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CHAPTER 4

Food webs in lakes—seasonal dynamics and the impact of climate variability

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Introduction

As a result of increased green-house gases, global surface temperatures increased strongly during the twentieth century and will most likely increase between 1.4–5.8°C within the twenty-first century (Houghton et al. 2001). Early signs of climate-related gradual changes in lake ecosystems have been reported (Schindler et al. 1990; Magnuson et al. 2000; Straile 2002; Livingstone 2003; Straile et al. 2003) and further changes are expected to come. Besides the increase in temperature, the increase in greenhouse gases per se (e.g. Urabe et al. 2003; Beardall and Raven 2004) as well as other associated phenomena, for example, increase in UV-B radiation (e.g. Schindler et al. 1996; Williamson et al. 2002), and their interactions will affect organisms in lake ecosystems (Williamson et al. 2002; Beardall and Raven 2004). This chapter can obviously not cover in detail these issues in global change research; instead the emphasis will be on possible food-web effects of temperature increase and variability. For recent reviews on various effects of climate forcing on lakes see (Carpenter et al. 1992; Schindler 1997; Gerten and Adrian 2002*a*; Straile et al. 2003).

Studying spatial shifts in species distribution and changes in phenology—although they are important and do undoubtedly occur also in lake food webs (Straile et al. 2003; Briand et al. 2004)—is not sufficient to predict the effects of climate change on ecosystems as they do not consider indirect effects and feedbacks within the food web (Schmitz et al. 2003). Food-web interactions may indeed play a key role for an understanding of the effects of climate change on lakes. Although food-web related impacts of climate change will probably be among the most difficult impacts to predict, they might have also some of the most severe consequences, for example, leading to regime shifts (Sanford 1999; Scheffer et al. 2001*a,b*).

Studies on lakes provide some of the most complete investigations on the structure, dynamics, and energetics of food webs encompassing organisms from bacteria to vertebrates. The life cycle of organisms in temperate lakes is adapted to a highly seasonal environment. Food-web interactions in these lakes depend on the seasonal overlap of the occurrence of potential prey, competitor, or predator species. This seasonal overlap, that is, the match–mismatch of food-web interactions depends strongly on the seasonal dynamics of the physical environment of lakes such as temperature, light availability, and mixing intensity. Consequently, climate variability influences food-web interactions and hence the structure, dynamics, and energetics of lake food webs. On the other side, a thorough understanding of climate effects on lakes will require information on lake food webs and—as will be shown below—on the seasonal dynamics of lake food webs. Hence, this chapter is separated into three sections: The section titled "The trophic structure of aquatic food webs" examines the trophic structure of lake food webs, especially of lake food webs as observed during the summer season. The section "Seasonal sucession" analyses the seasonal development of lake food webs, and hence provides the more dynamical viewpoint necessary for examining the effects of climate on the food webs of lakes (section "Climate variability and plankton food webs"). I will illustrate some aspects of lake food-web structure with examples from Lake Constance, which food web has been rather well studied during recent years (see Box 4.1).

The trophic structure of aquatic food webs

The most successful models on food-web regulation in pelagic lake food webs are based on the assumption that food webs can be aggregated into trophic chains, that is, that trophic levels act dynamically as populations. These assumption has its origin in the famous "green world" hypothesis of Hairston, Smith, and Slobodkin (1960) (hereafter referred to as HSS) although aquatic systems were not discussed by HSS. According to HSS, the relative importance of competition and predation alternates between trophic levels of food webs such that carnivores compete, herbivores are controlled by predation, which frees producers from predation and results into competition at the producer trophic level. Similar ideas developed more or less simultaneously in freshwater ecology. Already in 1958, Hrbáček (1958) provided seminal observations on trophic level dynamics in lakes: he noted the relationship between fish predation, the reduction of large-bodied herbivores, and the resulting decrease in transparency and increase in phytoplankton density in lakes. An increasing number of subsequent studies used the aggregation of food webs into trophic levels as a tool to analyze food-web interactions especially in plankton food webs. The theory of trophic level dynamics was further developed into the concepts of the trophic cascade (Carpenter et al. 1985) and biomanipulation (Benndorf et al. 1984; Shapiro and Wright 1984). Food chain theory (Oksanen et al. 1981) formally extended HSS "green world hypothesis" to more than three trophic levels based on the proposed relationship between primary productivity and food-chain length. The trophic cascade has received strong support in both mesocosm experiments (Brett and Goldman 1996) as well as in whole lake manipulative experiments (Carpenter and Kitchell 1993). Biomass relationships in a suite of 11 Swedish lakes (Persson et al. 1992) also largely corroborated the predictions of HSS and the food-chain theory in systems with three trophic levels (algae, zooplankton, planktivorous fish) and with four trophic levels (algae, zooplankton, planktivorous fish, piscivorous fish).

The success of HSS in aquatic systems is evidence that the complexity of aquatic food webs can indeed be aggregated into trophic levels (Hairston and Hairston 1993). Nevertheless, this assumption has hardly been tested explicitly with data from food webs. Recently, Williams and Martinez (2004) used highly resolved carbon flow models to provide a first test: based on mass-balanced carbon flow models, they estimated the trophic position of web components by computing their food-chain length and their relative energetic nutrition trough chains of different length (Levine 1980). They suggested that most species can be assigned to trophic levels and that the degree of omnivory appears to be limited. To provide another test of this idea, seasonally resolved carbon flow models, which were established for the pelagic food web of Lake Constance (Box 4.1) can be used. To calculate trophic positions in the Lake Constance food-web basal trophic positions of phytoplankton and detritus/DOC were set to one. The latter implies that bacteria, which derive their nutrition from the detritus/DOC pool, were assigned to a trophic position of two. As a consequence, two different flow chains can be recognized: a grazing chain starting from phytoplankton and a detritus chain starting from detritus, respectively bacteria (Figure 4.2(a)). However, as (a) in Lake Constance, bacterial production is considerably lower than primary production, and (b) one group, that is, heterotrophic nanoflagellates (HNF) are the major consumers of bacterial production, a strong impact of the detritus chain on the trophic position of consumers is only evident for HNF. All other groups rely energetically directly (ciliates, rotifers, herbivorous crustaceans) or indirectly (carnivorous crustaceans, fish) on the grazing chain (but see Gaedke et al. (2002) for the dependence of consumers on phosphorus). Trophic positions in the Lake Constance carbon flow models were not distributed homogenously

Box 4.1 The pelagic food web of Upper Lake Constance

Lake Constance is a large (500 km^2) and deep ($z_{max} = 254$ m) perialpine lake in central Europe, which has been intensively studied throughout the twentieth century. The lake consists of the more shallow Lower Lake Constance, and the deep Upper Lake Constance (Figure 4.1(a)). Due to its deep slope the latter has a truly pelagic zone, which seems to be energetically independent from littoral subsidies. Like many other temperate lakes, Lake Constance went through a period of severe eutrophication starting in the 1930s and culminating in the 1960s/1970s (Bäuerle and Gaedke 1998 and references therein). Beginning with the 1980s total phosphorus concentrations declined again. However, the response of the plankton community to oligotrophication was delayed. The pelagic food web of Upper Lake Constance during the oligotrophication period has been analyzed within several years of intensive sampling (Bäuerle and Gaedke 1998). Different food-web approaches, that is, body-mass size distributions (Gaedke 1992, 1993; Gaedke and Straile 1994*b*), binary food webs (Gaedke 1995), and mass-balanced flow networks (Gaedke and Straile 1994*a,b*; Straile 1995; Gaedke et al. 1996; Straile 1998; Gaedke et al. 2002) were applied to a dataset consisting of five, respectively eight (Gaedke et al. 2002) years of almost weekly sampling. A special strength of this dataset is that it encompasses both, the classical food chain as well as the microbial food web. For carbon flow models the pelagic food web was aggregated into eight different compartments (Figure 4.1(b)), of which five can be assigned to the ''classical food chain,'' that is, phytoplankton, rotifers, herbivorous crustaceans, carnivorous crustaceans, and fish, and three to the microbial loop, that is, bacteria, heterotrophic nanoflagellates, and ciliates (Figure 4.1(b)). In addition flows between these eight compartments and the detritus/DOC (dissolved organic carbon) pool were considered (exsudation of phytoplankton, egestion and excretion of consumers, DOC uptake by bacteria). To analyze seasonal changes in carbon flows data were subdivided into up to 10 seasonal time intervals per year lasting between 14 and 102 days. For all seasonal time intervals mass-balanced carbon and phosphorous flows were established and further processed with the techniques of network analyses (Ulanowicz 1986).
The results shown here are based on 44 different mass-balanced food-web diagrams for different seasonal time intervals from the study years 1987 to 1991 (Straile 1995, 1998).

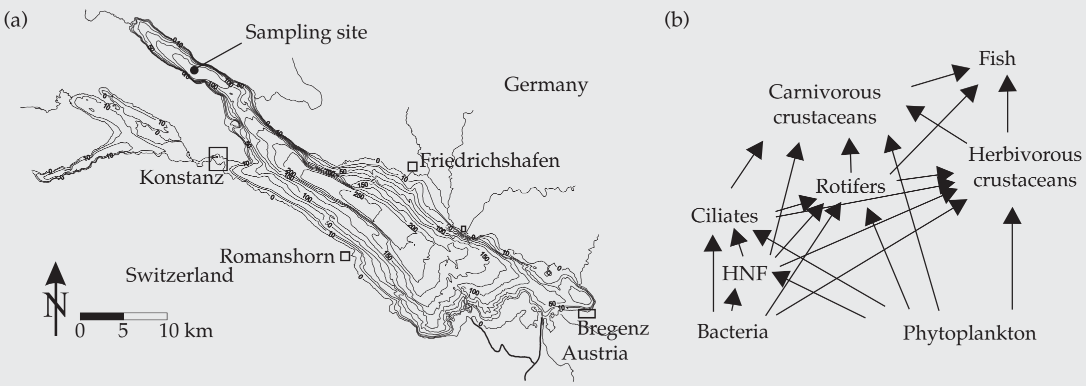

Figure 4.1 (a) Map of Lake Constance, and (b) aggregation of the Lake Constance pelagic food web into eight trophic guilds. Cannibalistic food-web interactions were considered for ciliates, rotifers, and carnivorous crustaceans, but are not shown here. Also not shown are the flows between these compartments and the detritus/DOC pool.

(Figure 4.2(b)). Rather, the distribution seems to be three-modal with peaks around trophic levels of two, three, and below four. This is especially remarkable as the inclusion of the microbial food-web with bacteria considered as second trophic level will cause an overestimation of trophic level omnivory, for example, herbivores do consume bacterivorous HNF (trophic level two to three, Figure 4.2(a)). Interestingly the distribution of trophic positions is not symmetrical around the

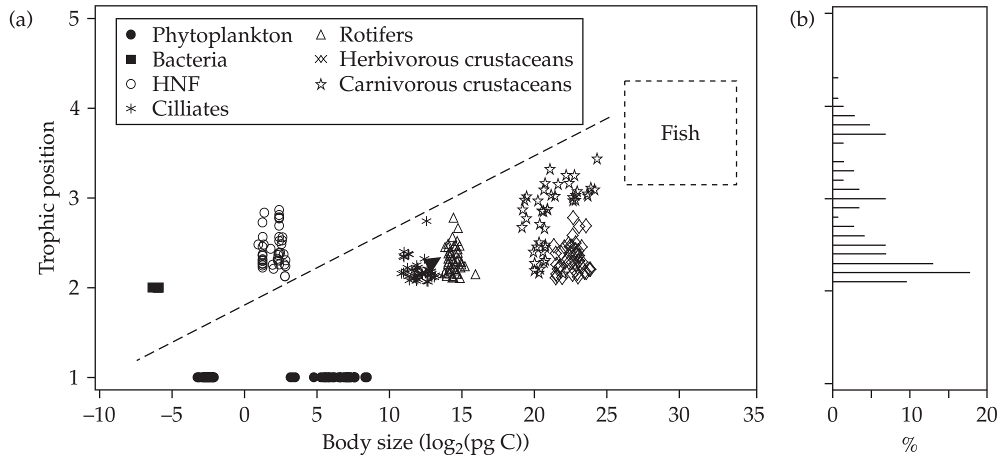

Figure 4.2 (a) Relationship between trophic positions in the carbon flow models and mean body size of trophic guilds; (b) percentage distribution of trophic positions (trophic positions of phytoplankton, bacteria, and HNFs not included).

different trophic levels, but rather skewed to the right, which might reflect the tendency of omnivorous consumers to gain most of their energy on the lowest trophic level on which they feed (Hairston and Hairston 1993).

Regarding the relationship of trophic position with body size, within both, detritus chain, and the grazing chain trophic position increases with body size. However, predominantly herbivorous groups do cover a large body size range between 2^{10} and 2^{24} pg C (Figure 4.2(a)), that is, more than four orders of magnitude. This data support a recently assembled binary food web for Tuesday Lake which also provides information on body size of species and in which a strong overall relationship between body size and trophic position (prey-averaged trophic position calculated from the binary food web) was observed (Cohen et al. 2003).

In many cases lake food webs hence provide text book examples for HSS and the trophic cascade. However, most of these examples are taken from the food webs of lakes during the summer situation. As climate variability will affect lakes throughout the season, it is necessary to consider seasonal variability of lake food webs.

Seasonal succession

The small size of planktonic organisms is the cause why it is necessary to consider seasonal succession in a discussion about climate effects on plankton food webs. Due to the small size and consequently high intrinsic growth rates of the food-web components, successional processes taking centuries in terrestrial systems will take place every year anew in the plankton. Environmental variations experienced by the plankton community in a lake during one year are considered to be scale analogous of gross climate change since the last glacial maximum (Reynolds 1997). Different successional stages are usually not considered together when examining terrestrial food webs, rather than food webs of for example, grasslands, shrubs, and forests are studied separately. This might suggests that there is in the pelagic zone of a specific lake not one food web, but rather a succession of different food webs. In fact, the classical paper on plankton succession in lakes, the PEG (Plankton Ecology Group) model (Sommer et al. 1986) distinguishes between 24 successional stages, in which the relative importance of abiotic forcing through physical and chemical constraints and of biotic interactions, that is, competition and predation, differ (Sommer 1989). Consequently, seasonal variability in driving forces will result into seasonal differences in for example, species composition, diversity, interactions strength between food-web components, and finally food-web configurations.

Food-web structure including the number of functionally relevant trophic levels changes during the season. During winter, primary productivity of algae in many lakes will be strongly limited by the availability of light, for example, due to deep mixing and/or the formation of ice cover, both preventing algal blooms. During this time period, growth of algae is constrained by abiotic conditions and not by the activity of herbivores. Reynolds (1997) considers this successional state as an aquatic analog to bare land. Only with ice thawing and/or the onset of stratification in deep lakes algal blooms can develop with subsequent growth of herbivores. Within a rather short time of several weeks different herbivore population increase in size and finally often control algae. Within this so-called clear-water phase (Lampert 1978) algal concentration is strongly reduced and water transparencies rise again to values typical for winter. During this successional phase the food web is functionally a two-trophic level system. However, the "green world" returns due to—at least partially—increased predation pressure on herbivores due to fish, whose larvae surpass gape limitation and/or due to invertebrate predators (Sommer 1989). In addition to predatory control of herbivores, the world in summer is also prickly and tastes bad (Murdoch 1966) as for example, large and spiny algal species develop which are difficult to ingest for herbivores. Hence the system has developed from a one level system in early spring where herbivores are not abundant enough to control phytoplankton development into a complex three–four level system in summer, which collapses again toward winter.

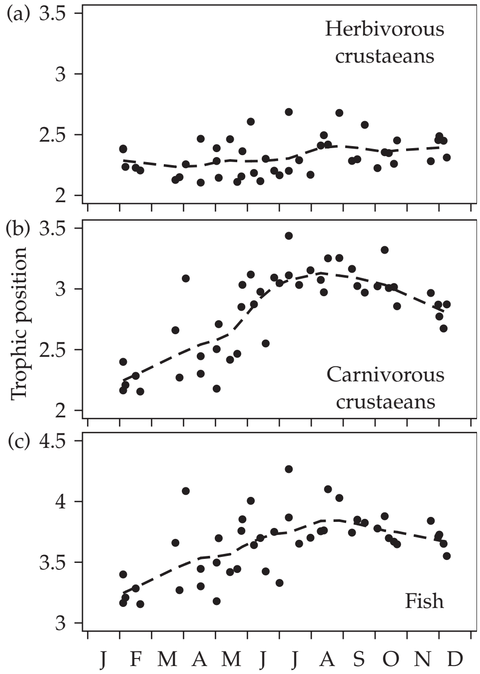

Figure 4.3 Seasonal changes in trophic position of herbivorous zooplankton, carnivorous zooplankton, and fish. Trophic positions are shown on the time axis at the midpoints of the respective time intervals. The dotted line represents a loess fit.

This development of trophic structure is also evident for the trophic positions of the different compartments of the Lake Constance flow model (Figure 4.3). The trophic position of herbivorous crustaceans remains rather constant throughout the year, at approximately two (Figure 4.3(a)). However, the trophic positions of carnivorous crustaceans and of fishes do increase seasonally (Figure 4.3(b) and (c)). This increase of both groups is due to the increase in trophic position of carnivorous crustaceans. During winter and early spring, carnivorous crustaceans consist of cyclopoid copepods. Although considered as carnivorous at least as more ontogenetically more advanced stages, there is simply not enough herbivorous production to sustain a carnivorous feeding mode for a major invertebrate group (Straile 1995). As a consequence, "carnivorous crustaceans" do rely largely on phytoplankton production, that is, they are in fact herbivorous during winter and early spring. Only from late spring/early summer onwards, herbivore production is large enough to sustain energetically populations of carnivorous crustaceans. This is also the time when more specialized carnivorous crustaceans, the cladocerans *Bythotrephes longimanus* and *Leptodora kindtii* develop from resting eggs and build up important populations in the planktonic community. Hence, the food web develops energetically from a three-trophic level system in winter/early spring to a four-trophic level system in summer. This is not due to the addition of a new top predator, as fish are present during the whole year, but due to the combined effects of diet switches of taxa, that is, cyclopoid copepods, and the addition of new intermediate predators, that is, *Bythotrephes* and *Leptodora*. This does not imply that the pelagic food web during summer can be considered dynamically as a simple four-trophic level system as among other things spatial (Stich and Lampert 1981) and size refuges (Straile and Hälbich 2000) of prey species at different trophic levels seem to blur cascading trophic interactions in Lake Constance.

However, despite these seasonal differences in food-web composition, structure, and dynamics, the season-specific pelagic food webs are clearly interconnected temporally. This is either due to the species which manage to persist during all food-web configurations within the year in the open water, or due to the existence of diapause and or dormancy stages. The latter allow species—given sufficiently correct cues for the start and termination of diapause—to exploit a specific season, respectively food-web configuration to ensure long-term persistence in a specific lake. These time-travelers (Hairston 1998) allow for the existence of a specific summer food web without the need for yearly new colonization events from other lakes. In addition, the latter is not really a possibility, as food webs in nearby lakes will be at a similar successional stage. This is also an interesting contrast to terrestrial system where a landscape mosaic of different successional stages offers the possibility of a new colonization. Recent research has shown that resting stages are important components of the life cycle of nearly all plankton taxa, for example, for phytoplankton (Hansson 1996), ciliates (Müller and Wünsch 1999), rotifers (Hairston et al. 2000), and crustaceans (Hairston and Cáceres 1996; Cáceres 1998; Jankowski and Straile 2004). Furthermore, bet hedging strategies even allow for multiyear dynamics and the persistence of species even when reproduction fails within specific years (Cáceres 1998).

On the other hand, lake food webs in the various successional stages or even within several successional cycles might be connected through the presence of long-living organisms, which are for example, top predators. This can have important dynamical consequences when for example, long-lived piscivores suppress planktivorous fish over several years (Post et al. 1997; Sanderson et al. 1999; Persson et al. 2003). Persson et al. (2003) provide evidence for shifts in trophic cascades caused by intrinsically driven population dynamics of top predators including size-specific cannibalism. This is an important case study showing that cannibalism and life-cycle omnivory can have important food-web consequences culminating in a trophic cascade, that is, less zooplankton and more phytoplankton biomass during high summer when large-sized "gigantic cannibals" produced high numbers of young-of-the-year fish (Persson et al. 2003). However, even for long-lived animals there is a need to adjust their life cycle to the seasonal environment, that is, to seasonal changes in the food-web structure. Any analysis of climatic forcing of pelagic food-web hence will need to consider fast changes in food-web structure occurring during seasonal succession and the adaptation of species to cope with this variability.

Climate variability and plankton food webs

Changes in climate may result into changes in the timing and duration of successional stages (e.g. Straile 2002) as well as in modifications of food-web structure within distinct successional stages (e.g. Weyhenmeyer et al. 1999). Climate warming has been shown to increase the stratification period in lakes (Livingstone 2003) which may in turn intensify nutrient limitation and phytoplankton competition. Species need to adapt their life cycles, for example, the timing of reproduction of long-lived species, the timing of critical life history shifts, for example, the timing of metamorphosis of copepod species, and the timing of diapause initiation and termination to temporal shifts in food-web structure, respectively food-web shifts. Match or mismatch of specific life-history events with the successional state of the food web may crucially influence population dynamics of species. This has been suggested for, for example, the interaction of fish larvae and their zooplankton prey (Cushing 1990; Platt et al. 2003) and the hatching of overwintering eggs (Chen and Folt 1996). The latter authors suggest that fall warming may result into the maladaptive hatching of overwintering eggs of the copepod *Epischura lacustris* possibly resulting into the loss of the species from the lake.

As a consequence of the strong seasonal dynamics within lake food webs, climate effects will be highly season-specific. Interestingly, and in contrast to many food-web studies, which consider the summer situation, there is a wealth of studies reporting ecological climatic effects of climate forcing in lakes during winter and early spring periods. Although climate forcing is also important in summer (see below), this might point to a special importance of winter meteorological forcing for temperate lake food webs. It is hence important to ask why this is the case: as often, there is not a single explanation, but meteorological, physical, and biological reasons contribute to this observation: (1) there are strong changes and there is a high interannual variability in winter meteorological forcing, (2) there is a high susceptibility of lake physics to meteorological forcing in the winter half year, (3) there is a high susceptibility of species physiology and life history and hence of successional dynamics to changes in lake physics during the winter half year.

1. Strong changes and high variability in winter meteorological forcing—the largest warming on our planet during the twentieth century has occurred (1) during winter and (2) over Northern Hemisphere land masses. Likewise, large-scale climatic oscillations such as the North Atlantic Oscillation (NAO) and the El Nino Southern Oscillation (ENSO) do have their strongest teleconnections to northern hemispheric meteorology during winter (Hurrell 1995; Rodionov and Assel 2003). In contrast, summer warming was not as pronounced during the twentieth century, and climate forcing during summer seems to be more controlled by local and regional factors, but less under the control of large-scale climate oscillations.
2. Lake physics will be especially sensitive to climate variability during the winter half year. During this time period important mixing events do occur and lakes may or may not be covered by ice. Physical conditions such as the presence/absence and intensity of mixing and the presence/absence and duration of ice cover may be highly sensitive—depending on lake morphology, latitude, and altitude—to changes in winter meteorology. For example, ice cover duration in European and North American lakes is associated with the NAO, respectively ENSO (Anderson et al. 1996; Livingstone 2000; Straile et al. 2003). Winter severity influences the mixing intensity in deep lakes, thereby influencing nutrient distributions (Goldman et al. 1989; Nicholls 1998; Straile et al. 2003) and oxygen concentrations in the hypolimnion (Livingstone 1997; Straile et al. 2003). In contrast, stratification is usually strong during summer and interannual meteorological variability might result into more or less steep temperature gradients but unlikely in mixing (but see George and Harris (1985) for more wind-exposed lakes). However, warmer summer temperatures may reduce mixing events in shallow polymictic lakes.
3. Species physiology and life history and hence plankton succession is highly sensitive to physical factors during the winter half year (Sommer et al. 1986). Ice cover duration (Adrian et al. 1999; Weyhenmeyer et al. 1999), mixing intensity, and timing (Gaedke et al. 1998) will have a strong impact on phytoplankton bloom formation. Temperature effects on growth rates of zooplankton and fish seem to be especially important during spring. During the phytoplankton spring bloom zooplankton growth is unlikely to be limited by food concentration. Consequently, temperature limits zooplankton growth rates (Gerten and Adrian 2000; Straile 2000; Straile and Adrian 2000). Similar arguments have been put forward regarding growth of whitefish larvae (Eckmann et al. 1988). As zooplankton is abundant in late spring—given that there is not a mismatch situation—fish growth depends on water temperatures. However, higher winter temperatures may also have negative impacts on consumers due to enhanced metabolic requirements at low food abundance. This has been suggested to have caused a decline of *Daphnia* abundance in high NAO winters in Esthwaite Water (George and Hewitt 1999). Additionally, competition with the calanoid copepod *Eudiaptomus,* which has lower food requirements and increased in abundance during winter in high NAO years might have contributed to the decline of *Daphnia* in Esthwaite Water.

Another important reason for the importance of winter is that winter represents a population bottleneck for many species. For example, in temperate lakes, the abundance of plankton is strongly reduced during winter, and populations rely on resting stages to overwinter (see above). Fitness benefits might be associated with the ability to overwinter in the plankton as opposed to produce resting stages. For example, the dominance of the cyanobacteria *Planktothrix* in Lake Zurich in recent years has been attributed to a series of mild winters resulting in less deep water mixis (Anneville et al. 2004).

Also winter is often associated with reduced consumption and starvation of juvenile fishes influencing fish life history (Conover 1992) and population dynamics (Post and Evans 1989). Furthermore severe winters associated with long-lasting ice cover and oxygen deficiency can cause winterkill of fish species with consequences for fish community composition (Tonn and Paszkowski 1986) and lower trophic levels (Mittelbach et al. 1995).

However, also summer food webs are affected by climate variability. This is due either to summer meteorological forcing or indirect food-web mediated effects of winter/early spring meteorological forcing (Straile et al. 2003). For example, temperature effects on the growth rate of the cladoceran genus *Daphnia* will change the timing of phytoplankton suppression, that is, the timing of the clear-water phase in early summer (Straile 2000). Higher temperatures associated with a positive phase of the NAO resulted into higher *Daphnia* growth rates and earlier phytoplankton depression in Lake Constance, in addition the duration of phytoplankton suppression increased (Straile 2000). Similar shifts in the timing of the clear-water phase were observed in a number of European lakes (Straile 2000, 2002; Anneville et al. 2002; Straile et al. 2003). Overall warming trends since the 1970s resulted into an advancement of the clear-water phase of approximately two weeks in central European lakes (Straile 2002). This phenological trend of a predator–prey interaction is of similar magnitude as phenological shifts in, for example, plant, insect, and bird populations (Walther et al. 2002; Straile 2004). In shallow lakes, the spring clear-water phase is of crucial importance for the growth and summer dominance of macrophytes (Scheffer et al. 1993). Hence, higher growth rates of daphnids during spring and an earlier onset of the clear-water phase has been suggested to promote a regime shift in shallow lakes from a turbid phytoplankton dominated to a clear macrophyte-dominated state. This might be an example on how even small temporal changes in the food-web interaction between phytoplankton and daphnids may result into large-scale ecosystem changes in lakes. However, the database used by Scheffer et al. (2001*b*) is confounded by management effects and cannot be used as a strong support of their hypothesis (van Donk et al. 2003).

Differences in winter meteorological forcing can also change the nutrient availability for phytoplankton due to changes in deepwater mixing or runoff with subsequent consequences for annual primary productivity. For example, primary production in Lake Tahoe and Castle Lake was related to winter mixing depth and precipitation, respectively (Goldman et al. 1989). Likewise, decreased summer transparency and increased epilimnetic pH and O_2 concentrations indicated that the phytoplankton summer bloom was more intense after mild winters in Plußsee (Güss et al. 2000). Food-web mediated effects of climate variability in summer will also occur when fish numbers are affected by winter severity due to starvation or oxygen deficiency under ice (see above).

Summer meteorological forcing can also have significant effects on lake food webs. For example, in Lake Windermere, interannual differences in June stratification linked to the position of the Gulf stream (George and Taylor 1995) are related to the growth of edible algae and finally to *Daphnia* biomass (George and Harris 1985). Also, copepod species have been shown to increase in abundance as a result of warm summers possibly due to development of an additional generation (Gerten and Adrian 2002*b*).

Effects of climate variability will also change the relative importance of species within successional stages. For example, phytoplankton species differ in respect to sedimentation and/or light limitation. Climate-related changes in stratification hence will favour different species. For example, in Müggelsee (Adrian et al. 1999) and Lake Erken (Weyhenmeyer et al. 1999), mild winters with less ice cover in response to high NAO years favored diatoms species over other phytoplankton. Diatoms need turbulent conditions to prevent them from sinking out of the euphotic zone, a condition not met under ice. In contrast, the dinoflagellate *Peridinium* can already build up a large population size under clear ice (Weyhenmeyer et al. 1999). Likewise, in Rostherne Mere, the intensity of summer mixing is crucial for which phytoplankton species will dominate: extremely stable stratification leading to the dominance of *Scenedesmus*, with increasing mixing favoring *Ceratium/Microcystis* and finally *Oscillatoria* dominance (Reynolds and Bellinger 1992). The establishment of a more stable stratification is of special concern since stratification may often favor buoyant species including toxic cyanobacteria over sedimentating species (Visser et al. 1996).

Also zooplankton growth rates will show different responses to interannual temperature variability. Based on a literature survey of laboratory data, Gillooly (2000) suggested that larger zooplankton species should respond more strongly to increasing water temperatures than small ones. According to his survey, difference in generation time between the large cladoceran *Eurycercus lamellatus* and the rotifer *Notholca caudata* is reduced from 88 days at 5°C to 15 days at 20°C suggesting that large zooplankton should be correspondingly favored with warming. A hypothesis that remains to be tested with field data (Straile et al., in prep.). Also the life history of zooplankton species is of importance. Population growth rate of parthenogenetically reproducing rotifers and cladocerans exceeds those of copepods which reproduce sexually and do have a long and complex ontogeny. As a consequence, daphnids should be able to benefit more strongly from spring warming than copepods. This can be demonstrated by examining interannual variability of daphnid and copepod biomass in relation to interannual variability to vernal warming. Both taxa are able to build up higher biomasses in years with early vernal warming and consequently high May water temperatures in Lake Constance (Figure 4.4). However, the effect is much more pronounced for daphnid biomass, which increases several orders of magnitude. Interestingly, an increase in spring temperatures seems to have a similar effect on the

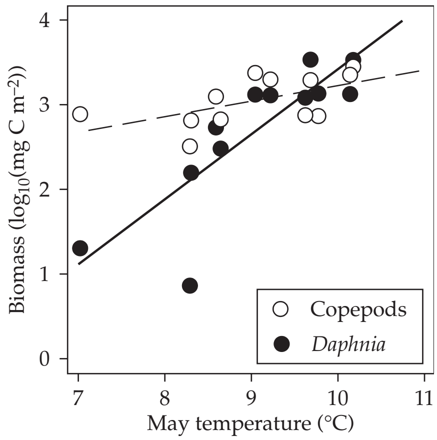

Figure 4.4 Response of *Daphnia* and copepod biomass in May to interannual differences in vernal warming as expressed as average May water temperatures (0–20 m water depth). Both taxa show a significant relationship with temperature ($n = 12$, $r = 0.84$, $p < 0.001$ for daphnids, and $n = 12$, $r = 0.57$, $p < 0.06$ for copepods).

relative abundances of daphnids and copepods in spring as an increase in food availability due to eutrophication (Straile and Geller 1998). Eutrophication as well as temperature increase seems to favor taxa with high intrinsic growth and developmental rates.

To summarize, due to the fast changes in food-web structure in pelagic systems, and the importance of food-web interactions, it is important to adopt a food-web approach when studying climate effects on lake ecosystems. Plankton systems seem to be especially suitable to study indirect food-web mediated effects due to the small size of the organisms concerned, their fast growth rates, and the relative promptness in which indirect effects will occur. On the other hand, food-web variability due to meteorological forcing, that is, so-called "natural experiments," can also be considered as an important tool to analyze food-web regulation. The highly seasonal signal of climate effects on lake food webs suggest that food-web studies in lakes need to consider seasonal variability. In addition, more attention should be paid to the winter period. Many studies in the past seem to have neglected the winter due to the admittedly overall lower biological activity during winter. Instead, the winter period may be a critical one for lake functioning, and for climate effects on lake functioning as it seems that the winter/early spring situation might set the stage for much what will come during the vegetation period. When adopting a seasonal approach, more emphasis should also be paid to time and season as resources. Resources, which will undoubtedly change with climate change and to which organisms have to fit their life cycle.

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