If there is an odd number of trophic levels such as in Lake Stechlin where the piscivorous fish level is almost absent (i.e., only three levels are present), the feeding by pelagic planktivores will modify the zooplankton assemblage structure substantially, with the further consequence that the zooplankton–phytoplankton link is functionally decoupled.

Finally, our results support the theoretical predictions of a lower biomanipulation efficiency threshold of P-loading by Benndorf et al. (2002). These authors concluded that zooplankton grazing cannot sustainably reduce total phytoplankton biomass (not only) in oligotrophic stratified lakes. However, the reason that zooplankton fail to control phytoplankton is not attributable to the low grazing rate of the less abundant zooplankton. Instead, the otherwise strong direct cascading effect of zooplankton on phytoplankton resources by reduction of pelagic P-concentrations via increased sedimentation (faecal material, exuviae), vertical migration of animals or P-accumulation in *Daphnia* biomass are not efficient at already low productivity conditions. Consequently, pelagic P-concentrations cannot be reduced further by these top-down mechanisms, and phytoplankton is continuously controlled bottom-up by resource availability in oligotrophic lakes, independent of the structure and biomass of zooplankton (Benndorf et al. 2002).

Acknowledgements

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