

Abstract

We compiled and analyzed long-term (1961–2005) zooplankton community data in response to environmental variations in Lake Biwa. Environmental data indicate that Lake Biwa had experienced eutrophication (according to total phosphorus concentration) in the late 1960s and recovered to a normal trophic status around 1985, and then exhibited warming since 1990. Total zooplankton abundance showed a significant correlation with total phytoplankton biomass. Following a classic pattern, cladoceran/calanoïd and cyclopoid/calanoïd abundance ratio was related positively to eutrophication. Zooplankton community exhibited a significant response to the boom and bust of phytoplankton biomass as a consequence of eutrophication-reoligotrophication and warming. Moreover, our analyses suggest that the Lake Biwa ecosystem exhibited a hierarchical response across trophic levels; that is, higher trophic levels may show a more delayed response or no response to eutrophication than lower ones.

We tested the hypothesis that phytoplankton community can better explain the variation of zooplankton community than bulk environmental variables, considering that phytoplankton community may directly affects zooplankton succession through predator-prey interactions. Using a variance partition approach, however, we did not find strong evidence to support this hypothesis. We further aggregate zooplankton according to their feeding types (herbivorous, carnivorous, omnivorous, and parasitic) and taxonomic groups, and analyzed the aggregated data. While the pattern remains similar, the results are less clear comparing with the results based on finely resolved data. Our research explored the efficacy of using zooplankton as bio-indicators to environmental changes at various data resolutions.

1 Introduction

Lakes, due to their vulnerability, have been considered as sentinels of environmental changes, such as anthropogenic effects and global warming (Williamson et al., 2009).

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feeding types may have determined the responses of zooplankton to changes in their prey field (Kawabata, 1988; Urabe et al., 1996; Yoshida et al., 2001b; Anneville et al., 2007). Such aggregation also allows us to investigate the effects of data resolution. Third, we examined whether the ratio of cyclopoid/calanoïd and of cladoceran/calanoïd can be used as an indicator to eutrophication (Ravera, 1980; Kane et al., 2009). Finally, we studied the total zooplankton abundance in response eutrophication and re-oligotrophication. In addition, we tested the hypothesis in each level of analyses that phytoplankton community can better explain the variation of zooplankton community than bulk environmental variables (such as total phosphorus, total phytoplankton biomass, or temperature). This hypothesis is based on observation that changes in zooplankton community may be critically affected by change in phytoplankton community through predator-prey interactions and species competitions (Kawabata, 1988; Yoshida et al., 2001b; Polli and Simona, 1992; Magadza, 1994; Anneville et al., 2007).

2 Materials and methods

2.1 Zooplankton data

Zooplankton samples were collected using a Kitahara's closing net (139 μm in mesh size and 25 cm in diameter) in four depth intervals (0–10 m, 10–20 m, 20–40 m, and 40–75 m) by the Shiga Prefecture Fisheries Experimental Station (SPFES) at five stations (Fig. 1). Numbers of depth intervals varied according to the bathymetry of stations (e.g. only 0–10 m samples taken in shallow stations 1 and 5). Samples were fixed in 5% formalin and enumerated under microscopes. While sampling was conducted monthly, zooplankton identification and enumeration was carried out only quarterly for most years. We digitized zooplankton abundance data from published annual reports by the SPFES from 1962 to 2005. For each species, we calculated the depth-integrated zooplankton density (10^4 ind./m^2) for each station, averaged the densities of the five stations into the quarterly mean, and finally averaged the quarterly data into the annual

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mean. While seasonality or phenology of zooplankton might also be affected by environmental variations (Anneville et al., 2007), we focus on interannual variation in this study. The taxonomic resolution of zooplankton changed over time and varied among groups. To ensure the consistency, only genus-level data were obtained for some taxa.

5 Only the taxa occurring in ≥ 15 years among the 44 sampling years were investigated for this study, which amount to a total of 20 taxa (6 species and 14 genera, Fig. 2). The only exception is the total zooplankton abundance, which consists of all zooplankton. To simplify, we call the species/genus resolved dataset “genus data” hereafter. Note that among these 20 taxa, *Trichodina* spp. is parasitic on aquatic animals and were often collected by plankton nets. We compared our data with that reported by Miura and Cai (1990) from 1965 to 1979 (visual investigation on their figures) and found generally a good agreement, although their zooplankton samples were collected from station I (Fig. 1).

2.2 Environmental and phytoplankton data

15 The details of environmental and phytoplankton data can be found in Hsieh et al. (2010). Here, we focused only on environmental data directly representing water warming and changes in trophic status in Lake Biwa. Lake surface water temperature data (average of 0–20 m) were obtained from SPFES for the same sampling stations (Fig. 1). The surface water temperature exhibited substantial interannual fluctuations superimposed on a long-term increasing trend (Fig. 3a). The average total phosphorus (TP) in the upper 20 m was used to represent the trophic status of the Lake (see Hsieh et al., 2010 for data source). The TP increased quickly after 1967, reached a maximum in 1974 and then declined until 1985, and fluctuated around a stable value thereafter (Fig. 3b). In addition to the local environmental data, climate indices were included in analyses. We investigated the Arctic Oscillation index (AO), a climate pattern that has been known to influence weather condition of Japan (Thompson and Wallace, 1998). The air and water temperature of Lake Biwa was significantly related to the AO index (Hsieh et al., 2010). We investigated also the Pacific Decal Oscillation (PDO)

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(Mantua et al., 1997) and Southern Oscillation index (SOI) (Trenberth, 1984). These basin-scale patterns have been shown to influence the climate of Japan through air-sea interactions (Miyazaki and Yasunari, 2008; Jin et al., 2005). Their influences on marine zooplankton have been studied (Chiba et al., 2006); however, their effects on lakes of Japan are not clear.

Phytoplankton community data include the time series from 1978 to 2003 collected by the Lake Biwa Environmental Research Institute (Station L in Fig. 1) and those from 1962 to 1991 collected by the SPFES (Stations 1 to 5 in Fig. 1), as detailed in Hsieh et al. (2010). We integrated these two time series to arrive at a phytoplankton total biomass (carbon) time series (Fig. 3c). While we admit uncertainty may exist in this integration, such proxy represents long-term variation of phytoplankton biomass in Lake Biwa. See procedure and justification in Supplement A.

2.3 Data analysis

Two main environmental issues are associated with the Lake Biwa ecosystem: eutrophication and warming. We investigated these environment effects on zooplankton community at four levels: (1) highly resolved zooplankton genus data, (2) aggregated zooplankton groups according to feeding types or a higher taxonomic level, (3) the ratio of cyclopoid/calanoïd and of cladoceran/calanoïd, and (4) total zooplankton abundance.

We started from the genus data (shown in Fig. 2). First, univariate correlation analyses (with lag up to two years considering the short generation time of zooplankton) were used to investigate long-term relationships between the environmental factors and the zooplankton abundance at an interannual scale. Stationary bootstrap approach (Politis and Romano, 1994) with accelerated bias correction was used to compute 95% confidence limits and to perform a hypothesis test in order to account for serial dependence in time-series data (Hsieh et al., 2009). Second, long-term variation of zooplankton communities were examined using principal component analysis (PCA) (Legendre and Legendre, 1998). Third, we linked the temporal pattern of zooplankton community to environmental variables using redundancy analysis (RDA) (Legendre and Legendre,

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zooplankton (Gillooly, 2000; Hansen et al., 1997), we do not have size information of each taxon through time and the size of many crustaceans can vary substantially. Those aggregated zooplankton data were analyzed with respect to environmental variables and phytoplankton community following the same manner as aforementioned.

5 Similarly, the ratio of cyclopoid/calanoïd and of cladoceran/calanoïd was analyzed likewise. Finally for the zooplankton abundance, simple stationary bootstrap correlation was employed to see how they responded to eutrophication and warming.

3 Results

3.1 Zooplankton community responding to eutrophication and warming

10 Zooplankton community exhibited a substantial change from 1962 to 2005 when we investigated the data at the species-genus level (Fig. 2). Results of univariate correlation analyses indicated that several taxa were either correlated with changes in the trophic status of the lake (e.g. *Cyclops* spp., *Daphnia* spp., *Diaphanosoma brachyurum*, *Eodiaptomus japonicus*, *Keratella* spp., *Mesocyclops leuckarti*, *Polyarthra* spp.,
15 and *Trichocerca* spp.) or water temperature and/or the Arctic Oscillation index (e.g. *Bosmina longirostris*, *Conochilus* spp., *Cyclops* spp., *Eodiaptomus japonicus*, *Epistylis* spp., *Keratella* spp., *Leptodora kindtii*, *Ploesoma* spp., *Synchaeta* spp., and *Trichodina* spp.), although still other taxa did not show any correlation (Table 1). The results of principal component analysis revealed the long-term variation of zooplankton community,
20 and the first and second principal components amount to explain 35.5% of variance (Fig. 4). The first principal component showed a first peak around 1970 and a second peak around 1980, possibly influenced by eutrophication (cf. Fig. 3b and c), and then changed to a negative phase around 1990 due to an increase in water temperature (cf. Fig. 3a). The second principal component also showed a first peak around 1970
25 and turned into a negative phase from 1974 to 1980, and then fluctuated since. The long-term zooplankton community variation was significantly affected by environmental

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changes (randomization test, $p < 0.05$), based on RDA results (Fig. 5a). The variation from early 1960s to late 1980s was related to the change in the trophic status of the Lake, while the variation from late 1980s onward was caused by warming. The result of RDA (Fig. 6a) based on data from 1978 to 2003 exhibited a similar pattern with that based on data from 1962 to 2005 (cf. Fig. 5a), showing that eutrophication (signified by TP) and warming significantly drove changes of the zooplankton community.

3.2 Responses of aggregated zooplankton to environmental variations

When we investigated zooplankton time series aggregated according to a higher taxonomic level (Cladocera, Copepoda, Rotifera, and Protista), we found that the aggregated taxa still showed significant correlations with environmental variables (Table 2). Rotifera correlated positively with TP with 1-year lag and concurrent phytoplankton biomass. Cladocera showed a positive correlation with TP and PDO with 1-year lag and phytoplankton biomass with 2-year lag. Copepoda did not show any correlation, and Protista correlated positively with water temperature and negatively with concurrent SOI and TP with 2-year lag. Note that when lagged and concurrent correlations were all significant, we considered the correlation of the strongest strength. The results of RDA based on the aggregated taxa also revealed the effects of eutrophication and warming (Fig. 5b), similar with the RDA results based on genus data (cf. Fig. 5a); however, the gradient of increased eutrophic status and warming is less clear.

When we aggregated zooplankton data according to their feeding types (herbivorous, carnivorous, omnivorous, and parasitic), correlations between zooplankton and environmental factors were also found (Table 2). Herbivorous zooplankton positively correlated with TP with 1-year lag and concurrent phytoplankton biomass. Carnivorous and omnivorous zooplankton did not show any correlation; parasitic zooplankton correlated positively with water temperature. The results of RDA based on the feeding types again revealed the effects of eutrophication and warming (Fig. 5c), similar with the RDA results based on genus data (cf. Fig. 5a); however, the gradient of increased eutrophic status and warming is less clear.

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3.3 Ratio of cladoceran/calanoïd and of cyclopoid/calanoïd and the total zooplankton abundance as an indicator to eutrophication

The ratio of cladoceran/calanoïd (Fig. 7a) and of cyclopoid/calanoïd (Fig. 7b) may be indicative of the trophic status of the Lake. The cladoceran/calanoïd ratio correlated positively with TP with 2-year lag and phytoplankton biomass with 1-year lag, and the ratio of cyclopoid/calanoïd correlated positively with concurrent TP with two-year lag and phytoplankton biomass with 1-year lag (Table 3). The total zooplankton abundance (Fig. 3d) correlated positively with TP with 1-year lag and concurrent phytoplankton biomass (stationary bootstrap test, $p < 0.05$).

3.4 Differential effects of environmental variables and phytoplankton community on zooplankton

We tested the hypothesis whether phytoplankton community can better explain the variation of zooplankton community than bulk environmental variables by comparing their relative contributions in explaining the temporal variation of zooplankton community. For this investigation, we used only data from 1978 to 2003 when phytoplankton community data are available. When considering genus-level zooplankton data, both environmental factors (mainly TP, phytoplankton biomass, and temperature) and phytoplankton community (aggregated according to their size, morphology, and taxonomic class) explained a significant amount of variance (Table 4). Together, these two matrices explained >50% of zooplankton variance. The environmental variables explained 38.05% of variance, and the phytoplankton community explained 15.69% to 38.05% of variance depending on how phytoplankton data were aggregated. Still, significant common fraction existed between the environmental variables and phytoplankton community. When we partitioned the variance, the environmental variables explained slightly higher variance than the phytoplankton data aggregated into either size or morphological groups, while phytoplankton class-level data explained slightly higher variance than the environmental variables (Table 4). However, the difference is not statistically

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different ($0.11 < p < 0.67$). The best combination of explanatory variables consisted of the environmental matrix and class-level phytoplankton data, which explained 72.1% of variance. The most parsimonious RDA results based on forward selection are shown in Figure 6b, and only temperature and biomasses of Cryptophyceae and Cyanobacteria were retained in the final model.

When considering the zooplankton feeding groups, the environmental variables explained a significant amount of variance (38.8%), but the phytoplankton community explained only a small amount of variance, except for class-level phytoplankton data (Table 5). Together, these two matrices explained about 50% of zooplankton variance. When we partitioned the variance, the environmental variables explained higher variance than phytoplankton data; however, the difference remained not statistically significant ($0.13 < p < 0.29$). Similar results were found when considering the zooplankton taxonomic groups (Table 5).

The ratio of cladoceran/calanoïd was better explained by the phytoplankton matrix than the environmental matrix, but the difference remained not statistically significant ($0.34 < p < 0.56$) (Table 6). The phytoplankton community explained a significant amount of variance (46.52–52.49%), and the environmental variables explained 28.41% of variance. Together, these two matrices explained >60% of the variance. The ratio of cyclopoid/calanoïd was also better explained by the phytoplankton matrix (40.9–68.84%) than the environmental matrix (36.34%), except for the comparison of environmental variables versus phytoplankton morphological groups (Table 6). However, the difference was not statistically significant ($0.15 < p < 0.87$). Together, these two matrices explained >50% of the variance. Similar with the results based on the genus data, the best combination includes the environmental variables and class-level phytoplankton data, each explaining 74.75% and 87.38% of variance for the cladoceran/calanoïd and cyclopoid/calanoïd ratio, respectively (Table 6).

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4 Discussion

4.1 Zooplankton community in response to the environmental variations

The ecosystem of Lake Biwa has experienced a dramatic change in trophic status (Fig. 3b and c) and thermo regime (Fig. 3a) in the past half century. These environmental changes in turn drove reorganization of the zooplankton community (Figs. 2, 4, and 5). This is particularly visible in the RDA results, where the gradient of trophic variation (TP and phytoplankton biomass) and temperature variation (lake surface temperature and AO) had significant effects on the evolution of zooplankton community (Fig. 5a). Such kind of effects of eutrophication-reoligophication processes and warming on zooplankton communities have also been observed in other lakes (Jeppesen et al., 2003; Stige et al., 2009; Straile and Geller, 1998; Lovik and Kjellberg, 2003; Anneville et al., 2007).

In Lake Biwa, the total zooplankton abundance showed a significant positive correlation with TP and phytoplankton biomass (Fig. 3b, c, and d), suggesting a bottom-up control. Nevertheless, not every taxon showed a significant positive response; among the 20 taxa, only six showed a significant positive correlation to TP or phytoplankton biomass (Table 1). We further investigated whether a taxon responded positively to trophic status is dependent on its feeding type or taxonomy (Supplement D) and found no significant relationship (logistic regression, $p > 0.4$). In addition to the bottom-up effects, thermo regime also had significant effects; nine out of the 20 taxa exhibited a significant correlation (negative or positive) with temperature (Table 1). Nevertheless, whether a taxon responded to water temperature is not dependent on its feeding type or taxonomy (logistic regression, $p > 0.4$). While warming effects on zooplankton has been widely documented (George and Harris, 1985; Molinero et al., 2007), the mechanisms underlying the complex pattern in Lake Biwa zooplankton are far from clear. Top-down effects from plantivorous fishes on zooplankton community may also be important (Carpenter and Kitchell, 1988) but cannot be examined here due to lacking

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of data. In addition, because water warming is accompanied by reoligotrophication process, it may be difficult to discern these two factors.

Among the 20 taxa, five showed a significant correlation with AO (Table 1). This linkage is likely due to the temperature effects, as AO showed a significant positive correlation with Lake Biwa water temperature (Hsieh et al., 2010). A few taxa showed a correlation with PDO or SOI (Table 1). While PDO and SOI has been shown to affect marine zooplankton through changes in circulation around Japan (Chiba et al., 2006), their effects on Japanese lake ecosystems are not known.

While 15 among the 20 taxa showed a significant correlation with environmental variables investigated here, strengths of all the correlations are small. We suspected complex competition among zooplankton (Einsle, 1983) or compensation mechanism may be at work within trophic level (defined as herbivores, carnivores, or omnivores). If compensation is important, negative covariance should prevail (Houlahan et al., 2007). Following Houlahan et al. (2007), we investigated the covariance structure among taxa within the same trophic level using the binomial test. We found no evidence of compensation within the same trophic level. Within the herbivorous level, 31/66 pair-wise comparisons in the covariance are negative (binomial test, $p = 0.712$), 2/6 for the carnivores (binomial test, $p = 0.688$) and 1/3 for the omnivores (binomial test, $p = 1$). Our results echo the findings of Houlahan et al. (2007) that compensatory dynamics are not common in natural ecological communities.

4.2 Issues on data resolution

We investigated the issue of zooplankton data resolution by aggregating the zooplankton time series according to their taxonomy or feeding types. The aggregation according to feeding type is akin to the trait-based approach (Menezes et al., 2010). As expected, herbivorous zooplankton showed a positive response to phytoplankton biomass (Table 2). Parasitic organisms (*Trichodina* spp.) showed a positive relationship with temperature (Table 2), likely due to the thermo effects. That is, growth of poikilotherms depends on temperature and thus parasites may be more productive in warm

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water, as they do not have food limitation. Carnivorous and omnivorous zooplankton did not show a clear response to changes in trophic status, although carnivorous zooplankton indeed peaked in 1970 when eutrophication is serious (Table 2 and Fig. 5b). The carnivores fluctuated but maintained long-term constancy (Fig. 5c). When aggregation was done based on taxonomy, we found that Rotifera (Supplement Fig. C1a) and Cladocera (Supplement Fig. C1b) exhibited a positive correlation with phytoplankton biomass (Table 2). This is not surprising because most of them belong to herbivorous (Supplement D). Protista correlated positively with water temperature, mainly attributable to *Epistylis* spp. and *Trichodina* spp. (Fig. 2 and Supplement Fig. C1d).

While the aggregated time series (reduced resolution) still revealed pattern of changes in trophic status and temperature regime, the community sensitivity to environmental variation was reduced. This is true for either aggregated taxonomic groups (Fig. 5b) or feeding groups (Fig. 5c). The RDA results remained significant, but the gradient was less clear. Together with the aforementioned findings that whether a taxon responded to water temperature or trophic status is not dependent on its feeding type or taxonomy, the trait-based approach provides limited additional information in interpreting the dynamics of Lake Biwa zooplankton.

4.3 Zooplankton as bio-indicators to environmental changes

Zooplankton community indeed signaled environmental changes in Lake Biwa such as eutrophication and warming, according to PCA (Fig. 4) and RDA results (Figs. 5 and 6). However, the PCA and RDA scores are not ideal indicators, because the scores change whenever new data are included in updated analyses. From the genus data, we found that *Cyclops* spp., *Keratella* spp., and *Trichocerca* spp. showed a clear response to eutrophication and *Epistylis* spp., *Ploesoma* spp., *Synchaeta* spp., and *Trichodina* spp. showed a clear response to warming (Fig. 2 and Table 1). These taxa can potentially be good bio-indicators.

The ratio of cladoceran/calanoïd (Fig. 7a) and of cyclopoid/calanoïd (Fig. 7b) represents good indicators to eutrophication. This is consistent with previous studies

suggesting that increasing lake trophic status will favor cyclopoid over calanoid copepods and cladocerans over calanoids (Rognerud and Kjellberg, 1984; Patalas, 1972; Straile and Geller, 1998). We noticed that these ratios generally showed a lagged response (Table 3). In fact for the ratio of cladoceran/calanoid, the correlation became stronger if more lags were taken (maximal at lagged 4 years). In such case, aggregated time series becomes informative.

4.4 Testing the hypothesis that the phytoplankton community explained better than bulk measurements

We tested the hypothesis that phytoplankton community can better explain the variation of zooplankton community than bulk environmental variables, because changes in zooplankton community may be critically affected by change in phytoplankton community through predator-prey interactions and species competitions. However, our results based either on genus data or aggregated time series do not support this idea. Generally, the bulk environmental variables explained slightly higher amount of variance (Tables 4 and 5). The only exception is the phytoplankton taxa, which explained almost equal amount of variance as the bulk environmental variables (Tables 4 and 5). By contrast, for the ratio of cladoceran/calanoid and of cyclopoid/calanoid, phytoplankton community explained better (Table 6). Thus, absolute group abundances followed better with bulk variables, while ratios followed better with phytoplankton community. Complex predator-prey interactions and species competitions play important roles in Lake Biwa ecosystem, which warrants further studies.

4.5 Hierarchical responses across trophic levels

From a system point of view, differential responses of different trophic levels to environmental changes are suggested (Allen et al., 1987). For example, one might expect a quick response of phytoplankton biomass to TP, but a delayed response of herbivores and even a more delayed response or no response of carnivores. Such concept is

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biologically intuitive, though, was rarely tested in lake ecosystems. The only comprehensive analysis was carried out in Muggelsee and revealed no such evidence (Wagner and Adrian, 2009). In Lake Biwa, the total phytoplankton biomass showed 1-year lagged response to TP (Hsieh et al., 2010). However, the total zooplankton abundance showed a concurrent correlation with phytoplankton biomass but not delayed response (Fig. 3). When taxonomic groups were considered, cladocera showed a delayed responses, but nor did other groups; when different trophic levels were considered, no delayed response was found (Table 2). Interestingly, while herbivores showed a significant correlation with phytoplankton biomass, the higher trophic levels (such as carnivores and omnivores) exhibited no correlation with either phytoplankton or herbivores. Particularly, omnivores showed a long-term constancy in abundance, perhaps because they can forage on a wider spectrum of food sources. These results suggest the effects of external forcing dissipated through up the trophic levels, as suggested by Allen et al. (1987). Furthermore, the ratio of cladoceran/calanoid and of cyclopoid/calanoid showed 1-year lagged response to phytoplankton biomass (Table 3). When considering individual taxon, six taxa showed a response to phytoplankton biomass; 66.7% among them are delayed responses (Table 1). By contrast, nine taxa showed a response to water temperature; 55.6% among them are delayed responses (Table 1). Thus for Lake Biwa, we saw some evidence of hierarchical responses across trophic levels, although the results are not unanimous. Moreover, whether a hierarchical response occurred may depend on the type of external forcings.

5 Conclusions

We compiled and analyzed long-term zooplankton community data in response to eutrophication-oligotrophication and warming in Lake Biwa. While the total zooplankton abundance showed a significant correlation with total phytoplankton biomass (Fig. 3), the zooplankton community changed substantially in response to changes in trophic status and water temperature (Figs. 4, 5, and 6). The food (phytoplankton) availability

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sets the carrying capacity for the total zooplankton; however, complex interactions occurred among zooplankton taxa. Similar observation has been found for the Lake Biwa phytoplankton community in response to TP (Hsieh et al., 2010). Our analyses suggest that the Lake Biwa ecosystem exhibited a hierarchical response across trophic levels; that is, higher trophic levels may show a more delayed response or no response to eutrophication than lower ones; but this kind of hierarchical response was not clear to temperature. Our results indicated that whether a taxon responded to eutrophication or warming is not dependent on its feeding type or taxonomy. Moreover, aggregating time series based on feeding types or taxonomic groups reduced the sensitivity of using zooplankton community as bio-indicators (Fig. 5). Other traits other than feeding and taxonomy should be investigated in the future. However following a classic pattern, cladoceran/calanoïd and cyclopoid/calanoïd abundance ratio (Fig. 7) was related positively to eutrophication and can be used as a good indicator. To summarize, zooplankton community may be reasonable bio-indicators to environmental changes in Lake Biwa; however, hierarchical responses across trophic levels should be bear in mind.

Our analyses did not support the idea that phytoplankton community can better explain the variation of zooplankton community than bulk environmental variables. In addition, we found no compensatory dynamics within a trophic level. Perhaps, complex nonlinear species competitions and predator-prey interactions prevail in Lake Biwa, which hampers the linear analyses employed here. Nonlinear methods may be required to clarify complex interactions (Hsieh et al., 2008; Hsieh and Ohman, 2006).

Supplementary material related to this article is available online at:
<http://www.biogeosciences-discuss.net/8/593/2011/bgd-8-593-2011-supplement.pdf>.

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Table 1. Results of correlation analyses between zooplankton abundance and environmental variables.

Taxa	Variables
<i>Asplanchna</i> spp.	
<i>Bosmina longirostris</i>	–LST lag 2 yr
<i>Brachionus</i> spp.	
<i>Conochilus</i> spp.	+LST
<i>Cyclops</i> spp.	+Phyto lag 1 yr, –LST lag 2 yr
<i>Daphnia</i> spp.	+TP, +Phyto lag 2 yr
<i>Diaphanosoma brachyurum</i>	–TP lag 2 yr, –Phyto
<i>Diflugia</i> spp.	
<i>Eodiaptomus japonicus</i>	–TP lag 2 yr, +AO
<i>Epistylis</i> spp.	+LST, +AO lag 1 yr, –SOI
<i>Filinia</i> spp.	
<i>Kellicottia longispina</i>	
<i>Keratella</i> spp.	+TP lag 1 yr, +Phyto lag 2 yr, –LST lag 2 yr, +PDO lag 2 yr
<i>Leptodora kindtii</i>	+LST lag 1 yr, +AO lag 2 yr, –PDO
<i>Mesocyclops leuckarti</i>	+TP lag 1 yr
<i>Ploesoma</i> spp.	+LST, +AO lag 2 yr
<i>Polyarthra</i> spp.	+Phyto
<i>Synchaeta</i> spp.	+LST, +AO lag 1 yr
<i>Trichocerca</i> spp.	+TP lag 1 yr, +Phyto lag 1 yr
<i>Trichodina</i> spp.	+LST, +SOI lag 2 yr

Note: only significant variables are shown (based on stationary bootstrap test with $\alpha = 0.05$). + indicates a positive correlation, – indicates a negative correlation, and lag 1 yr indicates that the zooplankton response is one year behind. If 0, 1, and 2 year-lag correlations are significant, only the best fit is retained. The results are not adjusted for multiple tests because we wish to explore potential relationships between zooplankton abundances and environmental variables. While correlation exists, the average explained variance is less than 15%. LST, Lake Surface water Temperature; TP, Total Phosphorus; Phyto, phytoplankton carbon biomass, AO, Arctic Oscillation; PDO, Pacific Decadal Oscillation; SOI, Southern Oscillation Index.

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Table 2. Results of correlation analyses of zooplankton abundances categorized according to their feeding types and taxonomic order versus environmental variables.

Feeding type	TP ($\mu\text{g L}^{-1}$)	Phytoplankton biomass (\log_{10} μgC)	LST ($^{\circ}\text{C}$)	AO	PDO	SOI
Taxonomic order						
Rotifera	0.214	0.323 ¹	-0.129	0.000	0.130	-0.099
Cladocera	0.299 ¹	0.268 ¹	0.084	0.111	0.107	-0.130
Copepoda	0.137	0.215	-0.082	0.285	0.188	-0.198
Protista	-0.005	0.033	0.433 ¹	0.212	0.004	-0.245 ¹
Lag 1 year²						
Rotifera	0.361 ¹	0.262 ¹	-0.163	-0.090	0.054	0.101
Cladocera	0.219	0.286 ¹	-0.085	-0.060	0.240 ¹	-0.035
Copepoda	0.052	0.136	-0.224	0.014	0.111	-0.200
Protista	-0.088	-0.017	0.326 ¹	0.355	0.074	-0.172
Lag 2 year²						
Rotifera	0.232	0.191	-0.047	-0.130	0.034	0.062
Cladocera	0.077	0.381 ¹	-0.182	-0.211	0.073	0.140
Copepoda	-0.166	0.086	-0.282	0.034	0.013	-0.066
Protista	-0.279 ¹	0.037	0.005	0.245	0.131	0.186
Herbivorous	0.227	0.337 ¹	0.056	0.092	0.133	-0.218
Carnivorous	0.225	0.043	-0.045	0.065	-0.143	0.183
Omnivorous	0.137	0.215	-0.082	0.285	0.188	-0.198
Parasitic	-0.068	0.134	0.389 ¹	0.161	0.170	-0.192
Lag 1 year²						
Herbivorous	0.323 ¹	0.268 ¹	-0.026	0.080	0.118	0.000
Carnivorous	0.068	-0.028	-0.043	-0.183	-0.032	-0.056
Omnivorous	0.052	0.136	-0.224	0.014	0.111	-0.200
Parasitic	-0.020	0.124	0.143	0.039	0.033	0.161
Lag 2 year²						
Herbivorous	0.121	0.240 ¹	-0.074	-0.020	0.106	0.125
Carnivorous	-0.094	0.045	-0.099	-0.188	-0.083	0.146
Omnivorous	-0.166	0.086	-0.282	0.034	0.013	-0.066
Parasitic	-0.141	0.076	0.139	-0.051	0.031	0.281 ¹

¹ Significant correlation based on stationary bootstrap test with $\alpha = 0.05$. The results are not adjusted for multiple tests because we wish to explore potential relationships between zooplankton group abundances and environmental variables.

² We investigated delayed responses of zooplankton, however, we included only 1 and 2 year lagged correlation, considering the short generation time of zooplankton.

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Table 3. Results of correlation analyses of zooplankton group ratio versus environmental variables.

Ratio	TP ($\mu\text{g L}^{-1}$)	Phytoplankton biomass (\log_{10} μgC)	LST ($^{\circ}\text{C}$)	AO	PDO	SOI
Cladoceran/calanoïd	0.246 ¹	0.171	0.132	-0.113	0.131	-0.133
Cyclopoid/calanoïd	0.448 ¹	0.218 ¹	-0.155	-0.186	0.075	0.088
Lag 1 year ²						
Cladoceran/calanoïd	0.269 ¹	0.326 ¹	0.102	-0.199	0.243	-0.082
Cyclopoid/calanoïd	0.429 ¹	0.379 ¹	-0.040	-0.158	0.030	-0.064
Lag 2 year ²						
Cladoceran/calanoïd	0.303 ¹	0.288 ¹	-0.105	-0.199	0.098	0.078
Cyclopoid /calanoïd	0.542 ¹	0.171	-0.165	-0.136	-0.162	0.067

¹ A significant correlation based on stationary bootstrap test with $\alpha = 0.05$. The results are not adjusted for multiple tests because we wish to explore potential relationships between zooplankton group abundances and environmental variables.

² We investigated delayed responses of zooplankton, however, we included only 1 and 2 year lagged correlation, considering the short generation time of zooplankton.

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Table 4. Results of variance partition to investigate relative contribution of environmental and phytoplankton matrices in explaining the variation of zooplankton community based on genus data.

Dependent variable: zooplankton community								
Factors: environment VS phytoplankton size groups			Factors: environment VS phytoplankton morphologic groups			Factors: environment VS phytoplankton taxonomic groups		
Total contribution Factors	Exp. Var.	Prob.	Total contribution Factors	Exp. Var.	Prob.	Total contribution Factors	Exp. Var.	Prob.
Environment + phyto size groups	0.5345	0.0004	Environment + phyto morph groups	0.5094	0.0004	Environment + phyto taxa groups	0.7210	0.0002
Environment	0.3805	0.0004	Environment	0.3805	0.0002	Environment	0.3805	0.0002
Phyto size groups	0.2743	0.0010	Phyto morph groups	0.1569	0.0974	Phyto taxa groups	0.3805	0.0004
Partitioning variance Fraction	Exp. Var.	Prob.	Partitioning variance Fraction	Exp. Var.	Prob.	Partitioning variance Fraction	Exp. Var.	Prob.
Unique to environment	0.2601	0.0328	Unique to environment	0.3525	0.0012	Unique to environment	0.2484	0.0074
Interaction	0.1204		Interaction	0.0280		Interaction	0.1321	
Unique to phyto size groups	0.1540	0.1558	Unique to phyto morph groups	0.1289	0.0770	Unique to phyto taxa groups	0.3405	0.0036
Residual	0.4655		Residual	0.4906		Residual	0.2790	
Testing difference in the two factors		0.5441	Testing difference in the two factors		0.1088	Testing difference in the two factors		0.6729

Prob.: p-value from randomization test of 5000 times. The interaction component cannot be tested statistically.

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Table 5. Results of variance partition to investigate relative contribution of environmental and phytoplankton matrices in explaining the variation of zooplankton groups.

Dependent variable: zooplankton feeding groups								
Factors: environment VS phytoplankton size groups			Factors: environment VS phytoplankton morphologic groups			Factors: environment VS phytoplankton taxonomic groups		
Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.
Environment + phyto size groups	0.4657	0.1840	Environment + phyto morph groups	0.4935	0.0386	Environment + phyto taxa groups	0.5546	0.5240
Environment	0.3880	0.0220	Environment	0.3880	0.0212	Environment	0.3880	0.0180
Phyto size groups	0.1403	0.6028	Phyto morph groups	0.1728	0.1396	Phyto taxa groups	0.3880	0.0182
Partitioning variance Fraction			Partitioning variance Fraction			Partitioning variance Fraction		
Exp. Var	Prob.		Exp. Var	Prob.		Exp. Var	Prob.	
Unique to environment	0.3254	0.1172	Unique to environment	0.3207	0.0746	Unique to environment	0.2421	0.4808
Interaction	0.0626		Interaction	0.0673		Interaction	0.1460	
Unique to phyto size groups	0.0777	0.8914	Unique to phyto morph groups	0.1054	0.3708	Unique to phyto taxa groups	0.1665	0.9644
Residual	0.5343		Residual	0.5065		Residual	0.4454	
Testing difference in the two factors		0.1384	Testing difference in the two factors		0.2909	Testing difference in the two factors		0.2324
Dependent variable: zooplankton taxonomic groups								
Factors: environment VS phytoplankton size groups			Factors: environment VS phytoplankton morphologic groups			Factors: environment VS phytoplankton taxonomic groups		
Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.
Environment + phyto size groups	0.4681	0.1678	Environment + phyto morph groups	0.4735	0.0478	Environment + phyto taxa groups	0.5883	0.3552
Environment	0.3560	0.0374	Environment	0.3560	0.0344	Environment	0.3560	0.0340
Phyto size groups	0.2085	0.1720	Phyto morph groups	0.1360	0.3202	Phyto taxa groups	0.3553	0.2912
Partitioning variance Fraction			Partitioning variance Fraction			Partitioning variance Fraction		
Exp. Var	Prob.		Exp. Var	Prob.		Exp. Var	Prob.	
Unique to environment	0.2597	0.2580	Unique to environment	0.3374	0.0626	Unique to environment	0.2330	0.4366
Interaction	0.0963		Interaction	0.0186		Interaction	0.1231	
Unique to phyto size groups	0.1121	0.6756	Unique to phyto morph groups	0.1175	0.3004	Unique to phyto taxa groups	0.2323	0.7680
Residual	0.5319		Residual	0.5265		Residual	0.4117	
Testing difference in the two factors		0.4341	Testing difference in the two factors		0.2368	Testing difference in the two factors		0.4821

Prob.: p-value from randomization test of 5000 times. The interaction component cannot be tested statistically.



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Table 6. Results of variance partition to investigate relative contribution of environmental and phytoplankton matrices in explaining the ratio of cladoceran/calanoïd and cyclop/calanoïd.

Dependent variable: cladoceran/calanoïd ratio								
Factors: environment VS phytoplankton size groups			Factors: environment VS phytoplankton morph groups			Factors: environment VS phytoplankton taxonomic groups		
Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.
Environment + phyto size groups	0.6161	0.3638	Environment + phyto morph groups	0.6161	0.3558	Environment + phyto taxa groups	0.7475	0.0860
Environment	0.2841	0.3298	Environment	0.2841	0.3316	Environment	0.2841	0.3150
Phyto size groups	0.4652	0.1466	Phyto morph groups	0.4651	0.1320	Phyto taxa groups	0.5249	0.0664
Partitioning variance Fraction	Exp. Var	Prob.	Partitioning variance Fraction	Exp. Var	Prob.	Partitioning variance Fraction	Exp. Var	Prob.
Unique to environment	0.1506	0.6442	Unique to environment	0.1506	0.6374	Unique to environment	0.1249	0.2302
Interaction	0.1335		Interaction	0.1335		Interaction	-0.0669	
Unique to phyto size groups	0.3320	0.3768	Unique to phyto morph groups	0.3320	0.3824	Unique to phyto taxa groups	0.3682	0.0750
Residual	0.3839		Residual	0.3839		Residual	0.5737	
Testing difference in the two factors		0.5521	Testing difference in the two factors		0.5597	Testing difference in the two factors		0.3449
Dependent variable: cyclopoid/calanoïd ratio								
Factors: environment VS phytoplankton size groups			Factors: environment VS phytoplankton morph groups			Factors: environment VS phytoplankton taxonomic groups		
Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.	Total contribution Factors	Exp. Var	Prob.
Environment + phyto size groups	0.5102	0.2050	Environment + phyto morph groups	0.5514	0.0904	Environment + phyto taxa groups	0.8738	0.0066
Environment	0.3634	0.1418	Environment	0.3634	0.1478	Environment	0.3634	0.1266
Phyto size groups	0.4090	0.0254	Phyto morph groups	0.2910	0.0582	Phyto taxa groups	0.6884	0.0118
Partitioning variance Fraction	Exp. Var	Prob.	Partitioning variance Fraction	Exp. Var	Prob.	Partitioning variance Fraction	Exp. Var	Prob.
Unique to environment	0.1012	0.7888	Unique to environment	0.2603	0.2270	Unique to environment	0.1853	0.0698
Interaction	0.2621		Interaction	0.1030		Interaction	0.1865	
Unique to phyto size groups	0.1469	0.3776	Unique to phyto morph groups	0.1880	0.1224	Unique to phyto taxa groups	0.5020	0.0054
Residual	0.4898		Residual	0.4486		Residual	0.1262	
Testing difference in the two factors		0.5873	Testing difference in the two factors		0.8674	Testing difference in the two factors		0.1544

Prob.: p-value from randomization test of 5000 times. The interaction component cannot be tested statistically.

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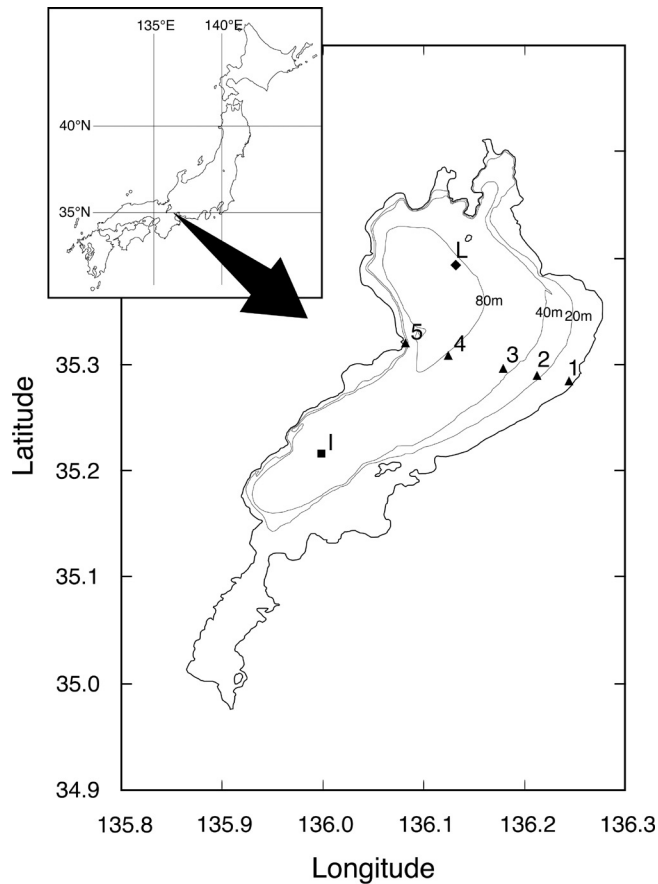


Fig. 1. Map showing sampling stations in Lake Biwa. Stations 1 to 5 are the Shiga Prefecture Fisheries Experimental Stations; station L is the long-term monitoring station of the Lake Biwa Environmental Research Institute; station I is the environmental monitoring station of the Kyoto University.

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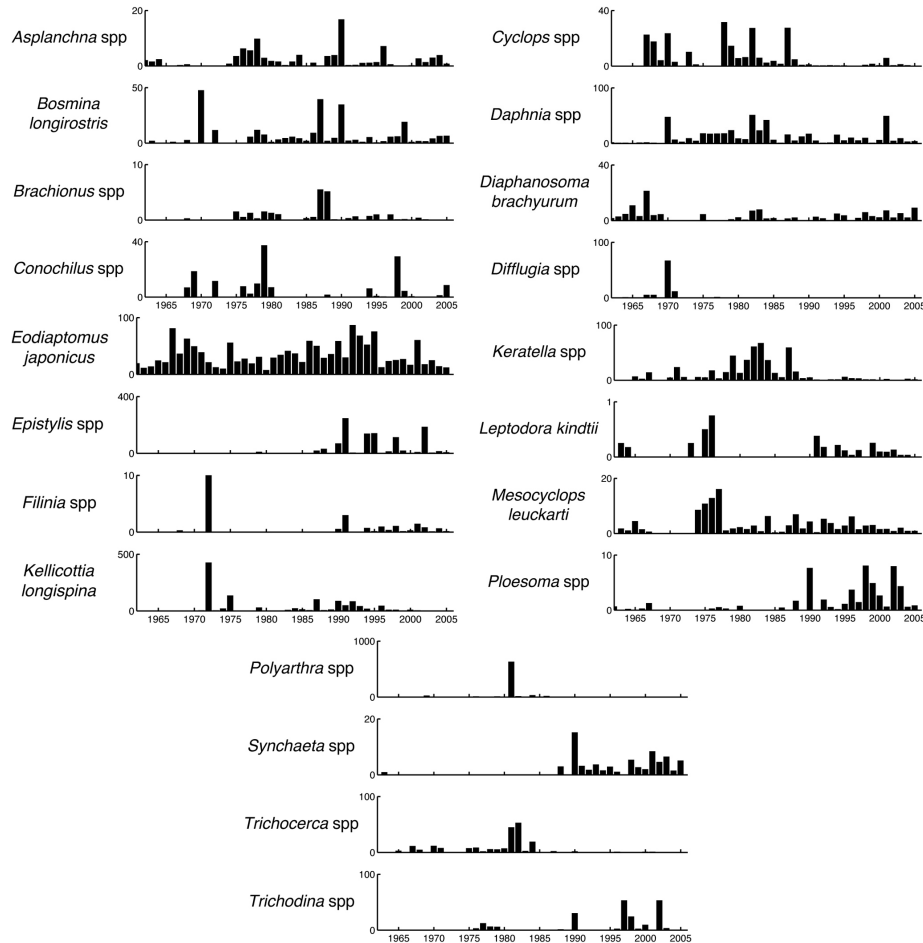


Fig. 2. Abundance (10^4 ind./m^2) time series of dominant taxa. Dominant taxa are defined as taxa with occurrence ≥ 15 years among the 44 sampling years.

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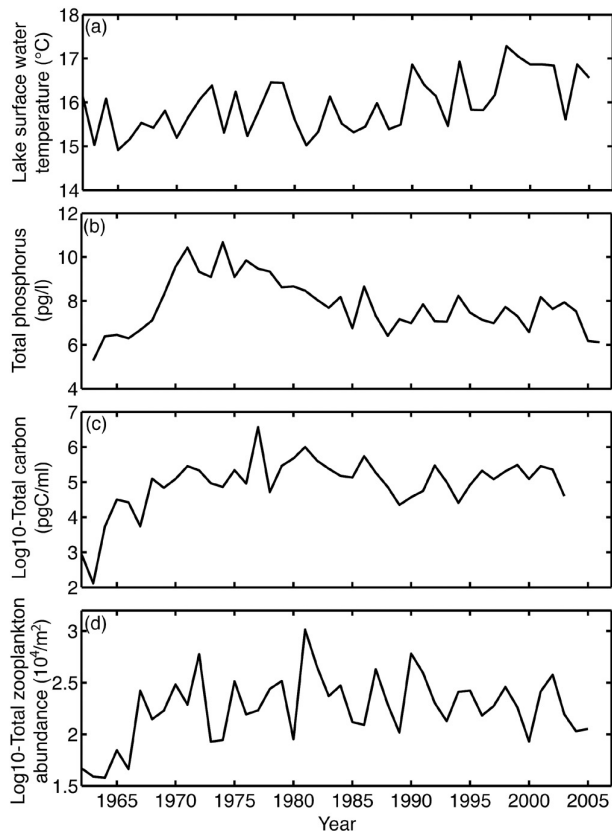


Fig. 3. Time series of **(a)** annual averaged lake surface water temperature and **(b)** estimated average total phosphorus in upper 20 m, **(c)** estimated phytoplankton carbon biomass, and **(d)** total water column integrated zooplankton abundance averaged over 5 stations. Zooplankton abundance is significantly correlated with total phosphorus with 1-year lag and concurrent phytoplankton carbon (stationary bootstrap test, $r = 0.387$ and $r = 0.534$, respectively, $p < 0.05$).

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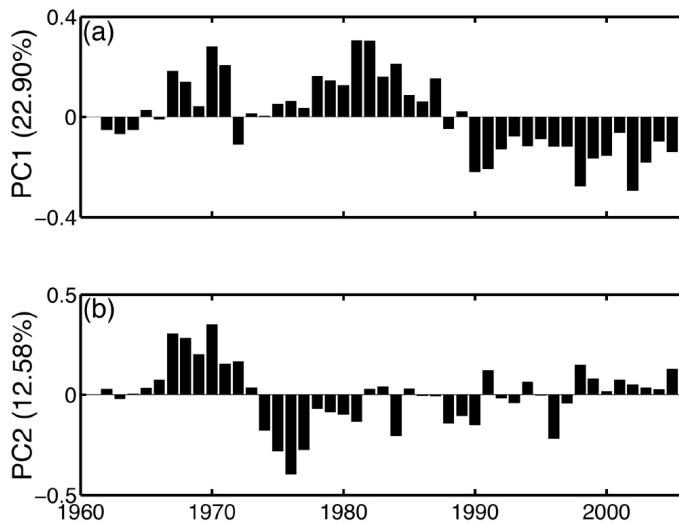


Fig. 4. Principal component analysis of dominant taxa. Zooplankton data were \log_{10} transformed prior to analysis.

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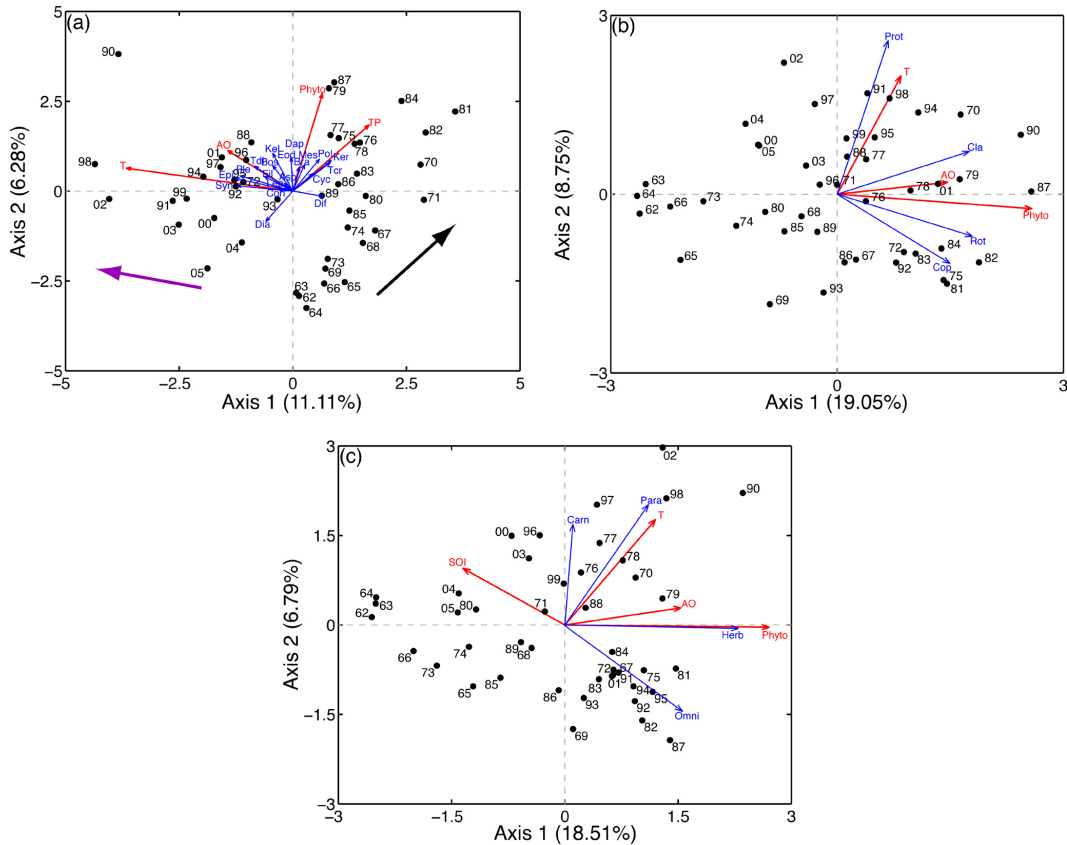


Fig. 5. Biplot of redundancy analysis relating years and zooplankton taxa and depicting how environmental factors affected zooplankton community dynamics based on data at **(a)** genus level, **(b)** aggregated higher taxonomic groups, and **(c)** aggregated feeding types. In **(a)**, the black arrow indicates a gradient of increased eutrophic status, and the purple arrow indicates a warming gradient. In **(b)** and **(c)** the gradient of increased eutrophic status and warming is less clear.

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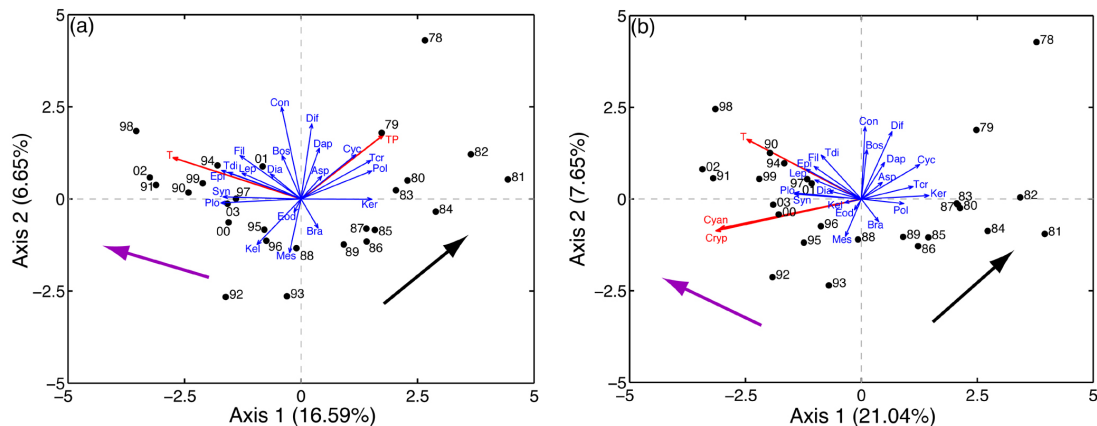


Fig. 6. Biplot of redundancy analysis relating years (1978 to 2003) and zooplankton taxa and depicting (a) how temperature and TP, and (b) how temperature, biomasses of Cryptophyceae and Cyanobacteria affected zooplankton dynamics. The black arrow indicates a gradient of increased eutrophic status, and the purple arrow indicates a warming gradient.

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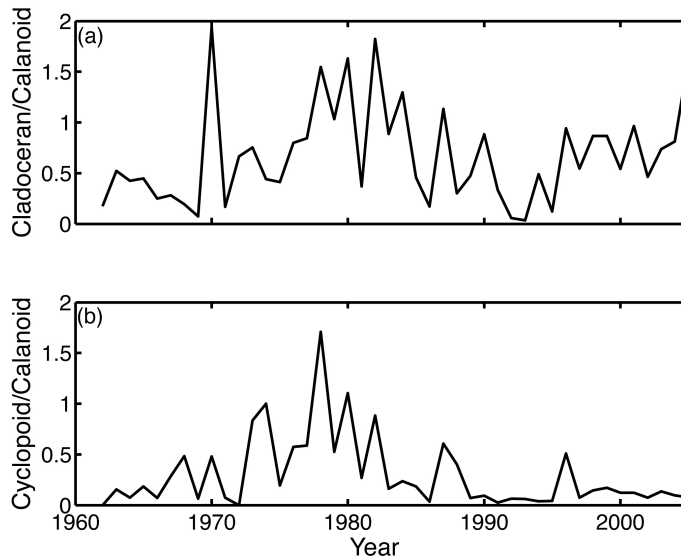


Fig. 7. Time series of abundance ratio of **(a)** cladoceran/calanoid and **(b)** cyclopoid/calanoid.

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