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Zooplankton ecology in high-mountain lakes

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Für meine Eltern

Vorwort

Das aquatische Leben unter extremen alpinen Bedingungen faszinierte mich bereits, als ich meine ersten limnogischen Erfahrungen an der Universität Innsbruck sammelte. Dies war meine Motivation, bei einem Projekt über die Ökologie des Zooplanktons in alpinen Seen und im speziellen über den Einfluss von Botenstoffen in der Nahrungskette in alpinen Seen an der EAWAG mitzuarbeiten. Die Auswahl eines geeigneten Bergsees stellte sich als problematisch dar, da nicht in jedem Bergsee (im Gegensatz zu Tieflandseen) Daphnien (Wasserflöhe) vorhanden sind. Daphnien sind wichtige Organismen in der aquatischen Nahrungskette und zudem hervorragende Modellorganismen. Auf der Suche nach einem *geeigneten* Bergsee mit Daphnien, lernte ich neben aquatischen Aspekten auch sehr viel über die sozio-ökonomische Bedeutung von Bergseen. Nach der Beprobung von fast 30 Seen war der Oberer Arosasee, immer noch der geeignetste. Somit ist der Hauptteil dieser Arbeit in Arosa durchgeführt worden. Diese Arbeit war ein sehr spannendes Abenteuer und nur möglich dank der Mithilfe von mehreren Personen. Ich möchte mich bei allen Personen bedanken, die durch ihr Zuhören, Ermutigen, Korrigieren, Anpacken, Helfen und Erdulden zum Entstehen dieser Arbeit beigetragen haben.

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Summary

The research of my thesis stresses the conflicting demands of zooplankton species inhabiting high-mountain lakes and attempts to clarify mechanisms by which zooplankton species maintain long-term persistence and coexistence with potential competitors and predators. In particular, I focus on the behaviour and life histories of the cladoceran genus *Daphnia*, an ecological important grazer in lakes. *Chapter I* contains a general introduction to high-mountain lakes, the trophic and chemical network in aquatic systems, habitat selection behaviour and describes protection strategies in zooplankton against unfavourable conditions.

In the first study (*Chapter II*) we addressed the questions of how the zooplankton community has changed during the last century in Swiss Alpine lakes and investigated the present genetic variation of *Daphnia* in various Alpine lakes. Re-sampling of lakes studied in the early twentieth century and comparing past and present zooplankton composition and taxa richness did not show a drastic overall change in planktonic crustacean composition. Taxa richness significantly decreased with increasing lake elevation, but no other environmental factor examined correlated with richness. The genetic diversity of *Daphnia* spp. was not related to lake elevation or to the proportion of sexual individuals. Large-bodied zooplankton taxa were found in lakes both with and without fish. Therefore, we conclude that the presence of fish can be excluded as the general factor explaining the occurrence or absence of large species of zooplankton in Alpine lakes (see also *Chapter III*). However, we do not know how fish altered the overall zooplankton community because fish introduction occurred in these lakes long before zooplankton data were available. The ability to create resting stages may be an essential factor for the maintenance of genetic diversity and the long-term persistence of *Daphnia* and other zooplankton taxa in Alpine lakes.

The following studies of this thesis were conducted in the Oberer Arosasee, a Swiss high-mountain lake, located at 1734 m a.s.l. Since in this lake, large zooplankters and fish coexist we were interested in the importance of predation and competition in structuring the zooplankton community (*Chapter III*). A comparison of patterns in the abundance, body length measures, fecundity and proportion of adults in the *D. galeata* population, strongly suggests that top-down effects of trout predation had no impact on the population and was not the cause for the population decline during the summer. There is some evidence for both exploitative and interference competition between some taxa. In the Oberer Arosasee, *D. galeata* is overall a consistently superior competitor, perhaps because of its broader food and spatial niches, stronger resistance to starvation or suppression of other herbivores by interference.

Food quality and quantity is a major factor influencing growth, reproduction and survival of zooplankton. We used carbon-length relationships to measure seasonal condition of the *D. galeata* population in different depth strata of the Oberer Arosasee (*Chapter IV*), where most individuals display a diel vertical migration (DVM). Low carbon content and fecundity indicate that *D. galeata* were food limited for much of the year. In addition, migrating *D. galeata* and individuals remaining in deep layer had better body conditions compared to non-migrating *D. galeata* during summer, when migration amplitude was highest.

Several hypothesis have been put forward to explain the adaptive significance of DVM in zooplankton. The ultimate cause for DVM of zooplankton is the avoidance of light-dependent mortality risk from visual predators in the surface waters. Remaining in the hypolimnion during the day, however, implies demographic costs due to the cold and nutrition-poor habitat. Reduced growth rate is thought to be the main cost of migration, and is thought to be the reason why daphnids move upwards to warmer food-rich surface waters at night. Since the Oberer Arosasee has deep-water food maxima it was of interest to investigate whether the deep food is of high quality. *Chapter V* reports on a study in which daphnids were cultured on seston taken from different depth strata. Growth rates of *D. galeata* were higher on seston of the deeper strata, even after temperature correction. Therefore, temperature and food optima are uncoupled and zooplankton should allocate their time in different depths depending on the temperature gradient. Seasonal migration patterns of *D. galeata* in the Oberer Arosasee (*Chapter VI*) showed that both adults and juveniles exhibit DVM behaviour throughout nearly the entire open water period. Daphnids did not increase migration amplitude when fish biomass or kairomone concentration was altered, neither in the natural fish stocking experiment nor in an *in situ* enclosure experiment. However, in a large laboratory experiment ('Plankton Towers') that mimicked lake summer conditions, daphnids increased mean day depth in the presence of fish kairomones, but did not migrate without fish chemical cues. This behaviour indicates that the alpine *D. galeata* population responds to the presence of fish and migrates into deeper colder water. Without fish kairomones and with fish kairomones at night, daphnids selected the habitat with the highest expected fitness outcome. The uncoupled optima of food and temperature might create ongoing migration to optimise fitness by allocating time spent in surface and deeper strata in the lake, without the enhancing effect of fish kairomones. Although daphnids response to fish kairomones in the tower experiment, there was no evidence of reaction in the field to changes in the amount of fish present in the lake or enclosures. Our results suggest that the major benefit of night-time movement to surface waters was an acceleration of embryo development due to warmer temperatures, not increased food intake.

Evidence presented in *Chapter VII* suggests that zooplankton of high-mountain lakes may avoid surface waters during the day because of the high ultraviolet radiation (UVR). In a life-history UVR experiment, *D. galeata* at the surface did not reach maturity. The deleterious effects of UVR on daphnids, however, decreased with increasing depth; although downward migration provides effective protection from UVR during the day, this does not explain the migration to deep strata.

In conclusion, the research presented in this thesis indicated that the behavioural and life-history plasticity of zooplankton are essential strategies to balance the conflicting demands and to maintain long-term persistence in high-altitude lakes.

Zusammenfassung

Die Untersuchung im Rahmen dieser Arbeit hebt die Anforderungen des Zooplanktons in alpinen Seen hervor und beschreibt Mechanismen, welche es dem Zooplankton ermöglichen, mit potentiellen Konkurrenten und Räubern zu koexistieren. Im speziellen fokusiert diese Arbeit auf das Verhalten und auf den Lebenszyklus von Cladoceren (Crustacea, Phyllopoda) der Gattung *Daphnia* (Wasserflöhe). Daphnien sind ökologisch wichtige Algenfresser in Seen. Das erste Kapitel enthält eine generelle Einleitung über alpine Seen, die trophische Kaskade, chemische Kommunikation im aquatischen Lebensraum, Habitatsauswahl und beschreibt verschiedene Strategien des Zooplanktons um ungünstige Bedingungen zu bewältigen.

Im zweiten Kapitel beantworten wir die Frage, inwieweit sich die Zusammensetzung des Zooplanktons in alpinen schweizer Seen während des letzten Jahrhunderts geändert hat. Zudem untersuchten wir die genetische Variation von Daphnien in diesen Seen. Ein Vergleich der Zooplankton Artendiversität mit ca. 100-jährigen Daten und der heutigen Diversität zeigte keine drastische Veränderung in der Zusammensetzung der Crustaceenarten. Die Artendiversität korreliert einzig mit der Höhenlage der Seen, d.h. je höher der See gelegen ist, desto geringer ist die Artendiversität. Im Gegensatz dazu korreliert die genetische Diversität von Daphnien weder mit der Seehöhe, noch mit dem Anteil von sexuellen Individuen. Grosse Zooplanktonarten kommen sowohl in Seen mit Fischen als auch in Seen ohne Fische vor. Aus diesem Grund ist anzunehmen, dass das Vorkommen von Fischen nicht der erklärende Faktor für das Vorhandensein oder Fehlen von grossen Zooplanktonarten in alpinen Seen ist. Da der Fischeinsatz in den ursprünglich fischfreien alpinen Seen jedoch schon vor einigen Jahrhunderten erfolgte, sind paläolimnologische Untersuchungen erforderlich, um den generellen Einfluss des Fischbesatzes auf die Zooplanktongemeinschaft zu untersuchen. Die Fähigkeit von vielen Zooplanktonarten Dauerstadien zu bilden ist bedeutend, um die genetischer Diversität und das Bestehen von verschiedenen Zooplanktonarten in alpinen Seen zu sichern.

Die anschliessenden Untersuchungen sind im Oberer Arosasee, einem Schweizer Bergsee auf 1734 m ü. M. durchgeführt worden. Da in diesem

See grosse Zooplanktonarten mit Fischen koexistieren, waren wir interessiert, wie potenzielle Räuber und Konkurrenten das Zooplankton strukturiert (*Kapitel III*). Die Dichte, Grösse, Eizahl und der Anteil von Adulten der *Daphnia galeata* Population deutet darauf hin, dass Räuberdruck von Fischen kaum der Grund für das Zusammenbrechen der Daphnienpopulation im Sommer war. Räuberdruck von *Cyclops abyssorum* beeinflusst die *D. galeata* Population. Es gab einige Annahmen für exploitative Interaktionen (Ausbeutung gemeinsamer Ressourcen) und Interferenzen (gegeneinander behindernde Konkurrenz) zwischen Zooplanktonarten.

Die Quantität und Qualität von Ressourcen bestimmt wesentlich die Wachstumsrate, Reproduktion und das Überleben von Zooplanktern. Wir verwendeten Kohlenstoff-Längen Verhältnisse, um die jahreszeitliche Kondition von Daphnien in unterschiedlichen Tiefenstufen zu bestimmen (*Kapitel IV*). Daphnien des Oberer Arosasees führen eine tagesperiodische Vertikalwanderung durch. Ein geringer Kohlenstoffgehalt und eine geringe Eizahl zeigten, dass *D. galeata* über einen Grossteil des Jahres futterlimitiert ist. Zusätzlich hatten wandernde und sich in tieferen Wasserschichten aufhaltende Daphnien bessere Konditionen im Vergleich zu nicht wandernden Daphnien während des Sommers.

Verschiedene Hypothesen sind aufgestellt worden, um die adaptive tagesperiodische Vertikalwanderung des Zooplanktons zu erklären. Der Ultimatfaktor der Vertikalwanderung ist die Verringerung der lichtabhängigen Mortalität durch das Meiden des Oberflächenwassers während des Tages. Jedoch ist der daraus resultierende Aufenthalt im kalten und nährstoffarmen Tiefenwasser für die Reproduktion der Zooplankter ungünstig. Dies ist auch der Grund, warum Daphnien in der Nacht ins warme nährstoffreiche Oberflächenwasser zurückkehren. Da der Oberer Arosasee ein Futtermaximum in tiefen Wasserschichten aufweist, waren wir interessiert, ob das Futter von hoher Qualität (nährstoffreich) war. Wir züchteten Daphnien in Wasser aus verschiedenen Tiefenstufen des Sees (*Kapitel V*). Daphnien, welche im Seston aus tieferen Wasserschichten des Sees gezüchtet wurden hatten eine grössere Wachstumsrate als Daphnien, die im Oberflächenwasser gezüchtet wurden. Selbst nach der Temperaturkorrektur waren die Wachstumsraten in tieferen Schichten höher. Da das Temperaturmaximum im Oberflächenwasser ist, das

Futtermaximum jedoch im Tiefenwasser liegt, sollten Zooplankter ihre Aufenthaltszeit in den verschiedenen Schichten je nach Temperaturunterschied verteilen. Saisonale Vertikalwanderungen von *D. galeata* zeigten, dass adulte und juvenile Daphnien eine tagesperiodische Vertikalwanderung fast über das ganze Jahr durchführten (*Kapitel VI*). Die Veränderung der Fischbiomasse oder der Kairomon Konzentration zeigte keine Erhöhung der Wanderungsamplitude der Daphnien. Dies wurde im See durch Fischbesatz und in einem *in situ* Enclosure-Experiment gezeigt. In einem Laborexperiment (‘Plankton Türme‘) hingegen, das die Sommersitutation des Sees simulierte, wanderten die Daphnien tagsüber in die Tiefe in der Gegenwart von Fischkairomonen. In Abwesenheit von Fischkairomonen wanderten sie jedoch nicht. Dieses Verhalten zeigte, dass die alpine *D. galeata* Population auf den Fischfaktor reagiert und tiefer in kältere Schichten wandert. Ohne Fischkairomone und mit Fischkairomonen in der Nacht, haben die Daphnien das Habitat mit der grössten erwarteten Fitness aufgesucht. Die gegenseitigen Optima von Temperatur und Futter könnten der Grund für die tagesperiodische Wanderung fast über das ganze Jahr sein. Daphnien versuchen ihre Fitness zu optimieren, indem sie sich zum Teil im Oberflächenwasser und in der Tiefenschicht des Sees aufhalten. Die nächtliche Wanderung ins warme Oberflächenwasser könnte ein Vorteil zur Beschleunigung der Eientwicklungs bei den Daphnien bieten, jedoch kein Futtervorteil.

Die phototaktische Reaktion von Daphnien auf Lichtintensität erklärt die synchrone Wanderung am Abend und am Morgen. Hohe Ultraviolett Strahlung (UV) an der Oberfläche erklärt das Meiden dieser Schichten während des Tages. Dies konnten wir anhand eines Lebenszyklus UV-Experiment mit *D. galeata* zeigen (*Kapitel VII*). An der Oberfläche starben die Daphnien vor der Reproduktion aufgrund des hohen UV-Lichtes. Der negative Effekt von UV nimmt jedoch mit der Tiefe ab. Daher gewährt das Wandern in tiefere Schichten während des Tages einen effektiven Schutz gegen hohe UV Einstrahlung, jedoch erklärt UV nicht die Wanderung in tiefere Schichten, wo der UV-Einfluss gering ist.

Diese Arbeit zeigte, dass Plastizität im Verhalten und im Lebenszyklus des alpinen Zooplanktons eine wichtige Strategie darstellt, um verschiedenste Konfliktsituationen auszugleichen und demzufolge das permanente Vorkommen in alpinen Seen sichert.

Contents

Chapter I

Introduction and thesis outline

High-mountain lakes

The definition of high-mountain lakes is based on a zonation scheme developed by botanists (Pechlaner, 1971). The vegetation, however, depends more on temperature than on altitude (Legros, 1992) and therefore on the latitude. In the western European Alps (45° N), the altitudinal belts (zones) of vegetation are arranged with increasing elevation as hilly belt – mountain belt – sub-alpine belt – alpine belt – nival belt (Ozenda, 1985). According to the elevation, the series of Swiss high-mountain lakes studied in this thesis are located in the sub-alpine and alpine vegetation zones. The alpine belt is the zone above the treeline consisting primarily of alpine meadow, whereas the sub-alpine belt is characterised by conifers adapted to higher altitudes (*Larix decidua*, *Pinus cembra*). In the Swiss Alps the alpine zone is between ~2000 and 2900 m a.s.l. and the sub-alpine zone between ~1300 and 2200 m a.s.l. (Ozenda, 1985). The position of the lakes with respect to the treeline imparts important chemo-optical characteristics to the water.

High-mountain lakes are, in general, much less influenced by pollution from agriculture and wastewater compared to lowland lakes. This condition does not necessarily imply that these ecosystems are pristine because many pollutants are introduced through regional and long-range atmospheric transport (Sommaruga, 2001). Most high-mountain lakes are naturally fishless; however, there is good historical evidence that man has been introducing fish to such systems since ca. 1500 A. D. in the European Alps (Roth, 1971; Pechlaner, 1981). The introduction of fish to previously fishless high-mountain lakes is accompanied by a change in the zooplankton community, including the local extinction of species (Gliwicz, 1985; Knapp et al., 2001).

High-mountain lakes in the European Alps originated after the last glacial retreat ~10,000 years ago (Pechlaner, 1981). Most of these lakes are small (area <5 ha) and generally shallow ($\text{depth}_{\text{max}}$ <15 m). Depending on their altitude, they are ice-and snow-covered for long periods, from late fall to early summer, at the highest elevations, and therefore have a short growing period. Under ice, low temperatures and low light levels are limiting factors for production (Ventelä et al., 1998). High-mountain lakes have little input of nutrients or humic substances; therefore, light penetration is high during the open season (Sterner et al., 1997). Because of shallow depth and wind exposure, thermal stratification is absent or transient during the open water period (Tilzer, 1972).

Organisms living in high-mountain lakes must cope with harsh environments—low nutrient conditions, low food availability, low temperature, short growing seasons (3 – 5 months), extreme seasonal changes in light conditions and periods of high solar radiation. As a result, biotic communities of high-mountain lakes are relatively simple, with a few dominant species (Rott, 1988; Starkweather, 1990). The dominant crustacean zooplankton representatives in European High-mountain lakes are the copepods *Cyclops abyssorum* and *Arctodiaptomus alpinus,* less frequently the cladoceran *Daphnia* spp. (Pesta, 1929; Sommaruga, 2001). Large-bodied zooplankton (e.g. *Chaoborus*, *Daphnia*) are absent in many lakes, probably due to the introduction of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). Phytoplankton populations in high-mountain lakes are often dominated by nanoplanktonic (2-20 µm diameter) and motile species of chrysophytes as well as by dinoflagellates, diatoms and cryptophytes. Other groups like Euglenophyceae, Xanthophyceae and Cyanophycae are numerically of minor importance (Nauwerck, 1966; Rott, 1988; Sommaruga et al., 1999).

The trophic cascade in lakes

The 'trophic network'

Two primary concepts have been proposed regarding the mechanisms regulating the biomass and abundance of different trophic levels, in both terrestrial and aquatic ecosystems. The producer-controlled model suggests that resource availability regulates the biomass on a trophic level from the bottom ('*bottom-up*'; Odum, 1969). In contrast, the consumer-controlled model supports the conclusion that the trophic level biomass is controlled from above by consumers ('*top-down*'; introduced by Hairston et al., 1960; reviewed by Northcote, 1988). For a long period of time, resource availability was considered to be a more important factor than predation in freshwater pelagic food webs (Schindler, 1978). However, in recent years top-down regulation has attracted more attention.

The idea of control flowing downward in the trophic pyramid is outlined by the '*Trophic Cascade Hypothesis*' (Carpenter et al., 1985). The potential biomass and production of organisms at a given trophic level is determined by bottom-up availability of nutrients (for autotrophs) and food (for heterotrophs), whereas the realised biomass at each trophic level is regulated by the trophic level above via top-down control (Carpenter and Kitchell, 1993; Chase, 2000). According to the trophic cascade hypothesis, keystone predators can strongly modify and impact the community composition at each trophic level (Shapiro and Wright, 1984; Carpenter and Kitchell, 1993). As a result, changes at higher trophic levels may cascade down to lower trophic levels in the food web (Carpenter and Kitchell, 1993; Pace et al., 1999). Most planktivorous fish are size-selective predators and feed preferentially on large zooplankton (Hall et al., 1976). An increase in planktivorous fish biomass leads to a concomitant change in zooplankton size structure towards smaller individuals and species (Spaak and Hoekstra, 1997). Small zooplankters are less efficient in grazing down phytoplankton than large ones ('*Size Efficiency Hypothesis*'; Brooks and Dodson, 1965) and the dominance of small zooplankton species often results in an increased phytoplankton biomass (Shapiro and Wright, 1984). An increase in the abundance of piscivores, on the other hand, will result in a lower abundance of zooplanktivores, a higher abundance of large zooplankton and a lower phytoplankton biomass.

The 'chemical network'

General food chain theory only considers the direct feeding links between predator and prey and neglects the possibility that some prey may detect and respond in behaviour, life history or morphology to the presence of potential predator (but see Abrams and Rowe, 1996; Hansson, 2000). These adaptive responses will increase the probability of survival for an individual prey organism and may also have population- and system-wide consequences. Numerous examples of predator-induced responses have been described and are ecologically important phenomena in aquatic ecosystems (Tollrian and Harvell, 1999). Prey species use a variety of tactics to avoid being eaten by their predators (see review Havel, 1987). Some are fixed in the course of evolution, such as spines of some fishes (Bond, 1996) and repellent tastes of many aquatic beetles and bugs (Scrimshaw and Kerfoot, 1987). Other reactions are plastic, being induced by chemical cues of potential predators (DeWitt et al., 1998).

Pioneering work on rotifers, the *Brachionus—Asplanchna* system (De Beauchamps, 1952; Gilbert, 1966), suggested chemical communication between planktonic animals. Further studies showed that plankton can recognise and discriminate chemical signals in the environment, which provide essential information for survival and profoundly influence their behaviour. Many terms have been designated for chemicals that convey information between organisms (Dicke, 1988); classification and terminology of infochemicals based on the costs and benefits of the interaction for both interactants are given in Table 1. Prey reactions induced by chemical signals from predators (called kairomones) are of particular interest, as they provide a means of avoiding costly reactions in the absence of predators. Prey reactions span from morphological changes to shifts in life history and changes in behaviour; all of which are expected to reduce the capture efficiency of the predator, enhance the escape ability of the prey or accelerate reproduction. The range of organisms showing chemically mediated phenotypic defences is wide and ranges from algae to ciliates, rotifers, molluscs, crustaceans and fish (Tollrian and Harvell, 1999). In the aquatic system, chemi-

Table 1. Infochemical terminology (after Dicke and Sabelis, 1992).

Infochemical: A chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response.

Pheromone: An infochemical that mediates an interaction between organisms of the same species whereby the benefit is to the producing organism, or to both.

Allelochemical: An infochemical that mediates an interaction between two individuals that belong to different species.

- *Allomone:* evokes in the receiver a behavioural or physiological response that is adaptively favourable to the sender, but not to the receiver.
- *Kairomone:* evokes in the receiver a behavioural or physiological response that is adaptively favourable to the receiver, but not to the sender.
- *Synomone:* evokes in the receiver a behavioural or phyisiological response that is adaptively favourable to the sender and receiver.

cally mediated traits have been especially well studied in the crustacean species *Daphnia*.

The influence of infochemicals on intraspecific and interspecific interactions is becoming increasingly evident. In spite of the unique property of water as a transmitter of biochemical signals, isolation and chemical identification of infochemicals in aquatic environments, however, is very limited (Faulkner, 1996). Except for two proteins that induce morphological changes in ciliates (Kusch, 1993), no other kairomone has been precisely identified. Only a few characteristics of a fish chemical factor and a *Chaoborus* chemical factor have been identified (Von Elert and Loose, 1996).

Infochemicals may influence the flow of matter within the trophic structure of an ecosystem. Trophic food web models that connect plastic responses of prey species are new approaches to understand the influences of kairomones on ecosystems (Chase, 1999). It can be hypothesised that infochemicals have a regulating function that influences the quantities of material transfer between trophic levels, ultimately influencing dynamics at the population and community levels. Figure 1 shows the linking of the information network with the material network in a simplified tritrophic food

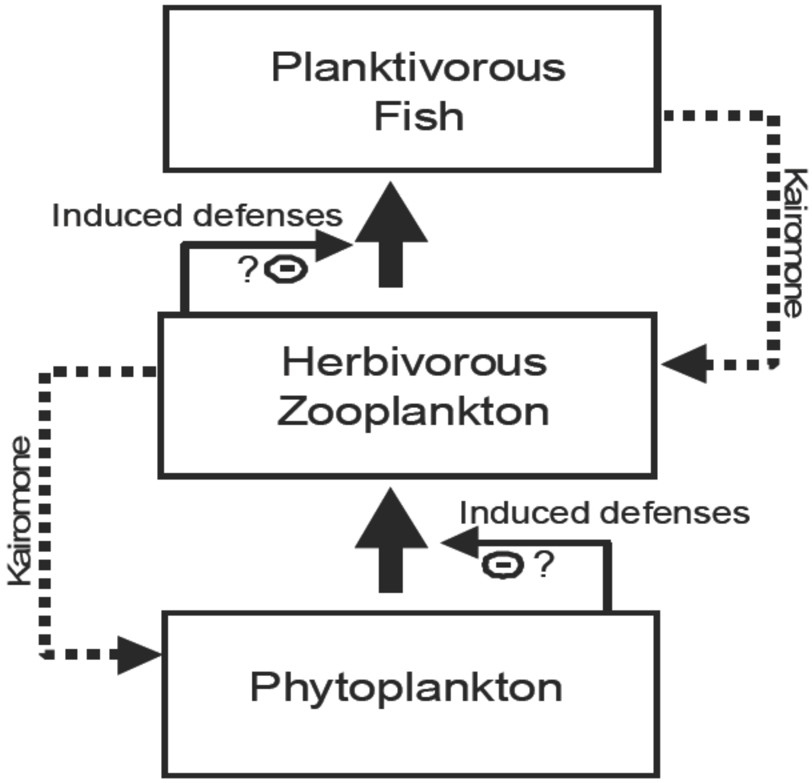

Figure 1. A scheme of flow of matter (thick arrows) between phytoplankton, zooplankton and fish and information which is carried by kaironomes (broken lines). Induced defenses (thin arrows) negatively inhibite the material flow.

chain. Two webs superimpose, the material web (thick arrows), which is the traditional food web, and the information network, which consists of infochemicals (kairomones) as carriers of information. Induced defenses (thin arrows) are thought to influence the quantities of transfer of material between trophic levels. In that way, the structure and functioning of the community is determined.

Selection for the optimal habitat

Habitat selection

The theory of habitat selection asserts that '*individuals should choose habitats that maximise their expected fitness*' (Rosenzweig, 1991). The habitat in which an organism is most commonly found is usually considered its optimal habitat. Hutchinson (1958) emphasised that organisms have ranges of tolerance for many environmental factors, rather than for only a single factor. Hutchinson distinguished between *fundamental* and *realised* niches, which are analogous to physiological and ecological tolerance ranges. Thus, the fundamental niche is the range in which a species can occur if there are no biotic interactions. The realised niche is the restricted niche into which the species is driven by competition and predation (Lampert and Sommer, 1997). Habitat selection has been identified as an important mechanism of niche segregation allowing the coexistence of similar species and different genotypes within species.

In zooplankton, habitat selection can be realised along temporal (Carvalho and Crisp, 1987) and spatial (Tessier and Leibold, 1997; De Meester and Weider, 1999) scales. For example, summer clones of the cladoceran genus *Daphnia* have their highest relative fitness at higher temperatures than winter clones and *vice versa*. Both horizontal and vertical spatial habitat selection in zooplankton has been realised in lakes and oceans. The open water zone consists of vertical habitat gradients, including variations in factors such as temperature, light, food and predation. The vertical partitioning of the water column enables planktonic organisms to reduce competition and mortality risk.

Depth selection behaviour

For many years, planktonic organisms were assumed to have limited abilities to cope with the challenges of the open water zone, being defined as organisms with reduced abilities to swim and to react to neighbouring organisms (the Greek word plankton means 'wandering'; Hutchinson, 1967). Studies during the last decades, however, have changed this view and have shown that freshwater zooplankton can recognise and react to the presence of other organisms and environmental cues and actively select for different habitats. In zooplankton, depth selection behaviour is defined as the '*behaviour by which the zooplankton maintains a particular (daytime, night-time) vertical distribution in relation to the vertical stratification of the water column*' (De Meester et al., 1999). Diel Vertical Migration (DVM) behaviour is a special case of depth selection behaviour, in which the preferred depth changes over a diel cycle.

Numerous organisms, representing 15 marine and freshwater phyla, change their vertical distribution in the water column on a daily basis (Orcutt & Porter 1983). For example, the cladoceran crustacean *Daphnia*, with a body length of ca. 1.5 mm may migrate over a vertical distance of 20 m within 24 hours, covering a distance of more than 26,500 times its own body length (De Meester et al., 1999). This behaviour is one of the most massive in animal migrations, involving tons of biomass changing its vertical position daily. The amplitude varies from less than one meter to several tens of meters in lakes or hundreds of meters in the open ocean (Hutchinson, 1967). The 'normal' migration pattern consists of a morning descent to deeper water and an evening ascent to shallow waters, although 'reverse' migrations have been described (Ohman et al., 1983; Lampert, 1989). These observations suggest that there might not be a single best habitat for a given species or population, rather the preferred depth changes over a diel cycle.

Protection against unfavourable conditions

Predation pressure

The relationship between predator size and prey size is a primary factor that determines the risk of predation in pelagic food webs. Many empirical studies showed that predators induce the production of defensive phenotypes in prey, implying that phenotypic plasticity can be an adaptative strategy (reviewed by Harvell, 1990). Planktonic species have a large repertoire of defence mechanisms against most kinds of predation by adjusting their morphology, life history or behaviour in such a way that they are less easily handled or detected (Havel, 1987; Hanazato and Yasuno, 1989; Scheffer, 1997). Numerous studies demonstrated that animals respond quickly and adaptively to changes in the risk of predation (Lima, 1998). The scent of predators provides detectable information on current risk for many aquatic organisms. Vertebrate predators often induce smaller body size (i.e. reproduce at a size that is less conspicuous to predators), reduced transparency (e.g. by reduction in eye pigmentation), swarming or increased amplitude or duration of DVM behaviour (summarised in Tollrian and Harvell, 1999). On the other hand, invertebrate predators are less efficient on larger prey and cause the opposite responses (Stibor, 1992).

DVM is a prime example of predator avoidance behaviour. It is generally accepted that the proximate cause for DVM is a phototactic reaction to relative changes in light intensity (Ringelberg, 1999). The adaptive significance of DVM is the diurnal avoidance of surface waters to prevent detection from visually feeding predators such as fish (Lampert, 1993). Several hypotheses have been proposed to explain DVM behaviour (Table 2 gives

Table 2. Hypotheses on the adaptive significance of DVM in zooplankton.

Hypothesis	Reference
Demographic and metabolic advantage	
Energy bonus for increased fecundity and storage capacity	McLaren (1963)
Feeding strategy – better utilisation of food resources	McAllister (1969)
Light adaptation – pathway analysis, isolume movement	Kerfoot (1970)
Size and fecundity advantage at low temperature	McLaren (1974)
Interaction with algae, net energy gain, control of timing	Enright (1977)
Reduction of interspecific competition by niche segregation	Lane (1975)
Energy conservation	
Avoidance of starvation	Geller (1986)
Light-related mortality	
Predation avoidance	Zaret and Suffern (1976)
Photo-damage	Hairston (1980)

an overview). The evidence that DVM can directly be induced by the presence of predators or predator-specific kairomones (reviewed by Larsson and Dodson, 1993) provides the strongest support for the predator-avoidance hypothesis. The sensitivity of prey to predators is usually associated with their physiological state, determined primarily by food condition and temperature (Gerritsen, 1982; Han and Straskraba, 1998). Dini et al. (1993) observed that food availability also is a significant factor for the migratory amplitude; zooplankton migrate less or even stop migrating in situations of food shortage (Johnsen and Jakobsen, 1987; Flik and Ringelberg, 1993).

Ultraviolet radiation (UVR) exposure

Light may have a direct deleterious effect on zooplankton during the day or may operate indirectly through increasing vulnerability to visual predation. High-mountain lakes receive generally higher incident solar UVR (290 – 400 nm) fluxes than low-elevation lakes due to the natural increase of UVR flux with elevation. Organisms living in lakes at high altitudes have developed various strategies to minimise damage from solar UVR exposure (Sommaruga, 2001). They often synthesise or concentrate compounds that directly or indirectly absorb UVR energy (e.g. melanin, carotenoids, mycosporine-like amino acids). These protective substances are especially important in clear or shallow lakes where water depth is insufficient to escape as a protectant against UVR exposure. In deeper lakes, however, zooplankton avoids surface waters during the day (Tartarotti et al., 1999; Williamson et al., 2001). Recently, it has been shown that *Daphnia* spp. respond to UVR by daytime downward migration (Rhode et al., 2001).

Suboptimal growth conditions

One mechanism of avoiding unfavourable conditions is to extend the life span by producing resting stages. Some planktonic species may undergo short-lived diapause as immature instars (e.g. cyclopoid copepods) or produce long-lived resting eggs (e.g. rotifers, calanoid copepods and cladocerans) when conditions deteriorate (reviewed by Hairston, 1996) and emerge when conditions become better. *Daphnia* spp., for example, reproduces by amictic parthenogenesis when environmental conditions are favourable (Fig. 2). In response to stimuli such as food shortage, high population density, changes in day length or deterioration of food quality (Hairston, 1987; Hobæk and

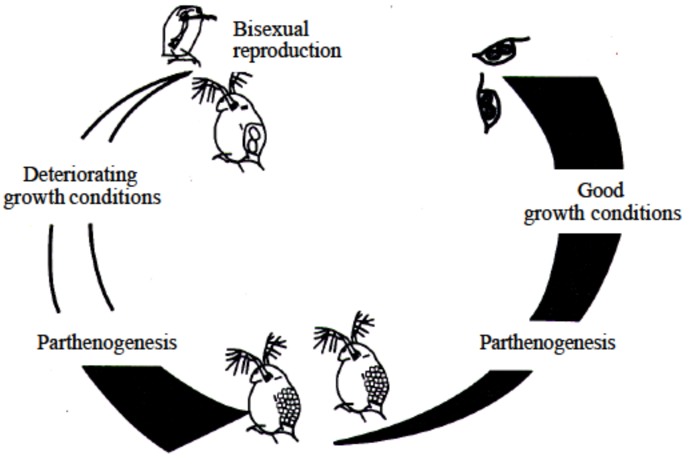

Figure 2. The cyclic parthenogenetic reproduction of *Daphnia*. Females reproduce by parthenogenesis as long as growth conditions remain favourable. When condition become unfavourable, males and sexual eggs are produced (modified after Hughes, 1989; De Meester, 1996).

Larsson, 1990; Alekseev and Lampert, 2000) daphnids start to produce males and sexually produced eggs. Sexual eggs are resting eggs that are protected by a structure called an ephippium that floats or sinks to the bottom to hatch later. When environmental conditions are again favourable, these eggs hatch and yield females that can reproduce by amictic parthenogenesis. Arctic clones, however, produce asexual resting eggs by parthenogenesis, most likely as an adaptation to the short growing season. Resting eggs provide insurance for long-term population persistence and reestablishment during low-mortality periods.

Costs and Trade-Offs

The trade-off between energetic gain and the risk of predation is of central interest in behavioural ecology (Sih, 1992; Lima and Bednekoff, 1999; Sih et al., 2000). The general idea is that by varying some aspect of behaviour an animal can balance its rate of energetic gain against the probability of being eaten by a predator (Fig. 3). Under unpredictable environmental conditions inducible defences are especially beneficial. Inducible defences are impressive examples of phenotypic plasticity that are ubiquitous in zooplankton. A directional difference in the size or value of a phenotype expressed by an individual in response to particular environmental change defines a plastic

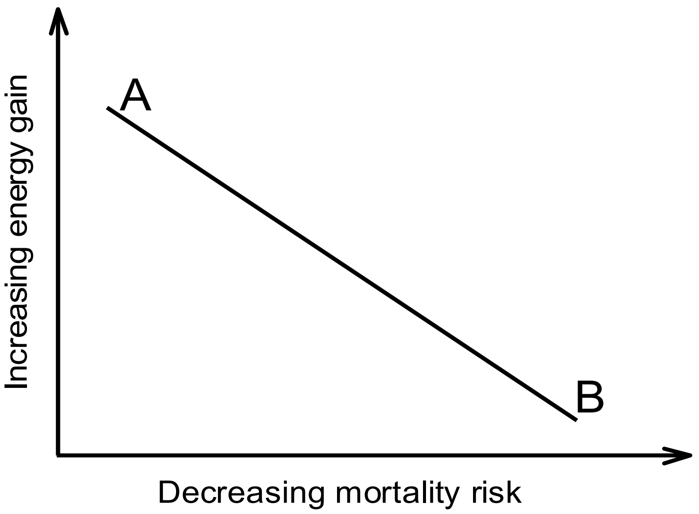

Figure 3. Hypothetical trade-off between light-dependent mortality risk (fish predation, ultraviolet radiation) and energetic gain in surface waters. The line indicates where the various genotypes may be situated; A and B are two extreme individuals genotypes.

character (Bradshaw, 1965). The associated costs, however, are often high (e.g. synthesis of extra body tissue or pigments, escape to suboptimal habitats), and might constrain the evolution of inducible defences (DeWitt, 1998). To demonstrate that a particular plastic trait is adaptive, one must show that modified phenotypes have greater fitness than unmodified ones. A cost of plasticity is usually assessed as a reduction in some fitness component, such as growth rate, reproductive output or survivorship (Harvell, 1990); quantifying the magnitude of the costs is often difficult.

Favourable habitats are often risky, causing zooplankton to move to areas of low food and cold temperature (Sih et al., 2000). DVM is a primarily mechanism by which organisms balance the conflicting requirements of maximising net reproduction and light-dependent mortality avoidance. The trade-off depends on the abundance and types of predators, the characteristics of the vertical gradients in temperature and food and the presence of competitors. The fact that DVM is inducible suggests that it involves a cost, otherwise a permanent migration behaviour would have been favoured (Stearns, 1992). Costs associated with DVM behaviour can be expressed as an increase in the development time of eggs and lower egg production due to reduced temperature and resource availability in the deep daytime refuge (Stich, 1989; Ringelberg et al., 1991; Loose and Dawidowicz, 1994), resulting in an overall reduced population growth rate. Model studies on DVM, however, have shown that the associated costs can be counterbalanced by reduced predation risk (Fiksen, 1997).

Study site description

The studies presented in this thesis were conducted in various high-mountain lakes (above 1618 m a.s.l.) located in the Swiss Alps and in the Oberer Arosasee particular. The Oberer Arosasee is located in the catchment of the River Rhine at an altitude of 1734 m a.s.l. in the Central Alps, Switzerland (46°13´N, 09° 41´E). The lake is situated over slate rocks. It is a dimictic, relatively small (surface area, 7.1 ha) oligotrophic lake. The major morphometric and environmental characteristics of the lake are listed in Table 3. Spring turnover is incomplete and the hypolimnion becomes anoxic twice a year. During summer, dissolved oxygen concentrations become < 3 mg liter^{-1} at depths > 9m.

The crustacean zooplankton community of the Oberer Arosasee consists of the herbivorous species *Daphnia galeata*, *Eudiaptomus gracilis*, *Bosmina longirostris* and the omnivorous *Cyclops abyssorum*. The fish community in the lake is dominated by salmonids, especially brown trout (*Salmo trutta*), charr (*Salvelinus alpinus*) and to a lesser extent rainbow trout (*Oncorhynchus mykiss*) and by minnow (*Phoxinus phoxinus*). The lake is regularly stocked with adult brown trout and charr.

Table 3. Oberer Arosasee: A) morphometric parameters, B) Environmental variables during the study period 1998 – 2000; given are maximum and minimum values.

A		B	
Surface area (m^2)	71,100	Temperature (°C)	3.3 – 13.8
Volume (m^3)	521,000	Ice cover (months)	5 – 6
Length (m)	390	Secchi depth (m)	2.5 – 12.0
Width (m)	250	Phosphorus (TP; µg l^{-1})	0 – 23.8
Maximum depth (m)	13	Conductivity (µS cm^{-1})	272 – 296
Mean depth (m)	7.3	pH	7.0 – 8.8
Relative depth (%)	7.7	Nitrate (NO_3-N;µg l^{-1})	17 - 146
		O_2 (mg l^{-1})	2.9 – 12.9

Research objectives and thesis outline

In the following chapters I address the central question of how zooplankton species in high-mountain lakes balance environmental demands, with special emphasis on the cladoceran species *Daphnia*. This question was approached in a three-year field study combined with different *in situ* and laboratory experiments. The research described in the second chapter was done in numerous Swiss high-mountain lakes and the studies described in the following chapters were conducted at the Oberer Arosasee.

In the last century, human activities have strongly altered high-mountain lakes. Such activities may have eliminated vulnerable and sensitive zooplankton species, thus creating impoverished communities. The human influence on zooplankton was studied in *Chapter II* by sampling Swiss high-mountain lakes that were studied in the early 20th century and comparing past and present zooplankton composition and taxon richness. We also studied how human induced changes may have influenced the genetic diversity of present-day populations of the widespread cladoceran, *Daphnia.* The introduction of fish in particular has a profound impact on zooplankton communities. In *Chapter III*, we present an overview of how salmonid fishes (especially brown trout and charr) influence the seasonal demography and structure of zooplankton. In addition, the importance of intra- and interspecific competition in zooplankton is evaluated.

It is difficult to directly estimate food availability for daphnids in the field: therefore, only indirect measurements of food availability are possible. The study reported in *Chapter IV* employed an indirect measurement of the condition of daphnids using carbon-length relationships. Because daphnids migrate vertically in the Oberer Arosasee, they are confronted with a variable food regime. In *Chapter V*, we address the question of whether food availability is poorer at greater depths compared to surface layers. Not only the quantity of food but its quality may be important. In laboratory experiments we studied the consequences (juvenile growth rates) of *Daphnia* species migrating over a food gradient, using populations from lakes with and without a deep-water chlorophyll maximum.

Vertical migration studies are largely based on observations during the summer, when planktivorous fish abundance is high. As a consequence, year-round studies are needed. The main objective of *Chapter VI* was to describe the seasonal vertical distribution of daphnids in a high-mountain lake in combination with an *in situ* enclosure experiment. In addition we conducted an indoor enclosure experiment ('Plankton Towers'), where the lake situation was mimicked, to study migration under controlled conditions. Specifically, we addressed the following questions: *i*) Do daphnids of a high-mountain lake still reacts to fish kairomones with DVM, although predation risk is low? *ii*) Do daphnids still migrate in the presence of a deep-water chlorophyll maximum? *iii*) Do daphnids select for the habitat where the highest birth rates can be realised under predator free conditions?

The research presented in the previous chapters' deal with the influence of disturbance, predation, food and temperature on zooplankton distribution and behaviour. *Chapter VII* examines the influence of ultraviolet radiation (UVR) on the life history traits of *Daphnia* in the water column and discusses the importance of vertical migration. Finally, in *Chapter VIII* the results presented in the previous chapters are put in a broader perspective and the significance of adaptive behaviour is discussed and suggestions for further research are made.

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Chapter II

Have human impacts changed alpine zooplankton diversity over the past 100 years?

with M. T. Monaghan and P. Spaak
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Abstract

Anthropogenic stress and fish introduction generally are thought to have eliminated vulnerable and sensitive zooplankton species from many alpine lakes, creating impoverished communities. To investigate this hypothesis we sampled 26 alpine lakes (1618 – 2757 m a.s.l.), 11 of which were studied in the early 20th century, and compared past and present zooplankton composition and taxa richness. We also studied how human induced changes may influence genetic diversity of present-day populations of the widespread cladoceran, *Daphnia.* Resampling did not show a drastic overall change in planktonic crustacean composition. Taxa richness significantly decreased with increasing lake altitude, but no other environmental factor correlated with richness. Large-bodied zooplankton taxa were found in lakes both with and without fish. Therefore we conclude that the presence of fish can be excluded as the general factor explaining the occurrence or absence of large zooplankton species in alpine lakes. Levels of chlorophyll *a* and POC best distinguished lakes with *Daphnia* from lakes without *Daphnia*. In 8 out of 12 lakes sexual *Daphnia* were more abundant than asexual individuals. Clonal diversity ranged from 0.01 to 1.3 but was not related to the proportion of sexual individuals. The ability to create resting stages may be an essential factor for the maintenance of genetic diversity and the long-term persistence of *Daphnia* and other zooplankton taxa.

Introduction

In the late 19th and early 20th century, many high-altitude lakes in the European Alps were characterized and their plankton fauna and flora described in detail (e.g. Zschokke, 1900; Stingelin, 1904; Zschokke, 1908; Stingelin, 1910; Kreis, 1921; Pesta, 1929). The most frequently observed zooplankton representatives were the rotifers *Notholca longispina, Keratella cochlearis* and *Polyarthra platyptera*. The cladoceran *Daphnia longispina* and copepods *Cyclops abyssorum*, *Arctodiaptomus alpinus* and *Acanthodiaptomus denticornis* also were common. Abundant zooplankton communities were observed up to 2780 m a.s.l. (Zschokke, 1900; Kreis, 1921). Zschokke (1900) observed no relationship between species richness and altitude but found that lakes located in granitic catchments generally had a more diverse aquatic fauna than lakes located in calcareous catchments. The physical characteristics of lakes (e.g. temperature, duration of winter ice cover, habitat structure) were even more important in determining the aquatic fauna present than water chemistry (e.g. calcium content).

Recent studies in the Tatra Mountains, European Alps and Colorado Rockies indicate that plankton species composition may be changing in alpine lakes (Lieberman, 1993; Cammarano and Manca, 1997; Medina-Sánchez et al., 1999; Straskrabová et al., 1999). These studies report an impoverished fauna consisting mainly of small copepods and rotifers. Alpine regions have been increasingly altered since the late 19th century by tourism, farming, recreation and the development of hydropower facilities (CIPRA, 1998) and the consequences for lakes include the introduction of fishes, eutrophication and lake retention times changed by repeated flushing and filling of reservoirs. Fish introduction, which has occurred in Swiss Alpine lakes since the 16th century (Roth, 1971), has been implicated as the major biotic factor contributing to impoverished plankton communities, including local extinctions of most large-bodied cladoceran and copepod species (Gliwicz, 1985). Acidification of alpine lakes located in poorly buffered granitic catchments also may cause local extinction of sensitive zooplankton species (Cammarano and Manca, 1997). The first goal of the present study was to examine how such human influence may have changed zooplankton diversity in alpine lakes.

Genetic diversity within and among species is an important component of zooplankton diversity. Just as species diversity typically decreases at high altitude and latitude (Rosenzweig, 1995), the same has been assumed to be true for genetic diversity within species (Hedrick, 1986). For the widespread and abundant genus *Daphnia*, the presence of hybrids results in species complexes in which species diversity and genetic diversity overlap (Schwenk and Spaak, 1995). Therefore, *Daphnia* are ideal organisms to study processes responsible for patterns and changes in both species diversity and genetic diversity. Their presence in alpine lakes allows for an investigation of how human activities may impact species and genetic diversity in the Alpine environment. The second part of our study addressed how factors related to human impact may influence genetic diversity of *Daphnia* in alpine lakes.

The reproductive biology of *Daphnia* suggests that different processes may influence genetic diversity at different times of the year. *Daphnia* reproduce by cyclic parthenogenesis. During the sexual phase, diapausing eggs encased in a resistant structure (termed an ephippium) are produced. These ephippia float or sink to the sediment and may hatch in the future when environmental conditions change (Banta and Brown, 1929). In lakes and ponds where sexual reproduction occurs regularly, genetic diversity is expected to be higher compared to those lakes where daphnids overwinter as parthenogenetic females (Hebert, 1974).

This study consisted of two parts. We first examined the hypothesis that species diversity in zooplankton communities has been reduced in alpine lakes during the last 100 yr. We resampled 11 Swiss Alpine lakes in 1998, 1999 or 2000 for which historic data were available from approximately 100 yr ago. To infer mechanisms responsible for species changes, we sampled 15 additional lakes with different levels of human impact and sought to determine the primary factors determining zooplankton richness in alpine lakes. The second part of our study concentrated on factors that influence the presence and absence of *Daphnia* and on factors influencing the present-day genetic diversity of populations. We hypothesised that genetic diversity would be higher in high-altitude lakes as a result of there being more sexually reproducing individuals in more harsh conditions. Further, we hypothesised inbreeding would be greater in lakes with a lower proportion of sexual individuals. Among years, we predicted that genetic turnover might be greater in lakes with more sexually reproducing individuals because of increased production of ephippia.

Study Sites

The study was conducted in 26 lakes (above 1618 m a.s.l.) located in the Swiss Alps (see Fig. 1 for locations and Appendix 1 for physical and chemical characteristics). Eleven of the lakes were chosen because data from the beginning of the 20th century were available. Four of the lakes contained no fish (Alteinsee, Prätschsee, Oberaarsee, Riffelsee II) and the remaining lakes had fish populations when sampled between 1997 and 2000. We assume that fish occur naturally in some of the lakes (Oberer Arosasee, Unterer Arosasee, Cadagno). We assume fish have been introduced to the remaining lakes because of their physical isolation (Table 1). Regardless, all lakes with fish currently are stocked with brown trout (*Salmo trutta*), charr (*Salvelinus alpinus*) or pike (*Esox lucius*) on a regular basis. The Oberaarsee and Lake Robiei have been greatly enlarged for hydropower production and water levels have been raised by dam construction in six other lakes (names in Appendix 1).

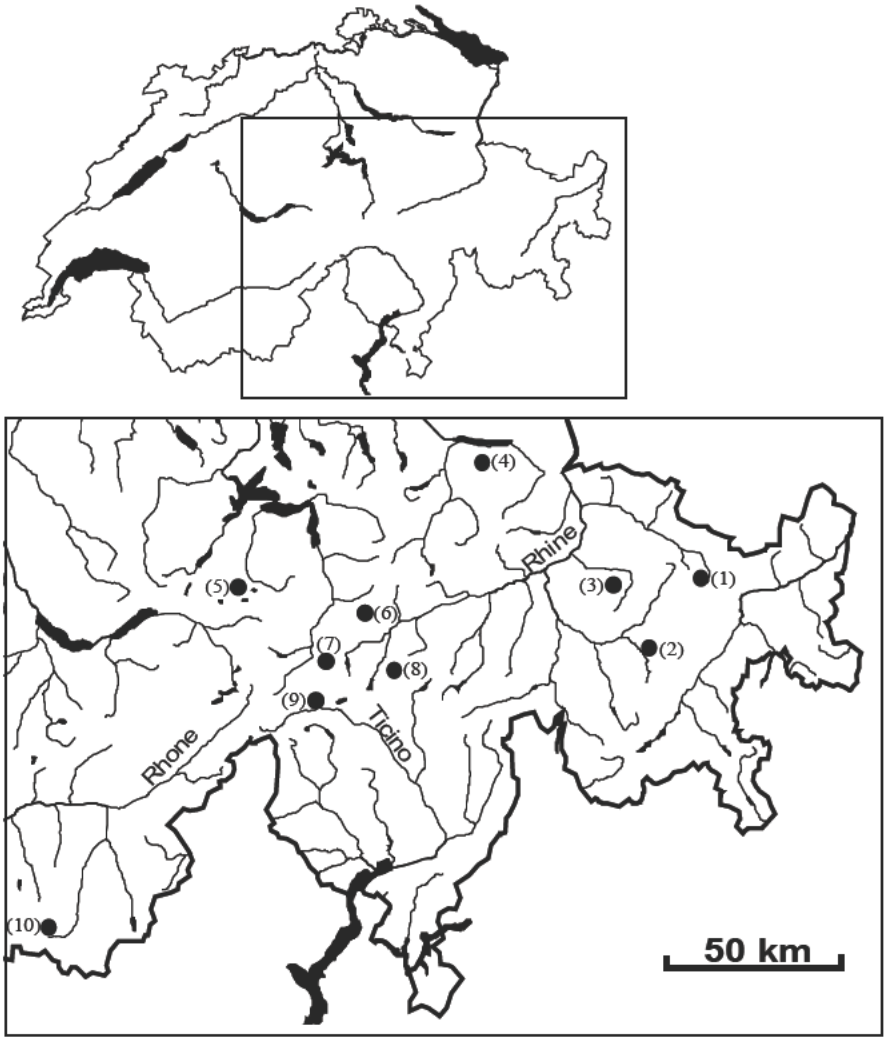

Figure 1. Map of the study region in Switzerland showing the locations of the lakes (dots: see Appendix 1 for names and altitudes).

Materials and Methods

Field sampling

For each lake, temperature, pH and conductivity were measured in the field. A tube sampler was lowered into the water from the surface to the bottom, stoppered and transferred to a bottle to collect an integrated water sample that was analysed for carbon and nutrient concentrations in the laboratory (for analytical methods see Tockner et al., 1997). Chlorophyll *a* was measured after extraction in 96 % ethanol using HPLC.

Zooplankton were collected using a 95-µm (for crustacean zooplankton) or a 50-µm (for rotifers) mesh plankton net. Simple vertical tows were taken from the deepest part of the lake to the surface. This was the same method used in the studies for which we have historical data. In four lakes (Alteinsee, Gruenseeli, Oberalppass, and Lutersee) horizontal tows were taken by retrieving plankton nets thrown by hand from the shore. Samples were concentrated and preserved in 96 % ethanol. Lakes were sampled in late summer or early autumn of 1997, 1998, 1999 or 2000. Three lakes (Oberer Arosasee, Unterer Arosasee and Prätschsee) were sampled monthly during the open water period from 1998 to 1999. In winter 1998/99 and winter 1999/00, Oberer Arosasee was sampled through the ice. In lakes with *Daphnia*, we collected ≥80 individuals (adult females) for genetic analysis. In Cadagno and Schwarzsee this was not possible and we collected approximately 50 and 30 individuals, respectively. *Daphnia* were returned to the laboratory alive and stored in liquid nitrogen for later analysis.

Species identification and allozyme electrophoresis

Organisms were identified in the laboratory using taxonomic keys of Koste (1978), Flößner (1972) and Einsle (1993). *Daphnia* species were identified using morphological characteristics (Margaritora, 1983; Flößner and Kraus, 1986; Flößner, 1993). However, *Daphnia* taxonomy is in transition (Taylor et al., 1996; Gießler et al., 1999) and several morphological species hybridize. Hybrids often are the most abundant taxa in lakes (Schwenk and Spaak, 1995). Individual daphnids were screened for genetic variation at four polymorphic allozyme loci using the methods of (Hebert and Beaton, 1989). Aldehyde oxidase (Ao, Enzyme Commission number (EC) 1.2.3.1), Phosphoglucose isomerase (Pgi, EC 5.3.1.9), Glutamate-oxaloacetate transaminase (Got, EC 2.6.1.1) and Phosphoglucomutase (Pgm, EC 5.4.2.1) were scored for all populations.

In brief, we use the term clone to designate distinct multilocus genotypes with the understanding that a given clone may actually represent a clonal group, which may range from one to many clonal lineages. Clonal diversity (*D*) was calculated as the negative log of Simpson's Index ($D = -\log\sum p_i^2$). Low values of *D* indicate that a single clone is dominant, while high values indicate that many clones are abundant at approximately equal frequencies. An inbreeding coefficient (F_{is}) was calculated for each lake (population) using FSTAT v.2.9.1 (J. Goudet, Université de Lausanne). Heterozygote deficiency (inbreeding) in each population was tested using the score test available in GENEPOP (Raymond and Rousset, 1995). Significant positive values indicate inbreeding. To determine which loci were responsible for inbreeding values we used the probability test in GENEPOP with a Bonferroni correction (4 loci in 14 populations). In the lakes sampled monthly over two successive years, autumn samples (i.e. August, September and October) were pooled and each year was treated as a separate population. Genetic distance (Nei, 1978) between years was calculated for each of these three lakes using BIOSYS-1 (Swofford and Selander, 1981) to examine temporal turnover in genetic structure.

Discriminant function analysis was conducted using STATISTICA to determine the lake characteristics that best predicted the presence or absence of *Daphnia*. All physical and chemical variables measured (in Appendix 1) were included and lakes were pre-assigned to two groups: with and without *Daphnia*. This resulted in a one-dimensional function analysis. Linear regression was used to investigate relationships between species or clonal diversity and environmental parameters and between proportion of sexual individuals and inbreeding. Where necessary, variables were transformed to normalise data (Sokal and Rohlf, 1995). Lakes with missing data were excluded from the analyses (see Appendix 1).

Results

Present-day species diversity

In total, 10 rotifer genera were identified, with *Keratella, Kellicottia* and *Polyarthra* being most widespread (Table 1). The cladoceran genus *Bosmina* and *Eubosmina* occurred in 10 of the 26 observed lakes. Individuals of *Ceriodaphnia pulchella*, *Holopedium gibberum* and *Scapholeberis mucronata* occurred only in single lakes. Among the copepods, *Cyclops* species, mainly *C. abyssorum*, were the most widely distributed zooplankters. The diaptomids *Acanthodiaptomus denticornis* and *Arctodiaptomus alpinus* were common. *Diaptomus castaneti* occurred only in Prätschsee, a temporary lake, and *Eudiaptomus gracilis* occurred in two lakes. The Diptera predator *Chaoborus crystallinus* was observed in the fishless lake Prätschsee. Genera richness was significantly related to lake elevation (regression $r = -0.55$, $P < 0.01$), but not related to DOC ($r = 0.18$), POC ($r = 0.32$), chlorophyll *a* ($r = 0.21$), nitrogen ($r = 0.22$) or phosphorus ($r = 0.06$), all $P > 0.05$.

Daphnia species occurred in 12 of the 26 lakes sampled. Three *Daphnia* species were identified and it appeared as though hybrids (*D. longispina* x *hyalina*) occurred in several lakes, although confirmation by use of molecular markers was beyond the scope of this study. Discriminant function analysis separated lakes with and without *Daphnia* (Fig. 2), marked by a negative

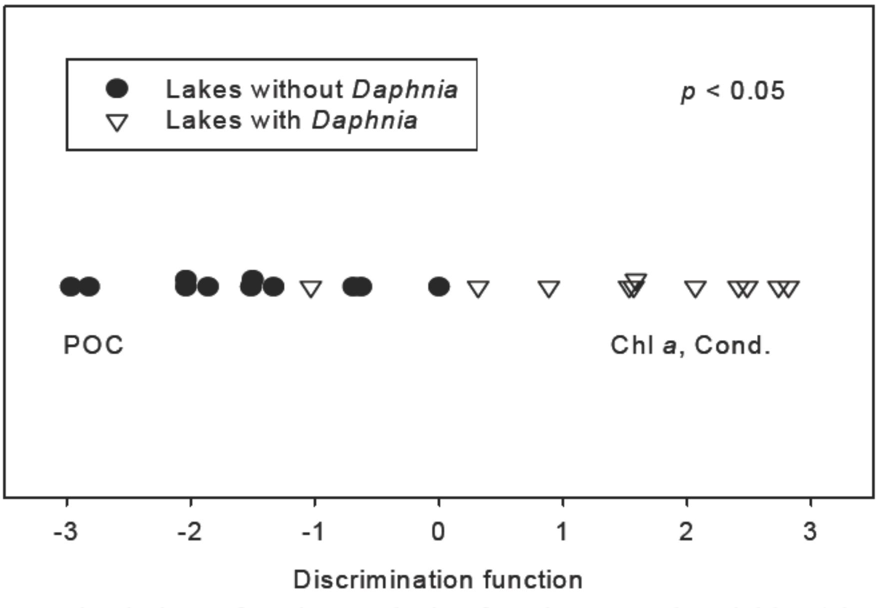

Figure 2. Discriminant function analysis of environmental variables (chemical and physical, see Appendix 1) and lakes with *Daphnia* and lakes without *Daphnia*. Some points were displaced vertically to show overlapping data points.

Table 1. Zooplankton composition and fish presence in sampling sites. An asterix (*) indicates taxa found in 1997 – 2000.

Species	1 Jörisee I	2 Schottensee	3a Älplisee	3b Alteinsee	3c Grüenseeli	3d Oberer Arosas.	3e Prätschsee	3f Schwellisee	3g Unterer Arosas.	3h Urdensee	4a Murgsee	4b Grosssee	5a Melchsee	5b Trübsee	6a Oberalpsee	6b Lutersee	7a Gotthardsee	7b Grimselsee	7c Triebtenseeroli	7d Oberaarsee	8a Cadagno	9a Robiei	10a Leisee	10b Riffelsee II	10c Riffelsee III	10d Schwarzsee
ROTIFERS		a													a	a										
Asplanchna						*	*		*												*	*				
Brachionus																										
Conochilus									*		*										*	*				
Filinia longiseta									*												*	*			*	
Kellicottia longispina	*		*		*	*		*	*	*	*		*	*			*					*				
Keratella cochlearis	*		*														*	*		*	*		*	*	*	
K. hiemalis																			*	*			*			
K. quadrata	*		*	*	*		*	*	*	*			*	*			*	*		*	*	*		*	*	*
K. ticinensis																	*		*				*			
Notholca squamula				*	*					*																
Polyarthra	*					*	*		*				*	*			*	*	*		*			*	*	
Synchaeta																		*								
Trichocerca																		*								
CLADOCERA																										
Bosmina longirostris							*					*	*								*	*				
Eubosmina longispina			*			*		*	*		*															
Ceriodaphnia pulchella												*														
Daphnia galeata						*			*																	
D. longispina									*		*						*				*			*		*
D. rosea							*		*				*	*				*					*			
Holopedium gibberum																	*									
Scapholeberis mucronata							*																			

Table 1. Extended

Species	1 Jörisee I	2 Schottensee	3a Älplisee	3b Alteinsee	3c Grüenseeli	3d Oberer Arosas.	3e Prätschsee	3f Schwellisee	3g Unterer Arosas.	3h Urdensee	4a Murgsee	4b Grosssee	5a Melchsee	5b Trübsee	6a Oberalpsee	6b Lutersee	7a Gotthardsee	7b Grimselsee	7c Triebtenseeroli	7d Oberaarsee	8a Cadagno	9a Robiei	10a Leisee	10b Riffelsee II	10c Riffelsee III	10d Schwarzsee
COPEPODA																										
Cyclops abyssorum						*			*	*	*						*			*	*	*				
C. spp.[b]	*	*		*			*	*				*		*	*	*		*	*							*
Acanthodiaptomus denticornis								*			*		*	*							*					
Arctodiaptomus alpinus	*		*																				*			
Diaptomus castaneti							*																			
Eudiapotmus gracilis						*			*																	
INSECTA																										
Chaoborus crystallinus							*																			
FISH (1997 – 2000)	yes	yes	yes	no	yes	yes	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	no	yes	yes	yes	no	yes	yes
Richness	5	-	4	3	3	7	9	5	10	4	6	3	6	6	-	-	6	6	3	2	9	7	3	3	3	3

[a] No rotifer data available.

[b] Only copepodites available - no species determination possible.

coefficient for POC ($P = 0.01$), a positive coefficient for chlorophyll *a* ($P = 0.02$) and marginally ($P = 0.08$) by a positive coefficient for conductivity. Among the lakes, only Schwarzsee was grouped incorrectly (Fig. 2).

Past and present zooplankton

Comparison of data collected 1997-2000 with those from the early 20th century shows both loss and gain of Cladocera and Copepoda genera in lakes (Table 2). Of the Cladocera, *Daphnia* has disappeared from Schottensee and Riffelsee III, while *Bosmina* appeared in Melchsee and *Holepedium* appeared in Gotthardsee. For the copepods, *Cyclops* and *Arctodiaptomus* species were not found in 3 lakes where they were reported previously. *Acanthodiaptomus* was not reported earlier in 2 lakes, but appeared in this study, and *Eudiaptmus* appeared in Oberer Arosasee (Table 2). The diversity of taxa (at the genus level) we studied remained unchanged in 5 of the 11 lakes.

Sexual reproduction in Daphnia

The proportion of sexual *Daphnia* was greater than 50% in 8 of the 11 studied lakes (Fig. 3). The proportion of males always was higher than the proportion of sexual females (Fig. 3). Riffelsee II, Gotthardsee and Grimselsee

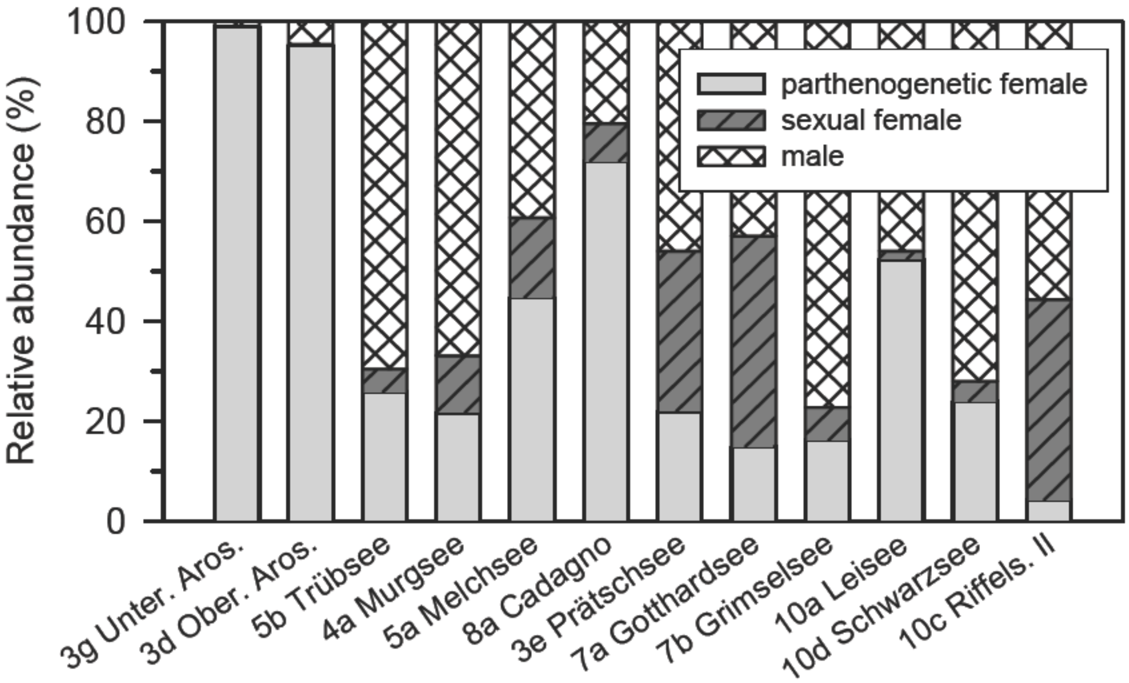

Figure 3. Proportion of parthenogenetic females, males and sexual (ephippial) females of various *Daphnia* species in the Alpine lakes containing *Daphnia* (for species see Table 1). Values are from autumn samples. Lakes are arranged from left with increasing altitude.

Table 2. Comparison of historical and present-day studies on zooplankton composition in 11 study sites. A minus (-) indicates that a genus disappeared, an asterix (*) indicates that a genus remained and a plus (+) indicates that a genus appeared.

Taxa	1 Jörisee I [a]	2 Schottensee [b]	3d Oberer Arosas[b]	5a Melchsee [c]	5b Trübsee [c]	7a Gotthardsee[a]	7b Grimselsee[a]	10a Leisee[a]	10b Riffelsee II[a]	10c Riffelsee III[a]	10d Schwarzsee[a]
CLADOCERA											
Bosmina			*	+							
Daphnia		-	*	*	*	*	*	*	*	-	*
Holopedium						+					
COPEPODA											
Cyclops	*	*	*	-	*	*	*			-	*
Acanthodiaptomus				+	+						
Arctodiaptomus	*						-	*			
Eudiapotmus			+								
Richness 1900	2	2	3	2	2	3	3	2	1	2	2
Richness 2000	2	1	4	3	3	3	2	2	1	0	2

Data from [a]Kreis (1921), [b]Zschokke (1900) and [c]Stingelin (1910).

had the highest percentage of sexual *Daphnia*. Unterer Arosasee and Oberer Arosasee contained very few sexual individuals. Proportion of parthenogenetic females was weakly negatively related to lake altitude (r = -0.59, P = 0.05).

Genetic diversity of Daphnia

Clonal richness (i.e. the number of unique clones per population) ranged from 2 to 54 and clonal diversity (*D*) ranged from 0.01 to 1.3 throughout the study. Highest values were observed for *D. longispina* in Lake Cadagno and in Grimselsee (Fig. 4). Clonal diversity was unrelated to chlorophyll *a* concentration (r = 0.30), POC (r = 0.45) and lake elevation (r = -0.34). Moreover, the genetic diversity of daphnids of alpine lakes was as high as that observed in lowland lakes (Fig. 4). Clonal diversity was unrelated to the number of sexual females, males or parthenogenetic individuals found (data not shown). In the Oberer Arosasee, *D* was fairly stable and lower than 0.4 throughout the year. In Unterer Arosasee, clonal diversity was lowest in late summer in both years but nearly always greater than 0.6. In Prätschsee the clonal diversity was intermediate (data not shown).

The inbreeding coefficient (F_{IS}) ranged from -0.765 to 0.439 among lakes and significant positive values of F_{IS} occurred in Murgsee, in Cadagno and in Prätschsee both 1998 and 1999 (Fig. 5). Examined by locus, the data indicate at least two loci were responsible for significant positive F_{IS} in each of these lakes (Fig. 5). We observed outbreeding (heterozygote excess) at the *Ao* locus in Unterer Arosasee 1999 and in Oberer Arosasee in both 1998 and 1999 (Fig. 5). This resulted in significant negative F_{IS} for all loci in the Oberer Arosasee 1998. For all populations, F_{IS} for all loci was not related to proportion of sexual female, sexual male or parthenogenetic individuals (data not shown). Genetic distance between years was highest in Prätschsee (0.032) and lower in Unterer Arosasee (0.011) and in Oberer Arosasee (0.003).

Discussion

Zooplankton changes over the past 100 years

At the beginning of the 20th century many Swiss Alpine lakes were characterised and the investigators documented a diverse aquatic fauna. Many of these lakes have been affected by human activities (e.g. fish stocking, hydropower construction); therefore, it is of interest to observe if the zooplankton composition has been altered in the time since these earlier studies. Because of changes to copepod and *Daphnia* taxonomy within the last 80 yr, comparison at species level with the former studies was problematic. We therefore made our comparisons at the genus level. Resampling of the 11 lakes did not show a drastic overall change in planktonic crustacean composition. In the Riffelsee III, the high fish density (M. Winder, pers. obs.) might explain the extinction of all planktonic crustaceans (*Daphnia* and *Cyclops*). In three other lakes, *Daphnia*, *Cyclops* or *Arctodiaptomus* disappeared. Since these taxa often are predominant during the open water period (Zschokke, 1900), they should have been detected if present even though we sampled these lakes only once. In three lakes, *Acanthodiaptomus* or *Eudiaptomus* were found where previous studies did not report them.

We found large-bodied zooplankton (e.g. calanoids and daphnids) in 15 of 22 lakes where they are exposed to fish predation. In the Canadian Rocky

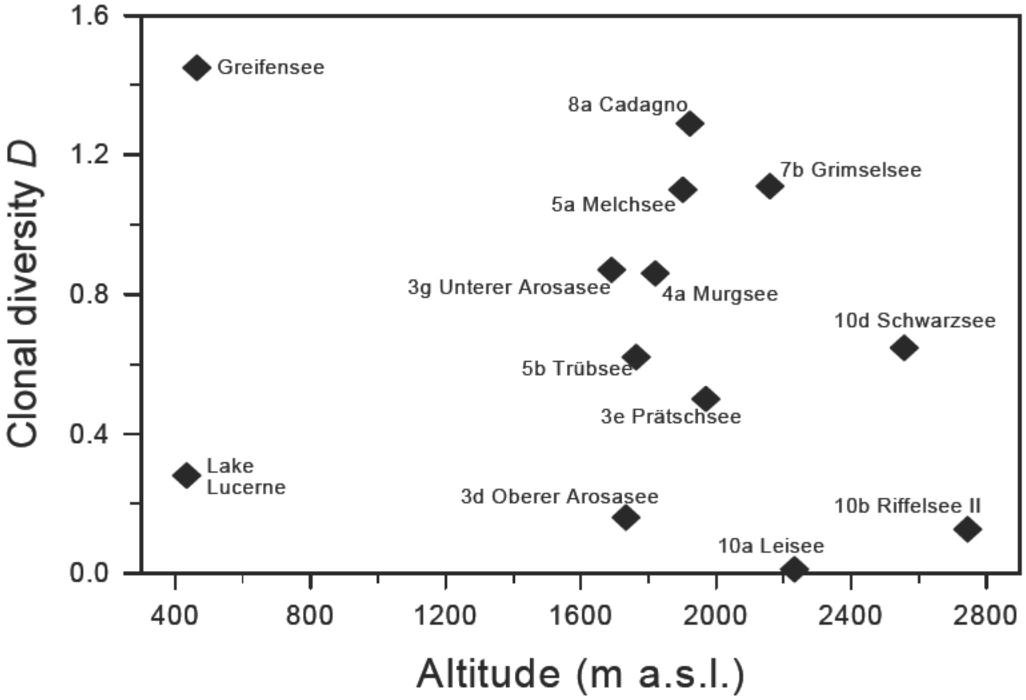

Figure 4. The relationship between altitude and clonal diversity '*D*' of *Daphnia* populations in 11 Swiss Alpine lakes. For comparison, data on two lowland lakes (Greifensee and Lake Lucerne; P. Spaak, unpublished data) are included in the graph.

Mountains, however, fish stocking in the 1960s resulted in the elimination of *Hesperodiaptomus* and *Daphnia* (McNaught et al., 1999), although *Hesperodiaptomus* can coexist with fish in lakes >16 m in depth (Donald and Anderson, 1994). We did not find such a general pattern. Daphnids and calanoids coexisted with fish, even in shallow lakes such as Leisee and Älplisee, and therefore fish presence can be excluded as the general factor explaining their occurrence or absence in these alpine lakes. The introduction of fish in Swiss Alpine lakes also started long before the historical studies were done. Many Swiss Alpine lakes were stocked with juvenile lake trout in 1599 (Roth, 1971). Since then, these lakes have been stocked regularly with salmonids and/or pike. Anglers commonly introduced minnow, roach and others. Only studies of crustacean subfossils in dated lake sediments may give more insight as to the impact fish introduction has had on zooplankton dynamics in the alpine region.

Food availability could be an important factor determining distribution of both zooplankton and fish at high elevation. For *Daphnia*, food availability is important for establishing a dominant population (Gliwicz, 1985) and the discriminant analyses showed that they occur in lakes with higher chlorophyll *a* concentration (discussed below). Further, salmonids are not

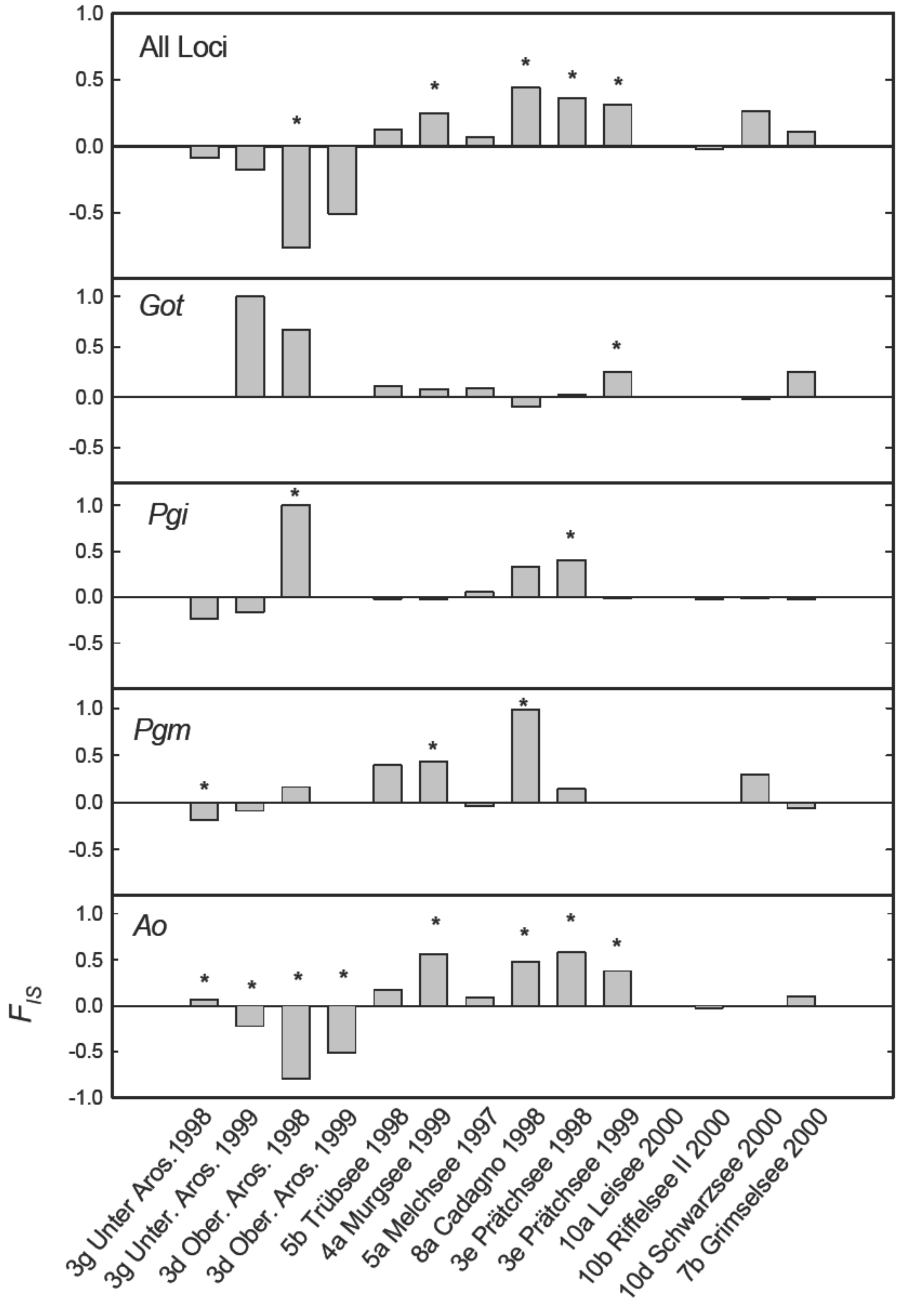

Figure 5. F_{IS} values of *Daphnia* for each locus at each lake, including multiple years at Oberer Arosasee, Unterer Arosasee and Prätchsee. An asterisk (*) indicates significant difference from zero. *Ao* = Aldehyde oxidase, *Pgi* = Phosphoglucose isomerase, *Got* = Glutamate-oxaloacetate transaminase, *Pgm* = Phosphoglucomutase.

strictly planktivorous fish, but stomach analyses have shown that they do prey on large zooplankton (Fitzmaurice, 1979). Thus, the magnitude of predation pressure on zooplankton might depend on the availability of alternative food sources. In alpine lakes some fish may live at the edge of their ecological limits, with little predatory impact on their prey. All lakes, except the Oberaarsee, are well buffered (Appendix 1), therefore acidification did not contribute to loss of species, which might be another reason for the little change in zooplankton.

Present-day zooplankton taxa diversity was unrelated to chlorophyll *a* and POC, as may have been expected if human influence (i.e. enrichment) was an important factor. Taxa richness decreased significantly with increasing altitude in the observed alpine lakes (1618 m – 2757 m a.s.l.), unlike the pattern observed by Zschokke (1900). The absence of fish also may explain the occurrence of *Scapholeberis* and *Chaoborus*—both rare in the alpine region—in the Prätschsee; however, the present study encompassed three other fishless lakes where these taxa were not found. Rotifers were the most diverse zooplankton group and were found in every lake except Grosssee. Unfortunately, comparison of past and present rotifer data was not practicable because of missing data from the former studies. Cladocerans and copepods were often represented by only two taxa. Copepods, particularly *Cyclops*, occurred in almost every lake, whereas calanoids were less widespread.

Daphnia *diversity*

Daphnids were the most prevalent cladocerans, occurring in almost half of the studied lakes, and were found up to 2745 m a.s.l. (Riffelsee II). In the discriminant analysis, chlorophyll *a* and POC content best separated lakes with and without *Daphnia*. Out of 11 lakes only Schwarzsee was not classified correctly, as it was grouped among the lakes without *Daphnia*. Different environmental conditions or lower susceptibility to predation might explain its occurrence there. Three *Daphnia* species were identified with the traditional taxonomic methods. However, daphnids are known to hybridise in nature and recent molecular analyses have revealed that lineages initially assigned to *D. longispina* or *D. rosea* were actually *D. galeata* or *D. hyalina* (Schwenk et al., 2000). In some of the observed lakes, hybrids of *D. galeata x D. rosea* and *D. galeata x D. longispina* might occur (e.g. Unterer Arosasee) but are not listed here because molecular DNA analyses were not used in this study.

This study showed that the percentage of sexual *Daphnia* in alpine lakes can be very high (Fig. 5). The data suggest a decrease in the proportion of parthenogenetic females with increasing altitude. This relationship did not appear to influence genetic diversity, as no relationship was observed between the proportion of sexual individuals and either clonal diversity (*D*) or inbreeding (F_{IS}). However, the presence of multiple species and their hybrids in lakes certainly can influence levels of genetic diversity as well. The allozyme data indicate inbreeding in 4 of the 14 populations. Two of these populations were in Prätschsee (1998 and 1999), a lake with a large proportion of sexual individuals (Fig. 3), and so contrary to our initial hypothesis. Thus, it is unclear if sexual reproduction and high genetic diversity were related in these *Daphnia* populations. Heterozygote excess or outbreeding occurred at the *Ao* locus in three populations (Oberer Arosasee 1998 and 1999, Unterer Arosasee 1999) and resulted in an overall significant negative F_{IS} in Oberer Arosasee in 1998. Heterozygote excess may result from a lack of recombination in this lake where clonal diversity is low and therefore the same, possibly fixed clones, persist. Heterozygote selection is possible, although from the scope of our study it appears to occur only in these two lakes and only in 1999 for Unterer Arosasee. Scoring errors are unlikely to occur in only 3 of 14 populations and the number and frequencies of alleles were approximately the same in other lakes (Appendix 1). What is clear is that inbreeding and outbreeding were not related to the proportion of sexual individuals in lakes, and that perhaps local processes and distinct genetic groups in individual lakes are responsible for the observed patterns. We observed genetic diversity in alpine lakes to be as high as in Swiss lowland lakes, e.g. 0.3 in Lake Lucerne, 1.4 in the Greifensee (P. Spaak, unpublished data), even though a shallow alpine lake constitutes a more homogenous habitat than a deeper lake. Whether this is a consequence of the genetic information possessed by the different species or imposed by the different habitats is not clear.

Results from the three lakes studied in multiple years provide indirect evidence that ephippia production and hatching may increase genetic diversity by creating turnover among years. In alpine lakes, more strenuous environmental conditions might favour sexual reproduction and the production of ephippial eggs. As a result, some clones may have a greater impact on the diapausing egg pool than other clones (Korpelainen, 1987). We did not study the hatching of ephippia, but the interannual genetic distance measures may provide some information regarding the hatching success of *Daphnia*. In the Prätschsee the *D. rosea* population was dominated by sexual individuals, in contrast to both Oberer Arosasee and Unterer Arosasee where almost no sexual daphnids were found. More sexual individuals will mean more genetic recombination and more resting eggs that might hatch in the future. Thus we expect more genetic turnover from year to year in lakes with more sexual individuals. This was the case, as the genetic distance was greater between 1998 and 1999 samples from the Prätschsee than between the same two years in the Oberer and Unterer Arosasee. This was despite Prätschsee harbouring only one morphological species (*D. rosea*), compared with three species in Unterer Arosasee (*D. galeata*, *D. longispina*, *D. rosea*). Several alternative hypotheses exist as well. The drying and re-wetting of Prätschsee may favour different genotypes in different years or may require the lake be recolonised each year. A large egg-bank also may result in lower interannual genetic diversity because similar genotypes return each year from the large egg reservoir of the sediments. The contribution of hatched ephippia to genetic structure in lakes within and among years requires further investigation.

We conclude that the zooplankton composition in the 11 resampled lakes has not been drastically altered in the last 100 yr. This is despite increased human influence in some of the alpine areas studied. Fish presence can be excluded as a primary determinant of zooplankton presence or absence in these lakes. The *Daphnia* data suggest that the formation of resting eggs might be essential for maintaining genetic variation over time. This ability to create resting stages might also be an essential factor for the long-term persistence of other zooplankton taxa.

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Appendix 1. Site overview and lake characteristics.

No.	Lake	Catchme., Utilization	Year sampled	Altitude (m a.s.l)	Surface (ha)	Max D (m)	pH	Spec. Cond. (µS cm^{-1} @ 20°C)	DOC (mg L^{-1})	POC (mg L^{-1})	Chl *a* (µg L^{-1})	TP (µg L^{-1})	TN (µg L^{-1})
1	Jörisee I[a]	R	00	2495	9.1	10.4	7.2	n.d.	n.d.	0.24	0.1	5.0	118.0
2	Schottensee [a]	R	97	2375	7.8	15.0	9.0	119.7	0.4	n.d.	n.d.	14.1	244.8
3a	Älplisee [b]	R	98-99	2156	1.9	4.0	8.4	166.6	2.3	0.67	0.9	4.0	318.0
3b	Alteinsee [a]	R	00	2251	0.7	1.5	8.5	195.0	0.3	0.28	0.3	2.0	148.0
3c	Grüenseeli [a]	R	00	1811	0.1	1.7	8.4	220.0	0.9	0.40	0.5	5.0	563.0
3d	Oberer Arosasee [b]	H	98-00	1734	9.1	14.0	8.5	383.5	1.5	0.71	3.4	14.4	350.0
3e	Prätschsee [b]	H	98-99	1970	0.4	4.5	8.4	119.9	2.3	0.56	2.7	10.3	238.4
3f	Schwellisee [b]	R	98-99	1933	1.9	13.0	8.3	200.7	1.4	1.21	4.8	2.7	300.7
3g	Unterer Arosasee[b]	H	98-99	1691	1.6	12.0	8.8	306.1	2.3	0.72	3.3	16.5	605.1
3h	Urdensee [b]	R	98-99	2249	1.8	10.0	8.4	171.0	1.3	0.23	0.1	2.7	230.3
4a	Murgsee [a]	R, HP	98-99	1820	25.0	24.0	8.6	n.d.	1.6	0.53	0.9	6.0	178.0
4b	Grosssee [a]	H	98	1618	5.4	11.0	8.2	192.1	2.5	1.39	6.8	26.0	609.0
5a	Melchsee [b]	H, HP	97	1891	50.0	16.0	8.3	n.d.	< 1.0	n.d.	0.5	n.d.	n.d.
5b	Trübsee [a]	R, HP	98-00	1764	30.0	10.0	8.2	121.0	0.8	0.30	0.8	5.0	313.5
6a	Oberalpsee [a]	R, HP	00	2025	19.5	15.0	8.1	44.0	0.8	0.63	2.2	10.0	236.0
6b	Lutersee [a]	R	98	2358	3.0	8.5	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
7a	Gotthardsee	R, HP	00	2091	8.0	12.0	8.7	27	1.6	0.41	1.8	5.0	319.0
7b	Grimmselsee	R,HP	00	2160	21.0	8.2	9.1	12.5	1.6	0.34	1.7	5.0	198.0
7c	Triebtenseeroli	R	00	2365	11.0	15.5	8.0	12.0	4.7	0.61	2.1	8.0	86.0
7d	Oberaarsee	R, HP	00	2303	187.5	34.0	5.0	27.0	13.0	0.19	0.6	24.0	240.0
8a	Cadagno [d]	H	98-99	1923	26.1	21.0	8.1	195.0	5.0	0.97	2.0	18.0	249.0
9a	Robiei [a]	R, HP	98	1940	40.0	44.0	8.0	147.0	2.4	n.d.	0.3	6.0	315.0
10a	Leisee [a]	R	00	2232	0.8	4.3	8.0	211	2.3	0.32	0.6	7.0	169.0
10b	Riffelsee II [a]	R	00	2745	02	1.8	9.0	75.0	5.6	0.21	0.1	6.0	215.0
10c	Riffelsee III [a]	R	00	2757	0.8	4.5	8.1	57.0	3.3	0.64	3.7	9.0	251.0
10d	Schwarzsee [a]	R	00	2552	0.6	3.8	8.3	37.5	2.4	0.64	2.9	11.0	233.0

DOC = dissolved organic carbon, POC = particulate organic carbon, Chl. *a* = Chlorophyll *a*, TP = total phosphorus and TN = total nitrogen. [a] pH, Spec. Cond, DOC, POC, Chl. *a*, TP and TN are the mean values for the water profile in late summer/early autumn; [b] pH, Spec. Cond, DOC, POC, Chl *a*, TP and TN are the mean values for the water profile during the open water period; [c] Values for Melchsee are from Emmenegger (1999); [d] Values for Lake Cadagno are from Deldon et al. (1998). R = Remote catchment (little influence by human), H = widely influenced by Human activities, HP = used for Hydropower Production. n.d. = not determined.

Chapter III

Seasonal zooplankton succession and demography in a high-mountain lake

with H. R. Bürgi and P. Spaak, submitted

Abstract

We studied the seasonal succession of phyto- and zooplankton and the impact of possible predation by salmonids on zooplankton population dynamics in a high-mountain lake (Oberer Arosasee, Switzerland). A comparison of patterns in the abundance, body length measures, fecundity and proportion of adults in the *Daphnia galeata* population, strongly suggests that top-down effects of trout predation had no impact on the population and was not the cause for the population decline during the summer. There is some evidence for both exploitative and interference competition between some taxa. Partial correlation analyses indicated that *D. galeata* depressed performance of other plankton species through exploitative competition. Even though *D. galeata* densities were relatively low, our results suggest that negative interference by *D. galeata* might be important in this high-mountain lake since growth rate and fecundity were more strongly depressed at high densities.

Introduction

Zooplankton species hold a central position in lentic food webs, and a combination of predation (top-down) and resource limitation (bottom-up) typically regulates plankton populations and drives seasonal successions (Threlkeld, 1987; Pace et al., 1999). Studies of freshwater communities have clearly demonstrated that fish predation can have a profound impact on the structure of zooplankton communities (Carpenter and Kitchell, 1993; Chase, 2000). The size-selective foraging behaviour of fish is considered a key factor in determining the community structure and productivity of prey populations (e.g. Brooks and Dodson, 1965). Large-bodied zooplankters such as *Daphnia* are preferred prey of visually foraging fish, and are therefore rare or absent when planktivorous fish are common (Brooks and Dodson, 1965; Vanni and Findlay, 1990). Conversely, smaller zooplankters such as *Bosmina* and smaller individuals within a species can coexist with planktivorous fish even at high densities (Hall et al., 1976; Arnott and Vanni, 1993). The seasonal fluctuations of large-bodied zooplankton are to a large degree often attributed to changes in fish predation pressure throughout the year (Spaak and Hoekstra, 1997). Young-of-the-year planktivorous fish often control the pelagic zone in summer, but this may differ between years due to differences in year class strength and the time of spawning. Size-selective fish predation may lead to a disproportionate decrease of adult individuals, therefore affecting the demography of prey populations by increasing mortality and reducing birth rates. Alterations in zooplankton community structure can, in turn, influence the algal community (Vanni and Findlay, 1990). Zooplankton grazing rates increase exponentially with zooplankton body size (Knoechel and Holtby, 1986). Thus, when fish remove large herbivores, grazing rates decline, allowing phytoplankton to increase.

The cascading effects of fish predation has been clearly demonstrated in freshwater systems, where fish density has been manipulated either by removal or stocking (Kerfoot and Sih, 1987). High-mountain lakes provide good examples of how fish introduction into fishless lakes can influence the community structure of zooplankton (Gliwicz et al., 2000). Many high-mountain lakes have been historically fishless but now are stocked with various trout species for recreational purposes. Trout are opportunistic feeders and rely largely on benthic prey. Nevertheless, trout are partly planktivorous and can consume plankton prey above a certain size range, whereas the often more numerous smaller individuals are ignored (Galbraith, 1967; Fitzmaurice, 1979). Fish introduction in fishless high-mountain lakes have caused dramatic changes in zooplankton communities, resulting in the elimination of large-bodied zooplankton such as calanoid copepods (e.g. *Diaptomus*) and large bodied cladocerans (e.g. *Daphnia*), in favour of smaller cladoceran species and cyclopoid copepods (Anderson, 1980; McNaught et al., 1999; Knapp et al., 2001).

Spatial heterogeneity and a multitude of predator avoidance strategies can dampen the effect of predation (Chase, 1999). In nature, prey species use a variety of tactics to avoid being eaten by their predators (Havel, 1987). Small size is advantageous for zooplankton when visually hunting fish are abundant. In *Daphnia*, for instance, size at first reproduction and average length decreases in the presence of fish mediated chemicals, called kairomones (Lampert, 1993). However, according to the 'Size Efficiency Hypothesis' large-bodied herbivorous zooplankters like *Daphnia* are superior exploitative competitors for shared food resources (Brooks and Dodson, 1965; Vanni, 1986). The consequence is a trade-off between competitive ability and vulnerability to predation that may be related to body size. Under reduced vertebrate (visual) predation pressure and fluctuating resource conditions, however, large-bodied species tend to have a competitive advantage over small-bodied species because of their ability to exploit rich resource conditions and withstand longer periods of resource depression (Lynch, 1980; MacIsaac and Gilbert, 1991; Walters and Vincent, 1973).

In addition to predation, food limitation and exploitative competition for shared food sources limit population growth and strongly determines the seasonal succession of herbivorous zooplankton (DeMott, 1983; Boersma, 1995). Exploitative competition implies that suppression of a given population is mediated only through the depletion of resources (Rothhaupt, 1990; Matveev, 1991). Positive correlation between fecundity and food availability and negative correlation between fecundity and animal density suggest demographic evidence of competition (Lampert, 1978; DeMott, 1983). However, zooplankton can also interfere with each other irrespective of food availability (Burns, 2000) and direct density effects predict a significant proportion of natural variance in *Daphnia* performance (Kerfoot et al., 1988). Some forms of mechanical and chemical interference also might be involved in zooplankton competition (Seitz, 1984).

In our study, we investigated the temporal changes in zooplankton population structure and demography in a high-mountain lake, where salmonids are the dominant fish species. If predation by salmonids is an important factor in structuring the zooplankton we would expect small-size zooplankton to be dominant due to a greater mortality of large-bodied zooplankters. In addition, we determined the relative importance of different biotic and abiotic factors contributing to the population dynamics and structure of crustacean zooplankton, with an emphasis on *Daphnia*, in an attempt to disentangle the effects of competition and predation by omnivorous copepods.

Material and Methods

Study area

The study was performed in a dimictic high-mountain lake, Oberer Arosasee, Switzerland, in the catchment of the River Rhine at an altitude of 1734 m a. s. l. It is a small (surface area = 7.1 ha), relatively deep ($depth_{max}$ = 13 m, $depth_{mean}$ = 7.3 m) lake with ice cover for about 6 months. In summer, the lake exhibits a weak thermal stratification, with a mean epilimnetic temperature of 14 °C and a hypolimnetic temperature of 7 °C. An anoxic zone (<0.5 mg oxygen L^{-1}) develops below 10 m during summer and winter. The crustacean zooplankton community consists of the herbivorous species *Bosmina longispina* Leydig 1860, *Daphnia galeata* Sars 1864, *Eudiaptomus gracilis* Sars 1863 and the omnivorous *Cyclops abyssorum* Sars 1863. The fish community in the lake is dominated by salmonids, especially brown trout (*Salmo trutta*), charr (*Salvelinus alpinus*), to a lesser extend by rainbow trout (*Oncorhynchus mykiss*) and by minnow (*Phoxinus phoxinus*). The lake is regularly stocked with adult brown trout and charr (>200 mm total length).

Field methods

During the ice-free period (May – November) the zooplankton community was sampled on a weekly basis in 1998 and fortnightly in 1999. During the period of ice cover, sampling was done twice in 1999 and five times in 2000. Zooplankton was sampled around mid-day at three stations situated in the deepest part of the lake at 2.5-m depth intervals up to 12.5 m depth using a duo-closing net (95 µm mesh size; Bürgi, 1983). Samples from each depth stratum of the three stations were pooled (300 L per depth stratum), concentrated and preserved in 90 % ethanol.

Phytoplankton was sampled at 6 depths (0, 2.5, 5, 7.5, 10 and 12.5 m) every third week during the ice-free period and once during the period of ice cover from May 1998 until January 2000 using a 5-L Schindler trap and fixed with Lugol's solution. Phytoplankton cells were analysed according to the Utermöhl settling technique (Rott, 1981). For each sample, a total of at least 200 cells were counted and identified up to genus or species level and for the most common taxa a minimum of 50 cells were counted. Biomass was calculated from volume measurements of each species (fresh weight). Cell size and shape distinguished edible from inedible algal cells (Infante, 1973; Porter, 1973; Conover and Mayzaud, 1984). Water transparency (using a Secchi-disk) and vertical temperature profiles were determined at each sampling occasion.

Zooplankton were identified to species level (Flössner, 1972; Einsle, 1993) and life stage; at least 100 individuals (if present) of each species and stage (i.e. juveniles, adults, copepodites, nauplii) were counted at each depth. Zooplankton biomass was calculated from length-weight regressions after Bottrell et al. (1976). For daphnids, body length and clutch size were determined for ≥500 randomly selected individuals per sampling date in 1998 and for ≥130 individuals in 1999 using an imaging programme connected to a microscope. In May and June this was not always possible and we measured fewer individuals. Size at maturity (SAM) of *D. galeata* was calculated according to Lampert (1988), which is the smallest size class that had at least one half of the average percentage of egg-bearing females in the adult population. Fecundity was calculated as the mean number of eggs per adult female. For *E. gracilis* body length was measured for 14 to 847 individuals per sampling date in 1998, depending on the number of individuals present.

Demographic rates

For each zooplankton taxon, the rate of population increase *r* was calculated from abundance estimates after conducting a three-point running average according to the formula of exponential growth

$$r = (\ln N_2 - \ln N_1) / (t_2 - t_1),$$

where N_1 and N_2 are the number of individuals at sampling time t_1 and t_2. In addition, for *D. galeata*, birth rate *b* was determined with the Edmondson-Paloheimo formula (Paloheimo, 1974)

$$b = \ln (E + 1) / D,$$

in which *E* is the average number of eggs per animal and *D* the egg development time. *D* was calculated according to an empirical equation relating egg development rates of several daphnids with temperature (Bottrell et al., 1976)

$$\ln D = \ln \mathrm{A} + \mathrm{B} * (T^2),$$

where A and B are regression parameters and *T* is the mean temperature (°C) of the water column encountered by adults. Death rate *d* was calculated as

$$d = b - r.$$

The time interval between sampling dates and the average values of egg development time of *D. galeata* (~8 days) in the Oberer Arosasee were approximately equal; such conditions provide the most accurate estimate of *b*, calculated by the Paloheimo (1974) method (Polishchuk and Ghilarov, 1981). In addition, mortality rates for juvenile and adult daphnids were calculated for 1998/99 by an approach similar to the discrete event model INSTAR (Vijverberg and Richter, 1982) according to Hülsmann and Weiler (2000). Growth rates were estimated from an *in situ* life history experiment (Winder and Spaak, in press).

Statistical analyses

The relationships between performance of crustacean zooplankton taxa (e.g. growth rate) and food availability, and biomass of the specific population, with potentially competing zooplankton taxa and predatory copepods was analysed using forward stepwise multiple regression and partial correlation analysis according to Declerck (2001). The subset of independent variables selected by the forward selection procedure were the (ln + 1) transformed biomass of zooplankton taxa and phytoplankton at the start of the respective time intervals, as well as temperature change during the time intervals. Missing phytoplankton estimates were obtained by exponential interpolation of the preceding and following sampling date. A Pearson correlation coefficient was calculated between the adjusted coefficients of determination calculated from the multiple regression models (adj. R^2) and the average mean body size of the zooplankton taxa.

Fecundity was used as an indicator for *D. galeata* condition. Since brood size depends on body length (Lampert, 1993), fecundity was estimated using the resulting residuals from linear regression between the average clutch size and body size of egg bearing females on each sampling date according to Declerck (2001). Multiple regression and partial correlation analysis between fecundity and species biomass and phytoplankton groups at 7 days before the sampling date were performed after selection of the variables by a forward selection procedure. The average time lag of 7 days takes into account the delay between ingestion of food and egg production (Seitz, 1980; Matveev, 1991); species biomass was estimated by exponential interpolation of the biomass of the preceding and current sampling date.

Top down control of zooplankton taxa on phytoplankton was analysed in 1998 using partial correlation between biomass of phytoplankton taxa and biomass of zooplankton taxa of the previous sampling date (average time lag of 7 days), since phytoplankton biomass is a delayed negative function of zooplankton biomass (Matveev, 1991).

Partial correlation analysis was used to disentangle the effects of food exploitation and direct interference effects according to Declerck (2001). Negative partial correlation between zooplankton population biomass and food availability, and also positive partial correlation between zooplankton performance (growth rate and fecundity) and food availability, may account for exploitative competition. In contrast, negative partial correlation between the biomass of a zooplankton taxon and its own performance or the performance of another taxon may indicate intra-specific or inter-specific interference competition, respectively, independent of food availability.

Regressions were individually checked for outliers; cases were excluded from the analyses when the residuals fell outside of the ± 2 x *sigma* limits (Feinstein, 1996).

Results

Plankton population dynamics

The phytoplankton peak at the beginning of the growing season consisted mainly of edible algae like diatoms (mainly *Achnanthes*, *Cyclotella*, *Synedra*), chlorophytes (mainly volvocales and *Schroederia*), cryptophytes (mainly *Cryptomonas* and *Rhodomonas*) and dinophytes (mainly *Gymnodinium*); in 1999 also Chrysophyceans (*Dinobryon*; Fig. 1). In May 1998 and August 1999 cysts of *Gymnodinium* and *Cyclotella* dominated the inedible algal biomass. The early season peak developed almost two months later in 1999, reaching the highest value of 3.15 mg FW L^{-1}. In both years, the early season peak was followed by a clear-water phase with varying biomasses of the different algal taxa and, later in the summer, by high biomasses of cyanobacteria (*Microcystis*, *Pseudanabaena*) and cryptophytes (*Cryptomonas*

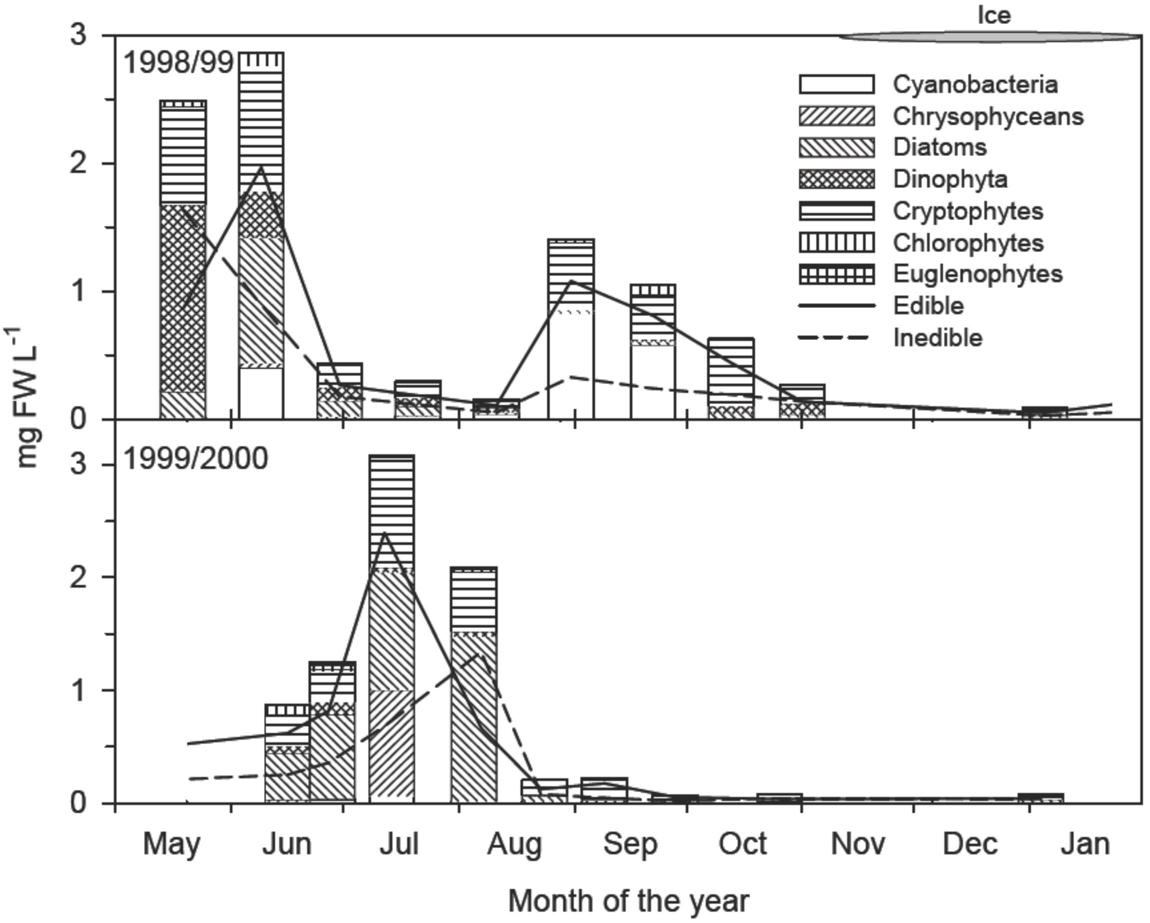

Figure 1. Biomass (mg FW L^{-1}) of the phytoplankton taxa and of the edible and inedible fractions in the Oberer Arosasee from May 1998 until January 2000.

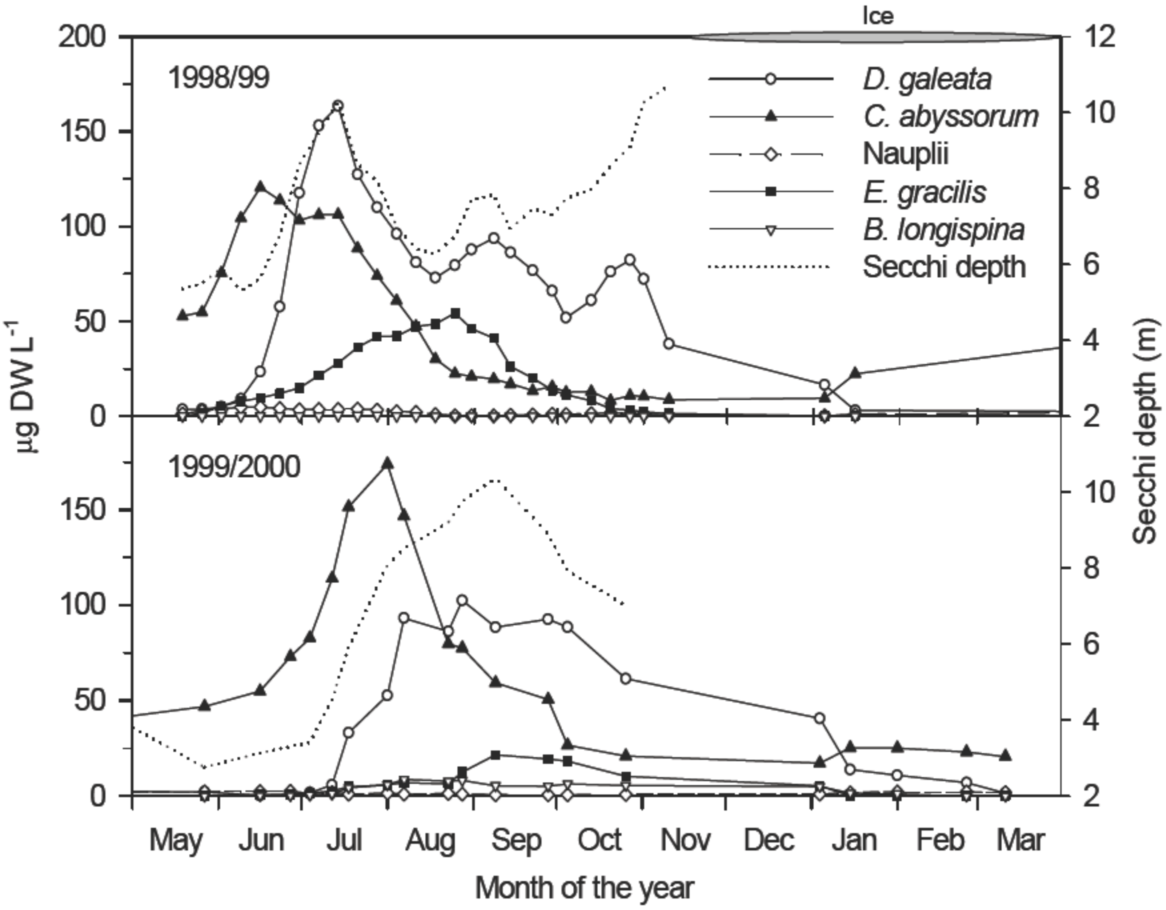

Figure 2. Biomass (mg DW L^{-1}) of crustacean zooplankton and Secchi disk depth in the Oberer Arosasee from May 1998 until March 2000.

and *Rhodomonas*) in 1998, whereas in 1999 no autumn phytoplankton peak was observed (Fig. 1). Phytoplankton biomass under the ice was low (~0.07 mg FW L^{-1}) and was dominated by cryptophytes and dinophytes.

The biomass of the crustacean zooplankton varied considerably within and between the two sampling seasons (Fig. 2). Average of the total crustacean zooplankton biomass ranged between 12.7 and 301.1 mg DW L^{-1} in the lake. In spring, *C. abyssorum* dominated the zooplankton community in both years, and was the most abundant zooplankter until mid August in 1999. *Daphnia galeata* contributed most to the zooplankton biomass from early summer until the lake was ice covered. Biomass of *E. gracilis* increased slightly during the summer months in 1998, but remained at a relatively low level in summer 1999 and increased slightly in autumn. The biomass contributions of *B. longispina* and copepod nauplii were low during the sampling period. Under ice cover, the biomass of all species was very low; *C. abyssorum* and *D. galeata* occurred most frequently. There was a significant positive relationship between *D. galeata* biomass and Secchi depth (Pearson r = 0.72, $P < 0.001$, N = 39).

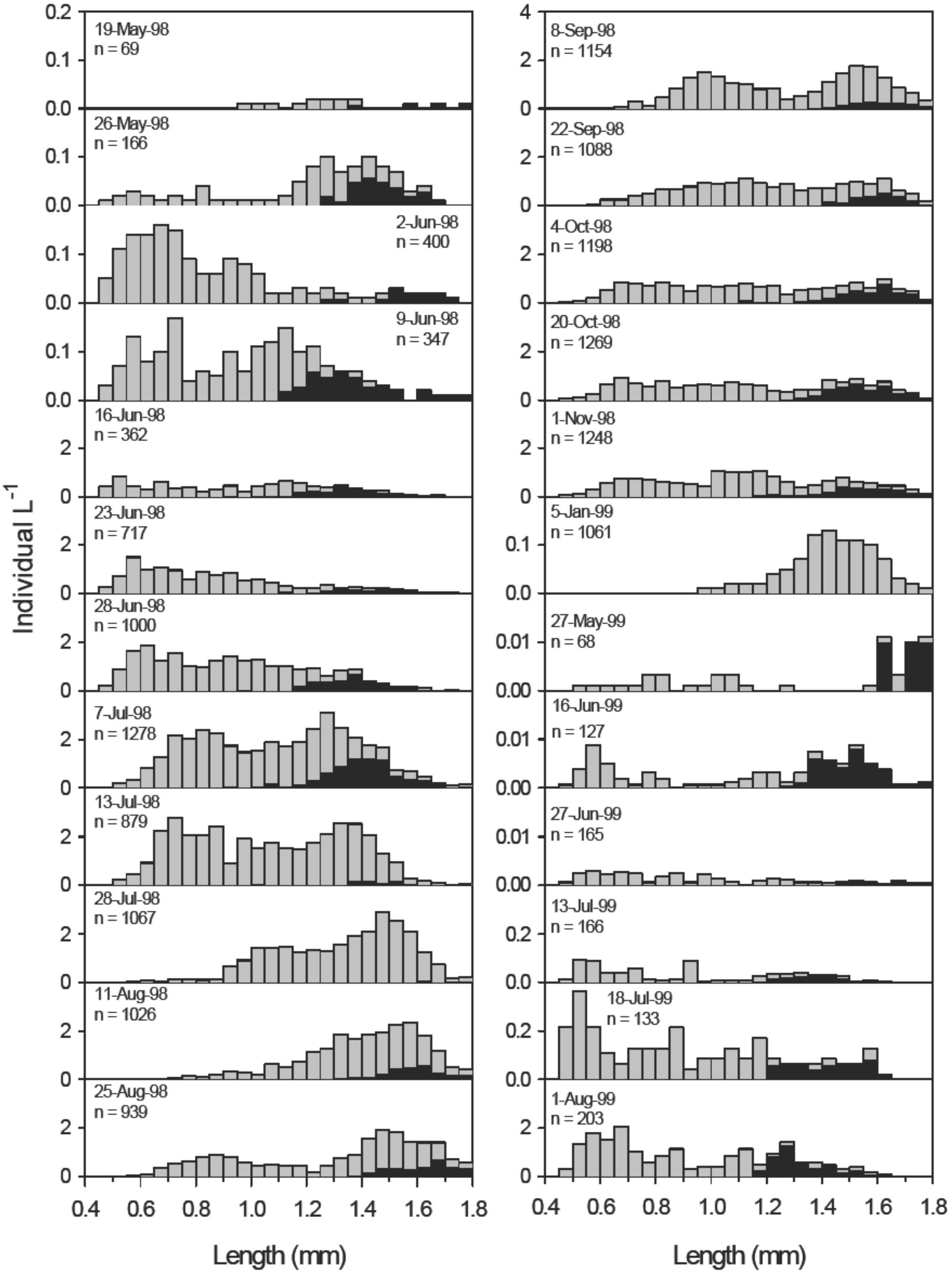

Figure 3. Length density distribution of the *D. galeata* population from June 1998 until August 1999; black bars indicate egg-bearing females.

Body size structure

The size structure of the *D. galeata* population changed considerably during the season in a consistent way (Fig. 3). After the lake became ice-free in May 1998 and 1999, juveniles were absent or rare and the population consisted of large daphnids, starting to produce eggs. In early June 1998 and July 1999, small daphnids dominated and a reduction in the population of large individuals was observed. The new generation started to produce eggs in July 1998 and August 1999. By the end of July 1998 the proportion of small-sized daphnids was reduced considerably, although they slightly increased in autumn. Only large size daphnids were observed under the ice cover (January 1999). The *E. gracilis* population started to reproduce in early summer (Fig. 4); in autumn the population consisted of large size individuals.

Maximum size of daphnids increased slightly in summer 1998 and remained high in autumn and under ice cover, but decreased in July 1999 (Fig. 5). SAM of *D. galeata* followed a similar pattern and was low at the beginning of the growing season (1.2 mm), increased in July 1998 up to 1.8 mm,

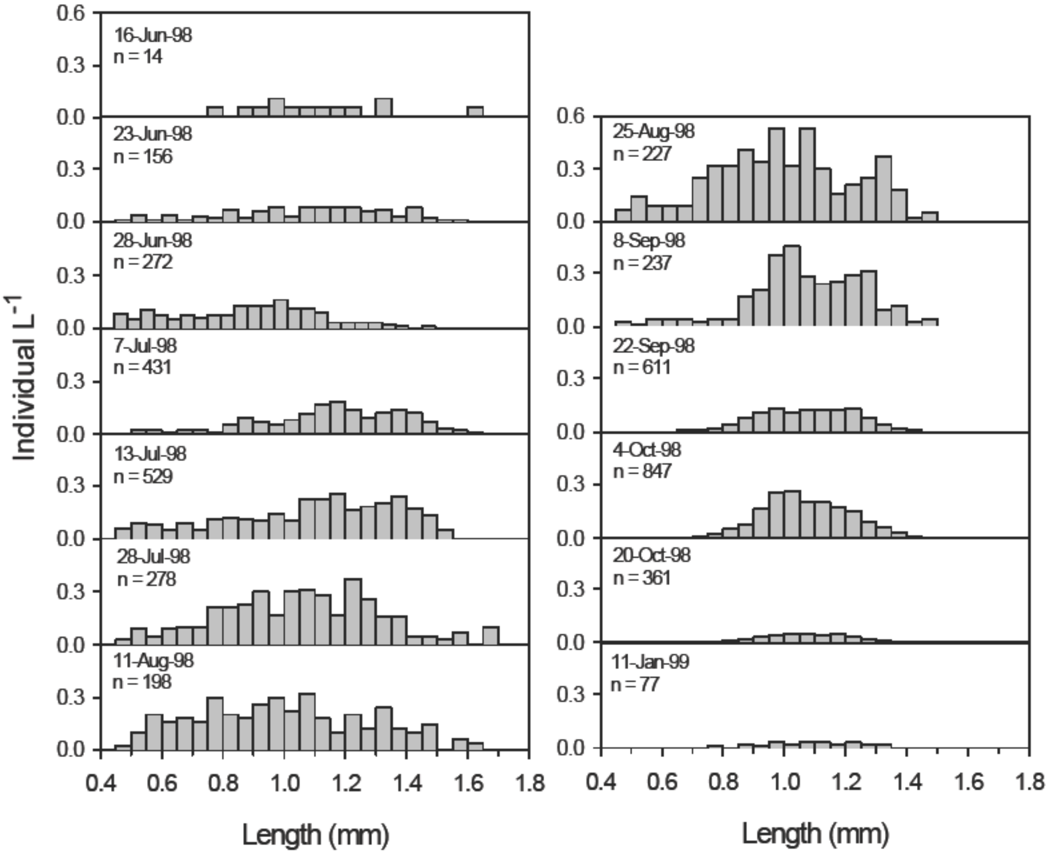

Figure 4. Length density distribution of the *E. gracilis* population from June 1998 to January 1999 in the Oberer Arosasee.

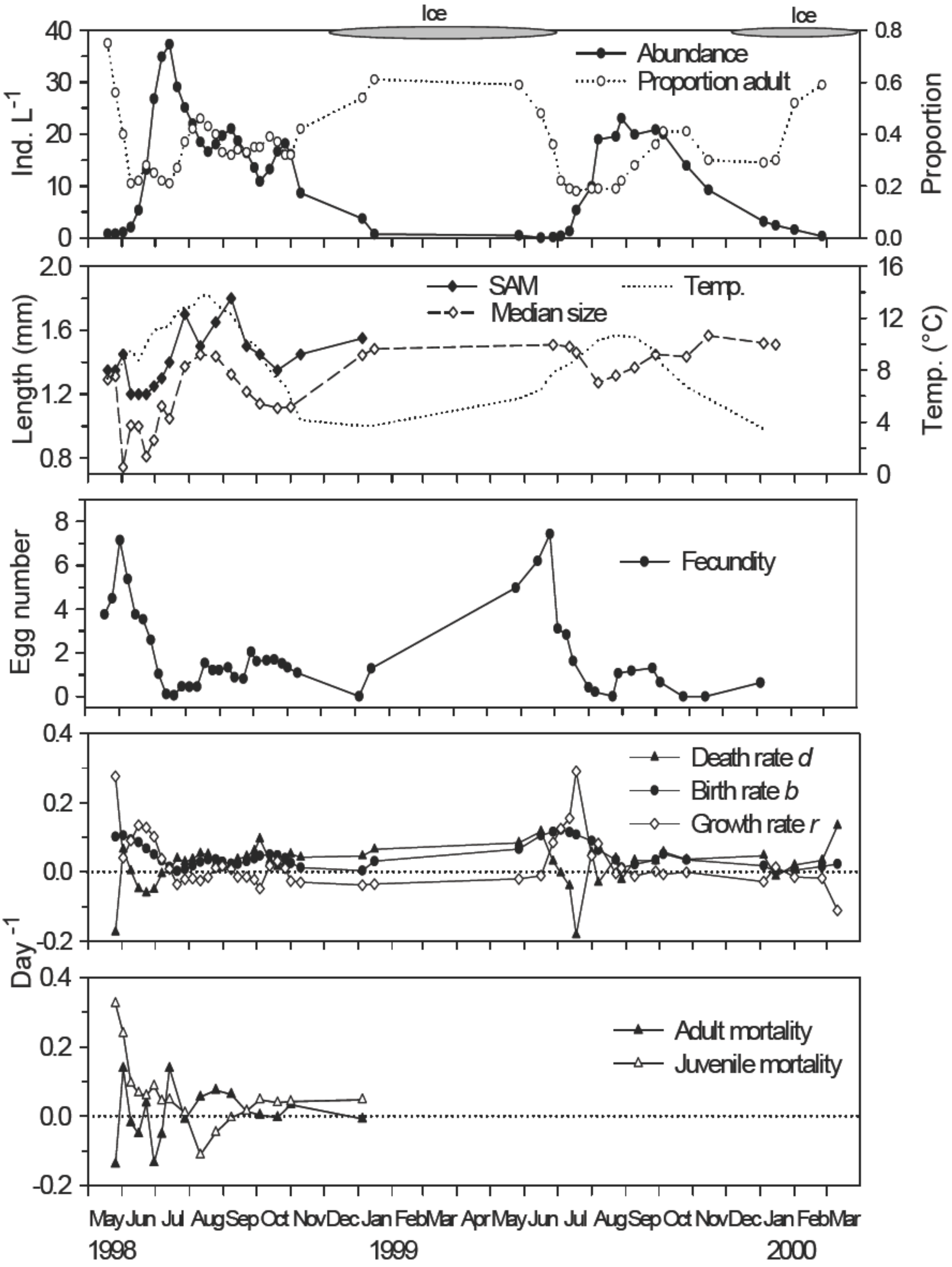

Figure 5. *Daphnia galeata* in the Oberer Arosasee: densities and proportion of adults, temporal changes of median length and size at maturity (SAM), mean lake temperature, mean fecundity (number of eggs per adult female), instantaneous rate of increase *r*, birth rate *b* and death rate *d* during the study period 1998 – 2000, as well as adult and juvenile mortality rates in 1998/99 calculated according to Hülsmann (2000); values are smoothed by a three-point running mean.

after decreasing in autumn to approximately 1.3 mm (Fig. 5). Due to the large percentage of juveniles in early summer 1998, median size was around 0.9 mm but increased in late summer and under the ice cover. Median size and SAM of *D. galeata* changed parallel to temperature changes; under the ice cover, when temperature was below 4 °C, median size (~1.4 mm) exceeded median sizes during the open water period (Fig. 5).

Fecundity

In both years, clutch size of *D. galeata* showed a similar pattern, although the peak shifted one month later in 1999 (Fig. 5). The over-wintering females produced large broods (maximum of 20 eggs and mean of 8 eggs per brood) for a short time at the beginning of the growing season (Fig. 6). In July 1998 and August/September 1999 clutch size was around zero. After the autumn turnover (early September), mean clutch size increased and fluctuated between 1 and 2 eggs, but decreased again under the ice cover. Highest egg numbers were found in spring samples with body sizes between ~1.5 mm and ~1.8 mm; in summer and autumn large oviparous daphnids with low egg numbers were found (Fig. 6).

Demographic rates

In 1998, the population growth rate of *D. galeata* was positive until July and fluctuated around zero until October (Fig. 5). Under ice cover and until June 1999 *r*-values were negative, but increased in July, followed by a sharp decrease and mostly negative values until January 2000. Birth and death rates (Fig. 5) reflected population development, birth rates were relatively high at the beginning of the growing season when clutch size was highest, and decreased later in the season. Death rates were negative at the beginning of the growing period, but remained positive during the rest of the year, except in January 2000. Rates of juvenile mortality were mostly positive, with negative values in August and early September 1998. Adult daphnids showed mostly positive mortality estimates in early June and July until September. Values remained low or around zero during the rest of the investigation period of 1998/99 (Fig. 5). Total death rates were in the same range as adult mortality. Depth rates strongly correlated with increasing SAM, proportion of adults and decreased with increasing fecundity (Fig. 7). Low natality (Pearson r = –0.90; $P < 0.001$), low population growth rates (Pearson r =

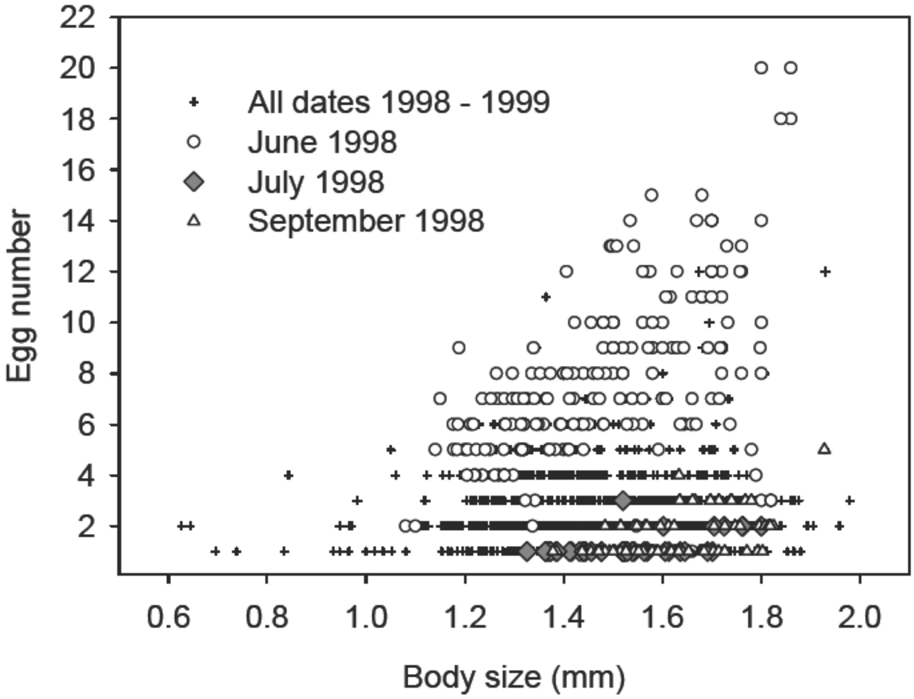

Figure 6. Relation between body size (mm) and brood size (number of eggs) of *D. galeata*, considering all egg-carrying individuals in samples taken between May 1998 and January 1999 from the Oberer Arosasee. June, July and September represent spring, summer and autumn, respectively, in this lake.

–0.78; $P < 0.001$) and high mortality (Pearson r = 0.74; $P < 0.001$) correlated with high *D. galeata* biomass (data not shown).

Multiple regression models

Multiple regression models significantly explained the growth rates of the zooplankton taxa and the variance ranged between 43 and 60 % (Table 1). Significant negative partial correlations were found between the *r*-values of *D. galeata*, *E. gracilis, B. longispina* and the biomass of *D. galeata* at the start of the time interval. In addition, *r*-values of *D. galeata* were negatively related to the biomass of adult *C. abyssorum,* as were copepod nauplii to the biomass of copepodite *C. abyssorum,* while *r*-values of *E. gracilis* were positively related to copepodite *C. abyssorum* and negative to nauplii. Growth rates of *D. galeata*, *C. abyssorum* and nauplii were positively associated with the edible algal fraction and copepod nauplii to temperature change (Table 1).

Fecundity of *D. galeata* was explained significantly by multiple regression models (adj. $R^2 = 0.93$, $P < 0.001$; Table 2). Its fecundity was positively related to the edible fraction of the phytoplankton biomass and biomass of

C. abyssorum and negatively to its own biomass and biomass of *E. gracilis* at 7 days before the respective sampling date. Also, birth rates and death rates of *D. galeata* were explained significantly by the multiple regression models (Table 2). Birth rate of *D. galeata* was positively related to the edible phytoplankton biomass and negatively to the biomass of its own population. Mortality rates were associated negatively with its own biomass, biomass of *C. abyssorum* and of the edible phytoplankton fraction and positively with the biomass of *E. gracilis* and the inedible phytoplankton fraction.

Partial correlation analyses between the biomass of phytoplankton and zooplankton taxa indicated that *D. galeata* biomass was negative related to all phytoplankton taxa, except cyanobacteria (Table 3), as was the biomass of *E. gracilis* significantly negative related to diatoms and dinophytes, and copepod nauplii to cryptophytes and cyanophytes.

Table 1. Multiple regression analyses of intrinsic population growth rate *r* of zooplankton species in the Oberer Arosasee on the following independent variables: biomass of the own population, of potential competitors, of predators and of edible and inedible algae biomass. Given are the partial correlation coefficients that were selected by a stepwise forward procedure (Sokal and Rohlf, 1995). Data are from 38 dates during the open water period of the Oberer Arosasee in 1998 and 1999. rp = partial correlation coefficient; adj R^2 = adjusted coefficient of determination of the multiple regression model, rDa = *r* of *D. galeata*, rEu = *r* of *E. gracilis*, rCyc = *r* of *C. abyssorum*, rNaup = *r* of copepodid nauplii, rBos = *r* of *B. longispina*. BiDa= biomass of *D. galeata*, BiEu = biomass of *E. gracilis*, BiCyCop = biomass of *C. abyssorum* copepodites, BiCyAd = biomass of *C. abyssorum* adults, BiNaup = biomass of copepodid nauplii, BiBos = biomass of *B. longispina*. PPed = biomass of edible algae, PPin = biomass of inedible algae. dT = temperature change. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	rp				
	rDa n = 38	rEu n = 37	rCyc n = 37	rNaup n = 36	rBos n = 36
BiDa	-0.60***	-0.63***	0.01	0.48**	-0.67***
BiEu			-0.41*		
BiCyAd	-0.37*			0.41*	-0.26
BiCyCop	0.33	0.71***	-0.27	-0.58***	0.40*
BiNaup	-0.22	-0.39*		0.43*	-0.43*
BiBos			0.31*		
PPed	0.41*	-0.28	0.41**	0.39*	
PPin				0.20	
dT				0.38*	
adj. R^2	0.60***	0.54***	0.55***	0.43**	0.47***

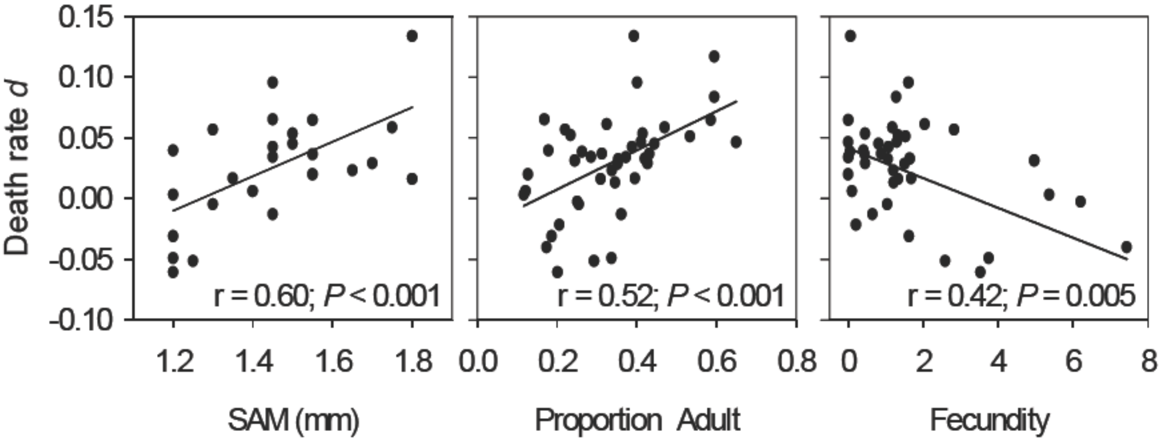

Figure 7. Correlations between death rate *d* of *D. galeata* with size at maturity (SAM), the proportion of adults and fecundity in the Oberer Arosasee.

Discussion

Influence of predation on zooplankton

Our results suggest that size-selective predation by salmonid fish contribute little to the seasonal succession of zooplankton in the Oberer Arosasee; there is, however, some evidence for both exploitative and interference competition between zooplankton taxa. Seasonal changes in the general size structure of the large-size zooplankton representatives, *D. galeata* and *E. gracilis* are indicative of non-selective mortality with respect to body size (Figs. 3 and 4). The large size fraction of *D. galeata* that diminished about a month after ice break may decrease because of senescence and not size selective fish predation (Spaak and Hoekstra, 1997). A decrease in SAM during summer is suggested to be a phenotypical adaptation of cladocerans to high fish predation (Lampert, 1993). In our study, however, SAM increased in July 1998 and in August 1999 (Fig. 5) as did the median length of daphnids. The positive correlation between death rate and SAM suggests that fish predation did not cause much mortality (Fig. 7). In addition, the increased proportion of adults during periods of increased mortality and decreasing mortality with higher fecundity (Fig. 7) provides further evidence that fish predation was not responsible for the population decline during the summer periods.

The wide variety of prey species available to fish in the Oberer Arosasee and the dominance of adult trout that mainly feed on benthic prey may buffer the effect of predation on the large zooplankton crustaceans. However, even adult trout may feed upon zooplankton; diet analyses of trout from high-mountain lakes contained beside benthic or terrestrial invertebrates also zooplankton species (Galbraith, 1967; Cacalli et al., 1998). Knapp et al. (2001) showed that *D. rosea*, a species that is in the size range of *D. galeata*, was unaffected by trout introduction in the Sierra Nevada mountains, but not the larger-size *D. middendorffiana*. In the Oberer Arosasee, *D. galeata* and *E. gracilis* are clearly able to sustain populations under a certain level of fish predation.

Multiple regression models that excluded measures of fish predation explained a high amount of variation in the population growth of crustacean zooplankton in the Oberer Arosasee. *Cyclops abyssorum* is the only potential invertebrate predator in the lake and a negative partial correlation may reflect that *C. abyssorum* preyed upon *D. galeata.* Cyclopoid copepodites also can prey on eggs by entering *Daphnia* brood pouches; however, predation on eggs is negligible under 2.25 mm *Daphnia* body length (Gliwicz and Lampert, 1994) and might be therefore not relevant in the Oberer Arosasee since the average size of egg bearing daphnids is 1.51 mm.

Table 2. Multiple regression analyses of residuals on *D. galeata* fecundity (= FecDa), birth rate (= *b*Da) and death rate (= *d*Da) on following independent variables: biomass of its own population, of potential competitors, of predators, and of edible and inedible algae; and temperature 7 days before the sampling dates during the open water period of the Oberer Arosasee. Given are the partial correlation coefficients that were selected by a stepwise forward procedure (Sokal and Rohlf, 1995). rp = partial correlation coefficient; adj. R^2 = adjusted coefficient of determination of the multiple regression model, BiDa= biomass of *D. galeata*, BiEu = biomass of *E. gracilis*, BiCy = biomass of *C. abyssorum*, BiNaup = biomass of copepodid nauplii, BiBos = biomass of *B. longispina*. PPed = biomass of edible algae, PPin = biomass of inedible algae. Temp = temperature. $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$.

	rp		
	FecDa n = 37	*b*Da n = 45	*d*Da n = 35
BiDa	-0.81^{***}	-0.81^{***}	-0.47^{**}
BiEu	-0.36^{*}		0.57^{***}
BiCyc	0.69^{***}	0.28	-0.57^{**}
BiNaup			
BiBos		0.27	
PPed	0.57^{***}	0.57^{****}	-0.83^{****}
PPin			0.71^{****}
Temp	-0.21		
adj. R^2	0.93^{***}	0.80^{***}	0.73^{***}

Plankton population dynamics

The seasonal pattern in biomass and species replacement of phytoplankton in the Oberer Arosasee varied among years (Figs. 1 and 2). In 1999 phytoplankton peaked about two months later compared to 1998, when phytoplankton biomass was highest after the lake became ice-free. Also the clear water phase started about 2 months later (end of August) in 1999 than in 1998 and a phytoplankton peak of cyanobacteria and cryptophytes was present in autumn 1998, but not in 1999. *Cyclops abyssorum, D. galeata* and *E. gracilis* dominated the zooplankton biomass in both years, whereas biomass of the small cladoceran *B. longispina* was low. The pattern of zooplankton species replacement was similar in both years. *Cyclops abyssorum* biomass decreased rapidly during the summer of 1998 and the autumn of 1999 and remained low until the lake became ice-free the following year. Immature cyclopoid instars might spent this period in the sediment as a dormant stage (Gliwicz and Rowan, 1984) and emerge in spring, when conditions are optimal (Hairston et al., 1990). This dormant stage might be induced through competition for food resources between *Cyclops* copepodites and *D. galeata*. Large *Daphnia* have been shown to negatively affect cyclopoids in enclo-

Table 3. Forward stepwise multiple regression analyses from the Oberer Arosasee of zooplankton biomass regressed against phytoplankton biomass (collected 7 – 9 days earlier) in 1998 (for abbreviations see Table 1 and 2) for 25 dates. Given are the partial correlation coefficients that were selected by a forward stepwise procedure (Sokal and Rohlf, 1995). Chloro = biomass of chlorophytes, Crypto = biomass of cryptophytes, Dino = biomass of dinophytes, Chryso = biomass of chrysophyceans, Cyano = biomass of cyanobacteria, Diato = biomass of diatoms, PPall = total algal biomass, PPed = biomass of edible algae, PPin = biomass of inedible algae. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	rp								
	Chloro	Crypto	Cryso	Cyano	Diato	Dino	PPall	PPed	PPin
	n = 25	n = 25	n = 24	n = 23	n = 24	n = 25	n = 24	n = 24	n = 23
BiDa	-0.45^{*}	-0.85^{***}	-0.89^{***}		-0.93^{***}	-0.84^{***}	-0.89^{***}	-0.83^{***}	-0.90^{***}
BiEu			-0.27	0.74^{***}	-0.69^{***}	-0.78^{***}		0.51^{*}	
BiCyAd	0.25	0.46^{*}		0.43	0.33		0.75^{***}	0.74^{***}	0.70^{***}
BiCyCop			0.90^{***}	0.54^{*}	0.69^{***}				-0.47^{*}
BiNaup		-0.64^{**}	-0.37	-0.83^{***}	-0.27		-0.40	-0.31	
BiBos		-0.35	0.27			0.66^{***}		-0.31	
Temp	0.34		-0.27	-0.53^{*}		0.57^{**}		-0.37	
adj. R^2	0.21	0.78^{***}	0.93^{***}	0.84^{***}	0.93^{***}	0.93^{***}	0.83^{**}	0.77^{*}	0.86^{**}

sure experiments (Soto, 1985). Cyclopoids have much lower clearance rates than daphnids and calanoids (Adrian, 1991), and cylcopoid nauplii are more sensitive to starvation than calanoid nauplii.

Daphnia galeata biomass fluctuated strongly in 1998, but maintained a relative stable population from August through October 1999. Peaks in *D. galeata* lagged behind algal peaks and the peak in *Daphnia* was associated with a clear-water phase. *Bosmina*'s greater foraging effectiveness upon highly edible flagellates at low density may allow coexistence with *Daphnia* (DeMott, 1982). De Mott and Kerfoot (1982) showed in an experiment that *Daphnia* was able to depress *Bosmina*, but not to exclude it, even when sharing the same food resources. The increase of *E. gracilis* at times when algal biomass was relatively low (e.g. July 1998) might be due to their ability of being efficient at low food concentrations and to grow at times when algal densities are too low for *Cyclops* (Santer, 1994). Competition experiments showed that calanoid copepods are often not affected by large *Daphnia* species (DeMott, 1989).

Population structure and demography of the D. galeata *population*

In the Oberer Arosasee a few large-sized individuals persisted over the ice cover period to produce the next generation when the lake became ice-free (Fig. 2). The dominance of egg-bearing adults after the lake became ice-free, and the occurrence of juveniles later in the season, indicates that the first generation started mainly with parthenogenetic eggs (Fig. 3); although hatching of resting eggs can not be excluded. Length distributions indicate that there are two generations, both resulting from parthenogenetic eggs. The decline of larger and thus older size classes after the lake became ice-free might be due to senescence or the inability of adults to cope with rising food concentrations because their feeding appendages are adapted to low food conditions (Voigt and Benndorf, in press). Fecundity and recruitment of *D. galeata* was low after the population established a high abundance in July 1998 (Fig. 3) and the population slowly rejuvenated in autumn.

In our study, SAM increased in July 1998 and was high until September 1998 when food was limiting. It has been shown that high SAM can result from both good and bad food conditions (McCauley and Murdoch, 1990). Under conditions of severe food limitation, however, the method of determining SAM has its limits, such that it may overestimate the size when individuals become adults (Stibor and Lampert, 1993). Nevertheless, the increase in SAM as well as the median size might be adaptive in daphnids in that period, since large individuals are superior competitors (Size Efficiency Hypothesis; Brooks and Dodson, 1965) when fish predation is low. Therefore, the increase in size could be the result of clonal replacement, adapted to poor food conditions (Stibor and Lampert, 2000). During periods of low food (summer and autumn), the size of egg-carrying females in summer and autumn was very similar (Fig. 6).

The decrease in birth rate and increase in death rate after the phytoplankton peak and the sharp decline in fecundity after the phytoplankton peak suggest a response to low food conditions during summer, since egg number is a good indicator of food conditions in *Daphnia* (Lampert, 1978). Food limitation after the early season and autumn peak is confirmed by low carbon values of daphnids during this period (Winder and Spaak, 2001). The relatively low levels of reproduction in autumn 1998 in relation to phytoplankton biomass suggest that the algae (mainly cyanobacteria) were of low food quality (Gulati and DeMott, 1997), or that daphnids show low sensitivity to resource richness (Hrbácek, 1977; Tessier et al., 2000).

The negative correlation of *D. galeata* biomass with birth rate and growth rate (Table 2), indirectly showed that a reduction in food availability, caused by high population densities, limited population growth. The decline of the population in July 1998 was caused mainly by enhanced mortality of adult daphnids (Fig. 5) and may be attributed to low food or ageing of the population and the simultaneous die-off.

Interactions between zooplankton species

In the Aroser Obersee, biomass of phyto- and zooplankton and temperature explained a substantial part of the total variance in population increase of crustaceans ($R^2 = 0.43 - 0.60$; Table 1) being highly pronounced in *D. galeata*. The intrinsic rate of increase *r* is assumed to be one of the essential components of competitive ability since it also incorporates food quality (Tillmann and Lampert, 1984; Matveev and Balseiro, 1990). Partial correlation analysis indicated that exploitative competition might have regulated the dynamics of planktonic crustaceans in the Oberer Arosasee, that is supported by the following: The strong negative relationships between the biomass of *D. galeata* with phytoplankton biomass suggest that this herbivore was able to suppress food sources (Table 3); the relationships were highly significant with all algal taxa, except for cyanobacteria. Further, there were positive relationships between the growth rate of *D. galeata*, *C. abyssorum* and nauplii with the edible phytoplankton fraction (Table 1) and a positive relationship of *D. galeata* fecundity with the edible phytoplankton fraction (Table 2). These relationships indicate that there is intra-specific exploitative competition in *D. galeata* and that *C. abyssorum* and nauplii suffer from exploitative competition with *D. galeata*.

In the Aroser Obersee, exploitative competition cannot fully explain the performance of *D. galeata*. A substantial amount of variation in their fecundity, population growth, birth rate and mortality rate was explained by a negative correlation with its own population biomass (Table 1 and 2), irrespective of food availability. Experimental studies showed that reproduction is the most sensitive indicator of interference and negative interference was measurable even at densities of 40 daphnids L^{-1} (Goser and Ratte, 1994). In the Aroser Obersee, maximal mean *D. galeata* density was lower than this value; however, daphnids complete a diel migration and aggregate during daytime in the deeper part of the lake, thus increasing densities up to 90 ind. L^{-1} in specific depth strata (M. Winder, *unpublished data*). The sharp decrease of fecundity in early summer may indicate that daphnids switch from producing many small offspring to fewer large offspring, which are more competitive under low food levels (Tessier and Consolatti, 1991). Hence, interactions might act as a self-regulating mechanism of *D. galeata* abundance and allow the population to react to food shortage very quickly.

To conclude, in the Oberer Arosasee, *D. galeata* is overall a consistently superior competitor, perhaps because of their broader food and spatial niches, suppression of other herbivores by interference, or stronger resistance to starvation (Matveev, 1991). The abundance of small-bodied cladocerans like *Bosmina* may be restricted in the Oberer Arosasee, and in other high-mountain lakes, both by invertebrate predation and competitive suppression by *Daphnia*. The results suggest that increasing densities of grazers effect herbivorous species indirectly through exploitative competition. Our study showed that when fish predation is low, invertebrate predation together with competition for food are the prevailing factors responsible for the dominance of large zooplankton species in high-mountain lakes.

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Chapter IV

Carbon as an indicator of *Daphnia* condition in a high-mountain lake

with P. Spaak, Hydrobiologia 442, 269-278 (2001)

Abstract

Carbon-length relationships can be used to indicate the condition of daphnids in natural situations. We examined the *Daphnia galeata* population of a high-mountain lake (Oberer Arosasee, Arosa, Switzerland), where most individuals display diel vertical migration behaviour (DVM). Normally, migrating daphnids face a trade-off between 'predator safe areas' in the hypolimnion and 'food rich areas' with high predation risk. However, in lakes, with chlorophyll *a* and POC maxima typically in deeper layers and weak temperature gradients, migrating species are confronted less with this trade-off. We investigated the seasonal changes in carbon content of *D. galeata* in different depth strata in relation to environmental parameters of the Oberer Arosasee. The carbon content of *D. galeata* was high in spring, but declined considerably in summer and increased slightly in autumn. The low values indicate that *D. galeata* are food limited for much of the year. The slopes of the regression lines between carbon content and body length varied seasonally, but were not significantly different among depths on a given date. In summer, *D. galeata* individuals residing in the deep layers during the day had a significantly higher carbon content than individuals in the surface layers. During the rest of the year, the carbon content of individuals was similar among all depth strata. We conclude that migrating *D. galeata* and individuals remaining in deep layers had better body conditions compared to non-migrating *D. galeata* that stayed in surface strata during the day in this high-mountain lake during summer, when migration amplitudes were highest.

Introduction

A number of studies have investigated the seasonal dynamics and production of zooplankton in temperate lakes (e.g. Sommer et al., 1986), and recognised that food limitation and predation are major factors influencing the size structure, reproduction and survival of zooplankton (Ghilarov, 1985; Lampert, 1988; Mitchell et al., 1992). In natural systems, however, it is difficult to disentangle the relative roles of food and predation, because of the complexities in measuring the effects of food limitation and predation separately (Boersma and Vijverberg, 1994c). Moreover, it is difficult to establish the amount of accessible food for herbivores in a lake, as in most cases the exact food source is unknown. Studies on daphnids, for example, reported that their diet is a mixture of algae and cyanobacteria (Bloem and Vijverberg, 1984; Vijverberg et al., 1993), bacteria (Urabe and Watanabe, 1991) and detritus (Kerfoot and Kirk, 1991). Furthermore, the biochemical content of algae differs among species, thus resulting in differences in food quality between them (Ahlgren et al., 1990; Groeger et al., 1991). Finally, other factors, such as selective feeding (DeMott, 1986), indigestibility of particles (Kirk, 1992; Van Donk and Hessen, 1993) and interference (Gliwicz and Siedlar, 1980), may result in only a small part of the available resources actually utilised by zooplankters. Thus, daphnids can be food limited even in eutrophic lakes (Boersma and Vijverberg, 1994b). In short, the actual measurement of food accessibility for herbivorous zooplankton is difficult. Hence, indirect measurements to assess the nutritional status of zooplankters have been proposed. For daphnids, laboratory experiments indicated that the number of eggs (Vijverberg, 1976), lipid content (Tessier and Goulden, 1982) and carbon content correlate positively with the quantity and quality of accessible food. As a result, parameters such as egg production (Hebert, 1977), number of eggs per female (Geller and Müller, 1985), lipid-ovary index (Tessier and Goulden, 1982), lipid content (Farkas, 1970) and carbon-length relationships (Duncan, 1985) have been used to assess the condition status of daphnids in the field. Fecundity is used most frequently, but reflects body condition only in a limited way (Berberovic, 1990), because the number of eggs depends on the size of the animal and lipid levels do not always correlate positively with animal growth rates (Sterner and Schulz, 1998).

The relationship between carbon content and body length of an organism seems most promising to evaluate a daphnid's condition. Duncan (1985;

1989) found that under controlled laboratory conditions the slopes of the carbon-length regression lines between length and weight were constant at different food levels, although the intercept, and hence the carbon content, significantly decreased as food levels became limiting. In contrast to animals reared in the laboratory, however, it is known from field populations that the slopes of the regression lines also vary during the year (Geller and Müller, 1985; Hessen, 1989; Boersma and Vijverberg, 1994b). Nevertheless, changes in the carbon-length relationships will reflect changes in the condition of the daphnids and hence yield information on their feeding environment. In addition, carbon-length (or dry weight) regressions are the most reliable method to estimate zooplankton biomass (Dumont et al., 1975; Bottrell et al., 1976; Persson and Gunnar, 1980).

In lakes with high fish densities, and hence a large risk of visual predation, zooplankton species typically exhibit diel vertical migration (DVM) (Ringelberg et al., 1991). Migration to deeper water layers during the day reduces the vulnerability to visual predation, although differences in food quality, quantity and temperature at different depths could result in metabolic costs for the migrating zooplankters (Orcutt and Porter, 1983; Gabriel and Thomas, 1988), even though the energetic costs of migration are thought to be negligible (Loose and Dawidowicz, 1994). Metabolic costs can be expressed as a reduction in growth and reproduction (Ringelberg et al., 1991). The susceptibility of prey species to potential predators is usually associated with their physiological state, which is primarily determined by food and temperature (Gerritsen, 1982; Han and Straskraba, 1998). Zooplankton species migrate less or even stop migrating under food limitation (Johnsen and Jakobsen, 1987; Flik and Ringelberg, 1993).

Guisande *et al.* (1991) and Duncan *et al.* (1993) used the relationship between length and protein, or length and carbon content, as an index of daphnids condition at different lake depths, to distinguish sub-populations that differed in their migration strategy. They showed that a trade-off exists between reduced mortality and poorer nutritive state at greater depths in lakes with food-rich surface waters and strong vertical temperature gradients. In lakes with high subsurface food abundance and weak temperature gradients, as is the case for many high-mountain lakes (Tilzer, 1973), however, migrating zooplankton may be confronted with this trade-off to a lesser extent. This should be reflected in a relatively good body condition of migrating daphnids.

The objective of this study was to evaluate the carbon content of a *Daphnia galeata* population across seasons, and the influence of seasonal biotic and abiotic fluctuations on the carbon-length regressions of the zooplankters in a high-mountain lake. In addition, carbon-length regressions were used to indicate the conditional status of *D. galeata* that undergo DVM. Hence, we compared the condition of *D. galeata* individuals caught at several depths. In addition, the carbon content of *D. galeata* was related to environmental parameters of the lake to test whether the seasonal variation in food availability was reflected in the condition of *D. galeata*. Furthermore, migrating *D. galeata* should have a better condition than individuals remaining in the surface water layers since migrating individuals can feed in the deep layers during their daytime refuge, whereas the individuals in the surface layers are confronted with low food conditions day and night.

Material and methods

Study area

The study was conducted at the Oberer Arosasee (Arosa, Switzerland), a dimictic lake (7.1 ha) situated 1734 m a. s. l. over slate rocks in the catchment of the River Rhine. Its maximum depth is 13 m and the lake is ice covered for about 6 months each year. During the open water period a distinct thermocline is absent, and a weak but relatively continuous vertical temperature gradient develops. Spring turnover is incomplete and the hypolimnion becomes anoxic twice a year. During summer, dissolved oxygen concentrations become < 3 mg l^{-1} at depths > 9 m.

Diatoms dominate the phytoplankton community in spring, whereas cyanobacteria and chlorophytes are abundant in summer, and cryptophytes in autumn. The zooplankton community consists of *Daphnia galeata*, *Cyclops abyssorum*, *Eudiaptomus gracilis* and *Bosmina longispina*. *Cyclops abyssorum* dominates in spring, but *D. galeata* is the most abundant crustacean in the rest of the year. The fish community in the lake consists of introduced brown trout (*Salmo trutta*), which are most dominant, and rainbow trout (*Oncorhynchus mykiss*) as well as of native minnow (*Phoxinus phoxinus)* and charr (*Salvelinus alpinus)*.

Field methods

Samples of zooplankton and water were taken on a weekly basis in 1998 and fortnightly in 1999 during the open water period, and twice in winter in both years. Zooplankton was sampled at mid-day from three stations around the deepest part of the lake at 2.5 m intervals from 0 to 12.5 m depth using a duo-closing net (95 µm mesh size; Bürgi, 1983). A total of 300 l per depth stratum was collected. Samples from each depth stratum were pooled, concentrated, and preserved in 90 % ethanol. In addition, *D. galeata* were sampled with the duo-closing net from each depth stratum at mid-day and midnight (in 1999) at one station and analysed for carbon content and egg number. In 1998/99 water samples from 6 depths (0, 2.5, 5, 7.5, 10, 12.5 m) and in 1999/2000 from 12 depths (1 m interval: 0 – 12 m) were used to determine the concentration of particulate organic carbon (POC) and chlorophyll *a* in the lake. Chlorophyll *a* was measured after extraction in 90 % ethanol using HPLC. Phytoplankton biomass was analysed every third week using the Utermöhl technique (Rott, 1981). Cell size and shape distinguished edible from inedible algal cells (Infante, 1973; Porter, 1973; Conover and Mayzaud, 1984).

Laboratory analyses

Directly after collection, animals were rinsed with distilled water, total length measured, number of eggs counted, and then individually transferred into clean (acetone washed and dried at 120°C) tin capsules and frozen at –20°C for transport to the laboratory. At the laboratory the samples were stored at -80°C until being analysed. The carbon content of individual *D. galeata* was determined using a CHNS Analyser (Carlo Erba, ANA 1500). A *t*-test showed that there was no significant difference ($P < 0.83$) in carbon content between fresh and frozen animals (but see Boersma and Vijverberg, 1994a). For total length, measures were taken from the base of the spine to the top of the eye. At least 30 individuals from each stratum, or all individuals in samples that contained fewer individuals were measured.

Statistical analyses

Linear regressions were calculated from log transformed values using individual length (L in mm) as the independent variable and carbon content (C in µg) as the dependent variable. The relationship is expressed as $C = a * L^b$.

The intercept *a* represents the carbon content of a *D. galeata* of 1 mm body length. Since the length of all measured *D. galeata* was close to 1.5 mm in 1998, the regression equation was used to estimate the carbon content an individual of 1.5 mm. This value is defined as the Standard Carbon Content (SCC; sensu Boersma and Vijverberg, 1994c).

Regressions were tested for differences in intercept, slope and regression coefficients using regression analysis with dummy variables (Sokal and Rohlf, 1995). Significance between depths was tested using ANCOVA followed by Tukeys post hoc comparison test (Sokal and Rohlf, 1995). Correlations between SCC and abiotic and biotic parameters were tested for significance by linear regressions.

Results

Chlorophyll *a* concentrations in the Oberer Arosasee reached a maximum in spring and early summer (Fig. 1). The concentration in the surface and middle layers decreased in July in 1998 and in August in 1999. During summer, chlorophyll *a* concentrations were low (0.5 – 7.0 mg l^{-1}) in the surface layer and middle layers, but higher in the deep layer in both years. After autumn turnover, chlorophyll *a* concentrations were low and uniformly distributed in the water column (0.5 – 1.0 mg l^{-1}). Pelagic POC concentrations ranged

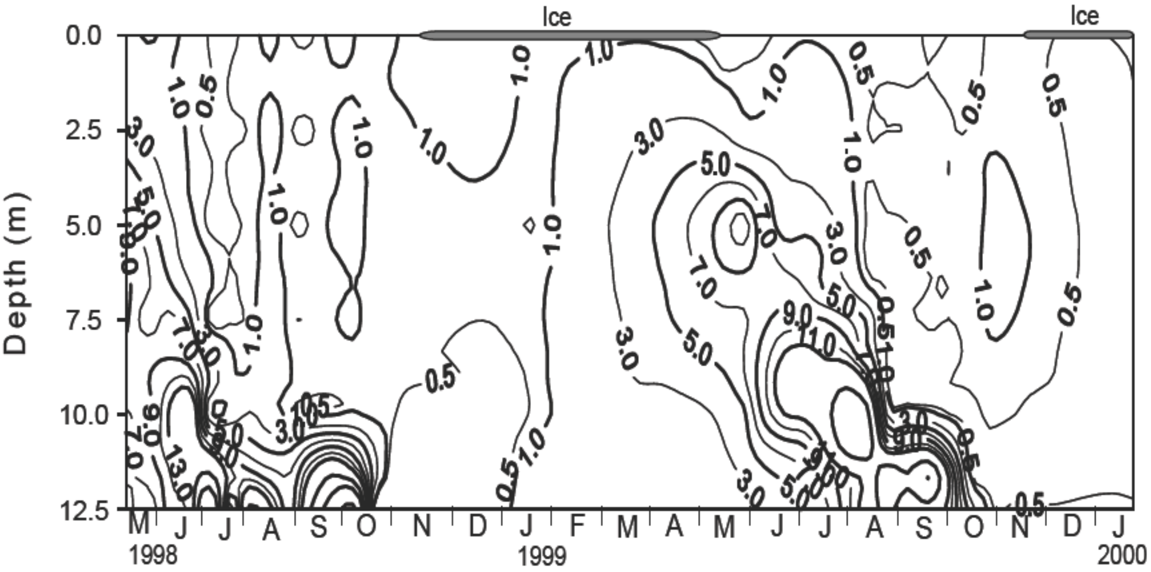

Figure 1. Distribution of chlorophyll *a* concentration (µg l^{-1}) in the Oberer Arosasee from May 1998 to February 2000.

from 0.2 to 1.3 mg l^{-1} and phytoplankton biomass from 0.08 to 4.0 mg l^{-1} with a high proportion of edible algal biomass at all times. Both parameters showed high values in the spring of 1998 and in early summer of 1999 (Fig. 2a).

In 1998, the population density of *D. galeata* was low in spring and increased considerably in late June to its highest abundance of 46 ind. l^{-1} (Fig. 2b). The density of *D. galeata* was relatively high for the rest of the open-water period but declined considerably in winter. In 1999, density increased in late June and reached its highest value of 31 ind. l^{-1} in late August. Adult females were rare, even in summer, never exceeding 12 ind. l^{-1} in 1998 or

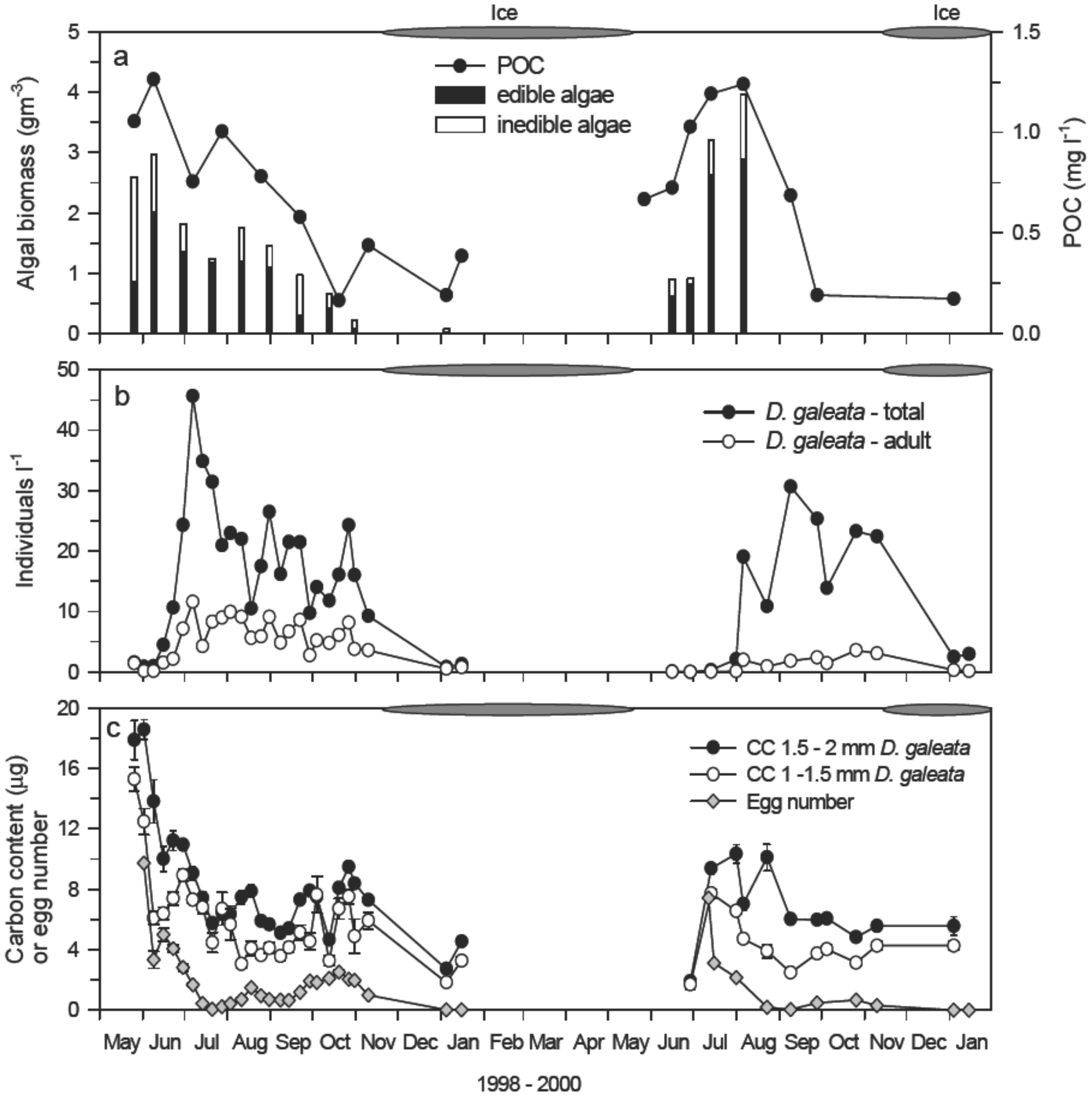

Figure 2. Seasonal variation in POC (line) and algal biomass (bars) (a); density of *Daphnia galeata* (b); number of eggs and carbon content (CC) of individuals for two size classes (1 – 1.5 mm and 1.5 – 2 mm) (c). Error bars equal ±1 standard error.

3.6 ind. l^{-1} in 1999. The average number of eggs per female was highest in June 1998 and July 1999, declining in both summers with low values (Fig. 2c). After autumn turnover, average number of eggs increased in 1998. Egg-bearing animals were rare during periods of ice cover.

Carbon content

The mean actual carbon content of individual *D. galeata* for two size classes (1 – 1.5 mm; 1.5 – 2 mm) was high in spring and then declined in summer to the lowest values of 5.10 µg C for 1.5 – 2 mm and 3.04 µg C for 1 – 1.5 mm (Fig. 2c). In autumn, the carbon content increased slightly for both size classes. In the spring of 1999, the carbon content was very low, but increased in August and declined again in autumn. *Daphnia galeata* had relatively low carbon content under periods of ice cover.

Linear regressions between the natural logarithm of the carbon content and the natural logarithm of the length were calculated separately for every sampling date (Table 1). On some dates, results of regression analysis between carbon content and length showed poor coefficients of determination, which was caused by the small size range of available animals present at that moment. The SCC of *D. galeata* was analysed both for (1) different slopes derived from each date from linear regressions and (2) a fixed slope of 2.92 derived from linear regressions estimated for all seasonal data (38 dates). When the slope of the different regression lines was fixed to a common slope, the explained variance was 71 %. SCC showed the same seasonal pattern as carbon content of the size classes and with values in the same range (Figs. 2c and 3b). The intercepts and the slopes differed among dates ($F_{38, 5210} = 138.6$; $P < 0.001$). Slopes declined toward early summer 1998, increased in July and August, and were more or less constant during the rest of the season. In 1999, slopes increased each month until September, and then declined (Fig. 3a, Table 1).

The SCCs of the *D. galeata* caught at different depths over each season were computed using carbon-length weight regressions (Fig. 3c). A test of parallelism showed that most slopes were not significantly different among the different depth strata for a given date (Table 1). After testing for significant differences among depths for each date, adjacent dates which did not significantly differ were pooled (Table 2). *Daphnia galeata* from the deep layer had a significantly higher SCC from July to September in 1998, as well as in September and October 1999, compared to the surface layer (Table 2). From mid August to mid November 1998, as well as in August and late September 1999, the number of eggs per individual were significantly higher in mid and deep layers than in the surface layer (Table 2).

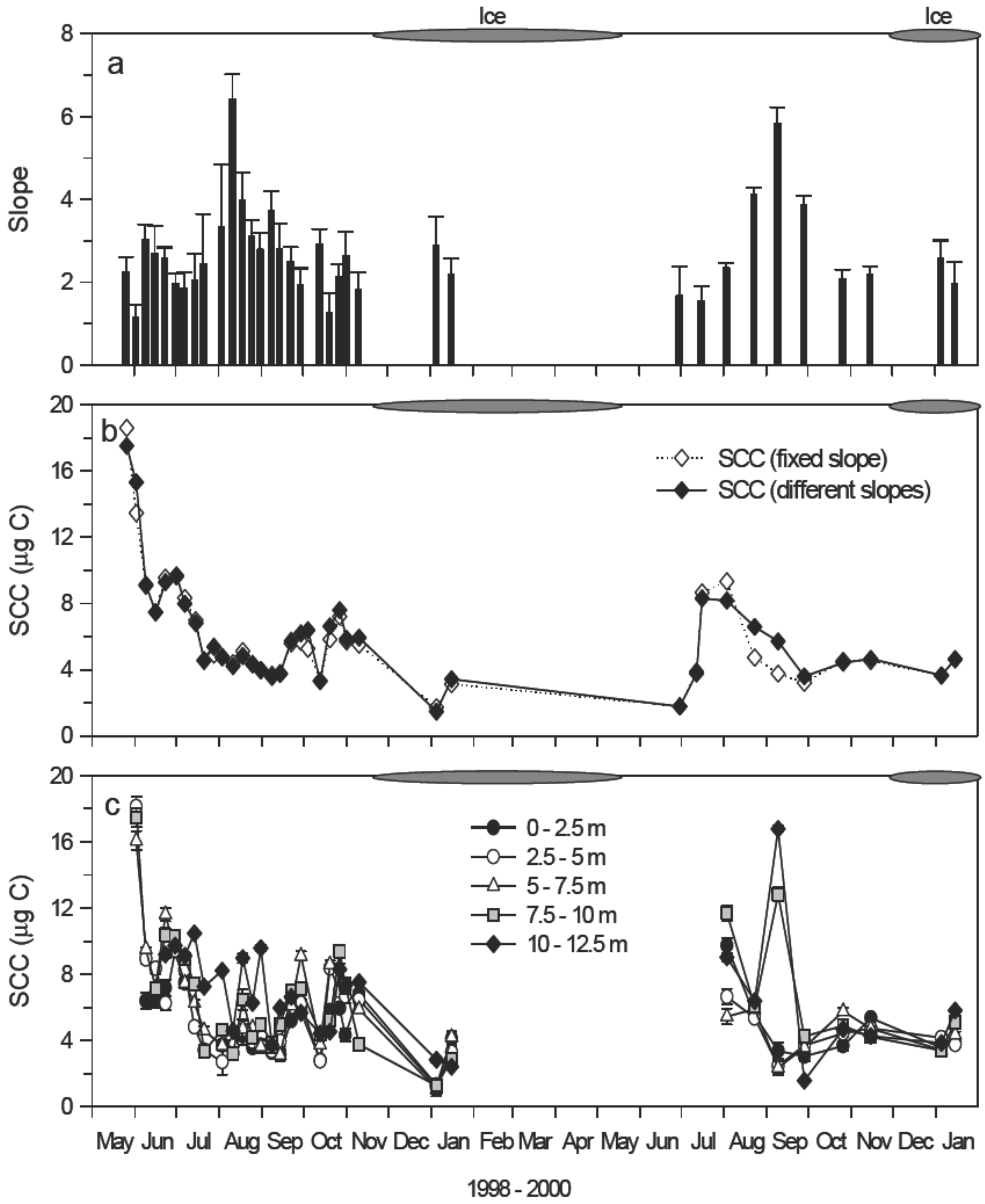

Figure 3. Seasonal variation in slope (*b*) (a), standard carbon content (SCC) of 1.5 mm *Daphnia galeata* individuals calculated using a fixed slope (2.92) and different slopes (b) and the seasonal SCC at 5 depths (c) computed from the carbon-length regression equation (ln C = ln *a* + *b* ln L) for each sampling date in the Oberer Arosasee. Error bars indicate ±1 standard error.

Comparing the SCC of the *D. galeata* population for different depth strata during day and night showed significantly higher SCC at night-time in the surface and middle layers in August, early September and October than at daytime (Fig. 4). In late September there was no day-night difference in the SCC.

Table 1. Carbon-length regressions for *Daphnia galeata* populations in the Oberer Arosasee on each sample date for all depths combined. Equation: $\ln C = \ln a + b \ln L$ (C in mg, L in mm). The intercept *a* represents the Standard Carbon Content (SCC) of an individual at 1.5 mm body length and *b* the combined slopes with the size range (mm) of the measured individuals; d. f., F, and *P* are the regression statistics and r the correlation coefficients. Comparisons of the slopes in the 5 depth strata of each date for significant differences were made with a Test of parallelism (P_b). * $P<0.05$, ** $P<0.01$, ***$P<0.001$; n. v. = no value, n. s. = not significant.

Date	Size range	$a_{1.5}$	b	d. f.	F	P	r	P_b
26-May-98	0.76 – 1.71	17.50	2.24	1, 60	35.57	***	0.61	n. v.
02-Jun-98	0.90 – 1.86	15.31	1.15	1, 77	15.01	***	0.40	n. s.
09-Jun-98	1.00 – 1.82	9.14	3.02	1, 68	61.89	***	0.69	n. s.
16-Jun-98	1.20 – 1.74	7.45	2.70	1, 78	16.58	***	0.42	n. s.
23-Jun-98	0.95 – 1.77	9.28	2.59	1, 103	102.17	***	0.71	n. s.
01-Jul-98	1.22 – 2.09	9.68	1.97	1, 106	60.51	***	0.60	n. s.
07-Jul-98	1.12 – 1.73	7.98	1.86	1, 126	22.93	***	0.39	n. s.
14-Jul-98	1.12 – 1.73	6.81	2.05	1, 102	10.22	***	0.30	n. s.
21-Jul-98	1.33 – 1.71	4.59	2.43	1, 99	3.94	**	0.20	n. s.
03-Aug-98	1.33 – 1.81	4.74	3.34	1, 57	4.91	**	0.28	n. s.
11-Aug-98	1.30 – 1.90	4.22	6.43	1, 132	117.97	***	0.69	**
18-Aug-98	1.37 – 1.86	4.83	3.97	1, 156	33.32	***	0.42	n. s.
25-Aug-98	1.16 – 1.94	4.31	3.12	1, 134	68.42	***	0.58	*
31-Aug-98	1.31 – 1.96	4.00	2.79	1, 139	45.60	***	0.50	n. s.
08-Sep-98	1.27 – 1.88	3.56	3.74	1, 143	68.64	***	0.57	n. s.
14-Sep-98	1.37 – 1.92	3.78	2.79	1, 140	19.07	***	0.35	n. s.
22-Sep-98	1.31 – 1.82	5.74	2.50	1, 137	51.26	***	0.52	n. s.
29-Sep-98	1.25 – 1.98	6.19	1.94	1, 94	23.72	***	0.45	**
13-Oct-98	1.24 – 2.03	3.32	2.92	1, 125	64.06	***	0.58	n. s.
20-Oct-98	1.22 – 1.90	6.62	1.26	1, 130	6.75	**	0.22	n. s.
27-Oct-98	1.14 – 1.84	7.59	2.12	1, 144	44.69	***	0.49	n. s.
01-Nov-98	1.28 – 1.90	5.86	2.64	1, 146	20.11	***	0.35	n. s.
10-Nov-98	1.29 – 1.86	5.92	1.82	1, 126	18.48	***	0.36	*
05-Jan-99	1.14 – 1.79	1.47	2.89	1, 215	17.24	***	0.27	n. s.
16-Jan-99	0.95 – 1.90	3.43	2.17	1, 179	27.22	***	0.36	n. s.
30-Jun-99	1.31 – 1.69	1.78	1.67	1, 3	5.42	**	0.80	n. v.
16-Jul-99	1.14 – 1.84	8.30	1.54	1, 89	17.99	***	0.41	n. v.
03-Aug-99	0.57 – 1.90	8.17	2.35	1, 304	428.31	***	0.77	n. s.
23-Aug-99	0.76 – 1.75	6.59	4.13	1, 287	664.33	***	0.84	*
09-Sep-99	0.91 – 1.71	5.71	5.82	1, 228	201.41	***	0.69	n. s.
28-Sep-99	0.99 – 1.84	3.59	3.86	1, 279	267.68	***	0.70	n. s.
26-Okt-99	0.76 – 1.86	4.41	2.08	1, 289	84.83	***	0.48	*
15-Nov-99	1.10 – 1.94	4.64	2.18	1, 144	107.63	***	0.65	n. s.
05-Jan-00	1.25 – 1.20	3.65	2.57	1, 141	34.88	***	0.45	n. s.
15-Jan-00	1.22 – 1.84	4.64	1.96	1, 124	13.97	***	0.32	*

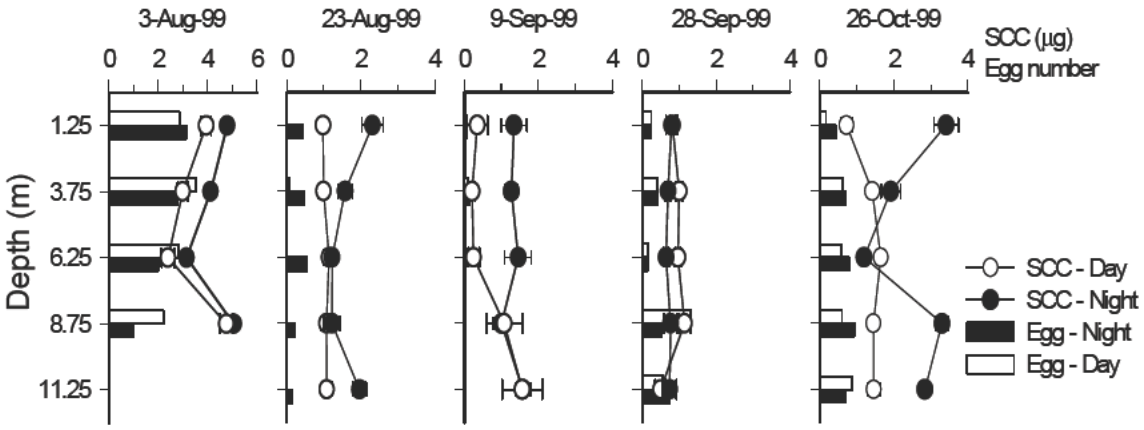

Figure 4. Standard Carbon Content (SCC) of 1 mm *Daphnia galeata* at different depths at mid-day and mid-night (lines) and mean number of eggs per individual (bars) in 1999 in the Oberer Arosasee. Error bars equal ±1 standard error.

SCC values include all body tissue of the females including the eggs in the brood pouch. Hence, we found a significantly positive correlation coefficient between SCC and the number of eggs (Table 3). Moreover, there were also a significantly positive relation with algal biomass, POC, chlorophyll *a* concentration and mean *D. galeata* length. Additionally, there was a significant negative correlations between SCC and slope, the density of *D. galeata* and water temperature.

Discussion

In this study, high intra- and interannual variability was found in the density, carbon content and number of eggs of the *D. galeata* population in the Oberer Arosasee (Fig. 2), comparable to the variation found in other studies of daphnids from lowland lakes (Geller and Müller, 1985; Berberovic, 1990; Boersma and Vijverberg, 1994b). Carbon content and number of eggs were high in the spring of 1998 when daphnids were rare and these parameters decreased toward summer as animal densities increased. Concomitantly, algal biomass and chlorophyll *a* also decreased. After autumn turnover in 1998 (mid September), the number of eggs of *D. galeata* and carbon content increased, whereas algal biomass remained low. A shift towards algae with better nutritional quality could be the reason for the relatively higher carbon content of *D. galeata* in autumn (Groeger et al., 1991). Carbon content increased only in August in 1999, and was constant after autumn turnover (end

Table 2. Standard Carbon Content (SCC) of *Daphnia galeata* (standardised to 1 mm body length) and egg number of measured individuals at different depths at mid-day calculated using a common slope of 2.92. Post hoc comparison was used to test for significant differences between the 0 – 2.5 m depth and the deeper strata following ANOVA. (* *P*<0.05, ** *P*<0.01, ****P*<0.001).

	1998					1999						2000
	15. Jun -	15. Jul -	15. Aug-	15. Sep-	15. Oct -	5. + 16.	3. + 23.	9.	28.	26.	15.	5. + 15.
Depth (m)	15. Jul	15. Aug	15. Sep	15. Oct	15. Nov	Jan	Aug	Sep	Sep	Oct	Nov	Jan
SCC												
0.0 – 2.5	2.45	1.31	1.08	2.14	1.79	1.34	2.31	1.01	0.99	0.94	1.68	1.27
2.5 – 5.0	3.03	1.38	1.12	1.93	1.91	1.40	2.13	0.58	1.19	1.52	1.44	1.29
5.0 – 7.5	3.07	1.52	1.12	1.73 *	1.99	1.72	2.04	1.28	1.14	1.79**	1.52	1.28
7.5 – 10.0	3.37 **	1.82 **	1.39 ***	1.60 **	1.62	0.79 *	2.84	1.48 ***	1.52*	1.58	1.33	1.36
10.0 – 12.5	3.14	2.56 ***	1.72 ***	1.90	1.77	1.29	1.67	2.21 ***	0.78	1.75 *	1.35	1.58
Egg number												
0.0 – 2.5	2.4	0.5	0.2	0.8	1.0	0.0	1.7	0.0	0.25	0.18	0.4	0.0
2.5 – 5.0	4.0	0.6	0.3	1.4 *	1.7 **	0.0	1.8	0.1	0.40	0.62	0.3	0.0
5.0 – 7.5	4.6 *	0.6	0.6 *	1.9 ***	2.0 ***	0.0	1.4	0.0	0.17	0.60	0.4	0.0
7.5 – 10.0	4.8 **	0.7	0.8 ***	1.9 ***	2.3 ***	0.0	0.9 **	0.0	1.31 *	0.61	0.1	0.0
10.0 – 12.5	2.3	0.8	1.6 ***	1.9 ***	2.3 ***	0.0	0.1 ***	0.0	0.57	0.88	0.2	0.0

	r	P
Density	-0.430	0.046
Mean length	0.037	0.013
Egg number	0.715	0.000
Temperature	-0.210	0.021
Chlorophyll *a*	0.304	0.007
POC	0.384	0.008
Slope	-0.244	0.007

Table 3. Correlation coefficients (*r*) between Standard Carbon Content (SCC) and life-history traits and abiotic and biotic field parameters ($P<0.05$, Analysis of variance).

September). The maximal value in 1999 was about half the maximal carbon content in 1998. In comparison to other studies of more eutrophic lake (Geller and Müller, 1985; Hessen, 1989; Boersma and Vijverberg, 1994b) the mean carbon content values of *D. galeata* in this high-mountain lake were low. Under the assumption that the carbon content and number of eggs measured in spring 1998 and summer 1999 indicate a period of no food limitation, the low SCC and fecundity during the other parts of the year implies that the *D. galeata* population were food limited during most the year (Duncan, 1985; Berberovic, 1990).

Contrary to laboratory studies, regression lines varied for intercepts and slopes during the year, as was shown before (Geller and Müller, 1985; Hessen and Van Donk, 1993; Boersma and Vijverberg, 1994b; Manca et al., 1994). However, the seasonal SCC patterns as well as the absolute values of the intercepts were similar irrespective of whether they were calculated with a fixed slope or with varying slopes (Fig. 3b). The calculated slope for SCC using all seasonal data was close to 3, which is the exponent for isometric growth. As the slopes changed through the year (Table 1), we found that the condition of larger *D. galeata* was low relative to smaller *D. galeata* in spring and early summer. In summer, when chlorophyll *a* concentrations decreased in the surface and middle layers, the regression lines were steeper, indicating that large animals were in better condition relative to small individuals. After turnover, the condition of smaller individuals increased as indicated by the decrease in slopes, even though the chlorophyll *a* concentration was low in the water column. Similar seasonal patterns in slopes are shown for other lakes (Geller and Müller 1985, Boersma and Vijverberg 1994b). In addition, the SCC and slopes from the regression lines were negatively correlated (Table 3), suggesting that when food conditions were good smaller animals benefited more than larger ones (Persson and Gunnar, 1980; Geller and Müller, 1985; Boersma and Vijverberg, 1994b).

In lakes with high food concentrations in the epilimnion, non-migrating daphnids are higher in carbon (Duncan et al., 1993) and protein (Guisande et al., 1991) per unit length. In many high-mountain lakes, as in the Oberer Arosasee, however, chlorophyll *a* accumulates in the deep layers during summer (Tilzer, 1973). In the Oberer Arosasee, when food was highest in the deep layer and low in the surface and middle layers (mid July to mid September 1998, September to October 1999), the SCC of *D. galeata* in the deep layer was significantly higher compared to the surface layer (Table 2). During these months, migration amplitude also was highest (Chapter VI). After autumn turnover, the SCC of *D. galeata* was equal throughout the water column. Since the number of eggs per individual did not show the same pattern and average number of eggs was low, changes in SCC may be mainly caused by a change in somatic carbon (Boersma and Vijverberg, 1994b). Further, after the autumn turnover, when the number of eggs per individual was significantly higher in the deep layer, SCC was not. Since the egg stage structure of measured *D. galeata* did not significantly vary between depths major differences of SCC are not expected to be associated with the egg stage structure (Tessier and Goulden, 1982).

These results indicate that migrating *D. galeata* and individuals that remain in the deep layer during night have an advantage over animals that stay in the upper layers in summer, since they can exploit the better food in the deep layer. The significantly higher carbon content in the surface and middle layers at night during this major migration period supports this. It seems that individuals with high body conditions migrate upwards at night, thus overcoming the costs associated with DVM (Loose and Dawidowicz, 1994). However, there was also a group of *D. galeata* in the deep layer during the night.

The density of *D. galeata* showed a negative relationship with SCC suggesting that competition may affect the condition of *D. galeata*. We found a significant positive correlation between SCC and egg number; *D. galeata* had more eggs when SCC was high. Food concentration, as chlorophyll *a*, POC and algal biomass showed a significant positive relationship with SCC. The average length of *D. galeata* correlated closely with SCC on a given date, which suggests that the reduction in mean adult length was caused by food limitation rather than by other factors such as positive size-selective predation by fish (Tessier et al. 1992). Nutritional deficiencies may be one of the main seasonal factors controlling *D. galeata* dynamics in the

Oberer Arosasee, rather than predation.

In general, we found that changing environmental conditions were almost immediately reflected in carbon-length ratios. Therefore, the carbon content is a reliable parameter to measure the animal's condition since there is no appreciable time lag between environmental changes and response (Hessen, 1989). Geller and Müller (1985) found that thermal lake stratification combined with an increase of temperature, food supply and egg production were the major factors influencing the carbon-length regressions of daphnids. Also in the Oberer Arosasee *D. galeata* carbon-length regressions changed mainly with the stratification state of the lake. In this high-mountain lake, similar seasonal dynamics in density, number of eggs and carbon content of *D. galeata* were found compared to lowland lakes, although high-mountain lakes have a shorter growing season. In the Oberer Arosasee with a chlorophyll *a* maximum in deeper layers, migrating daphnids and individuals remaining in deep layer have a better condition than daphnids from the surface layer. Hence, the main question arising from this study that needs to be answered is why daphnids migrate upwards in this high-mountain lake, since the food accessibility and condition are so good in the deeper water layers.

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Chapter V

On the cost of vertical migration: are feeding conditions really worse at greater depths?

with M. Boersma and P. Spaak

Abstract

The ultimate explanation for diel vertical migration (DVM) of zooplankton is the avoidance of visual predation in surface waters. Remaining in the cold and food-poor hypolimnion during the day, however, has demographic costs. Higher temperatures and food concentrations in the surface waters are thought to be the main reasons why daphnids move upwards at night. In this study, we investigated the growth condition of daphnids raised on seston taken from different depths from a lake with and without a deep-water chlorophyll maximum. Juvenile growth rates of *Daphnia galeata x hyalina* from the lake without a deep-water chlorophyll maximum were similar for all treatments. After temperature correction, however, growth rates were significantly higher on seston taken from the surface layers. In contrast, in the lake with the deep-water chlorophyll maximum *D. galeata* growth rates were higher in deeper strata, even after temperature correction. Although, this lake had a weak temperature gradient, *D. galeata* leaves the food rich strata at night and migrates into the surface food-poor environment. Invertebrate predation and oxygen depletion are probably not the reasons for the nocturnal upward migration into the surface strata. Therefore we assume that *D. galeata* migrates up to take advantage of higher temperatures.

Introduction

The pelagic habitat of lakes is characterised by pronounced vertical gradients in light, temperature, resources, competition strength and predation risk (Zaret, 1980; DeMott and Kerfoot, 1982; Geller, 1986). The vertical stratification of these factors strongly affects the vertical distribution of zooplankton. Many zooplankton species avoid the surface layers during daytime, migrating downward to deep layers and returning to surface waters at night (Gliwicz, 1986; Stich, 1989; Ringelberg et al., 1991a). The reaction to relative changes in light intensity (secondary phototaxis) is the primary physiological mechanism underlying this diel vertical migration (DVM) behaviour (Ringelberg, 1999). Changes in DVM behaviour can be induced by chemical cues exuded from potential predators (for a review see Pijanowska et al., 1993). The daytime distribution is determined largely by vertical differences in predation pressure (i.e. juvenile fish) or by the deleterious effect of ultraviolet radiation (UVR) in surface waters and is often related to zooplankton body size, transparency and pigmentation (Ringelberg, 1999). It is generally accepted that DVM is an adaptive predator avoidance strategy (Lampert, 1993). However, migrating deeper into cold and food-poor waters has pronounced costs (Orcutt and Porter, 1983; Gabriel and Thomas, 1988). These costs are expressed as a reduction in somatic growth and egg production due to reduced temperature and food in the deep daytime refuge, thereby resulting in an overall reduced growth rate (Stich, 1989; Ringelberg et al., 1991b; Loose and Dawidowicz, 1994). Hence, migrating species normally trade-off light-dependent mortality risks (i.e. visual hunting fish, UVR) against reduced growth to optimise their fitness (Ringelberg, 1999; Lampert et al., submitted).

The nocturnal upward migration of zooplankton is usually explained by the higher food quantities and higher temperatures in surface waters (Lampert, 1989). However, little is known how food quality changes in the water column, and vertical distribution of food resources are seldom measured in combination with migration patterns (but see Stich and Lampert, 1981; Gliwicz and Pijanowska, 1988; Schöps, 1999). Recent studies have demonstrated that resource availability may not necessarily be worse at greater depths (Williamson et al., 1996). This experimental study by Williamson and co-workers is one of the first to indicate that food availability can in fact be better in deeper compared to surface waters. This study also showed that the reduced food effect in the deeper daytime refuge might have been overestimated under natural conditions in many DVM studies. Thus, low temperature, rather than food availability, may be the most important cost for animals that migrate downward and stay in dark daytime refuge, as was already suggested by Kerfoot (1985).

Some lakes have deep-water chlorophyll maxima, especially during the summer months (Fee, 1976; Tilzer and Schartz, 1976; Williamson et al., 1996). For example, increased algal biomass in deeper strata is typical for alpine lakes and is attributed to higher nutrient availability and reduced solar radiation at depth (Tilzer and Schartz, 1976). These deep-water chlorophyll maxima may be dominated by filamentous cyanobacteria with low food value (Kasprzak et al., 2000), and hence chlorophyll or particulate organic carbon (POC) measurements might not be an adequate indicator of food availability for zooplankton. Quantitative food measurements do not consider edibility, changes in quality (e.g. biochemical composition) or microbial communities that might change with depth (Uehlinger and Bloesch, 1987; Bennett et al., 1990; Müller-Navarra and Lampert, 1996). The quality of natural seston as food for zooplankton can be highly variable and the importance of mineral and biochemical composition in algae for zooplankton growth is evident from recent studies (Boersma et al., 2001; Elser et al., 2001). An approach to quantify food quality is to raise zooplankton on natural seston and measure life-history traits (Boersma and Vijverberg, 1995; Müller-Navarra and Lampert, 1996).

Given the occurrence of deep-water chlorophyll maxima, we hypothesised that food conditions at depth in lakes with a deep chlorophyll maximum should be much better relative to those at the surface than in those lakes where these deep chlorophyll maxima are absent. This would imply that in lakes with a deep chlorophyll maximum the effect of temperature as a cost should be more pronounced than in those lakes that do not have higher food levels at depth. Hence, we addressed the question whether the feeding conditions at greater depths are as good as in surface water in a lake with and without a deep-water chlorophyll maximum. *Daphnia* species were raised at a standard temperature on seston collected from different depths. Thus, any changes in life-history traits should be caused by differences in food availability and not temperature. In the lake with a deep-water chlorophyll maximum we expected better *Daphnia* growth conditions when raised on water taken from deep strata compared to surface strata. In contrast, in the lake without a deep-water chlorophyll maximum we expected that growth conditions should be better on water taken from the surface layers.

Material and Methods

Field sampling

Two lakes differing in the distribution of algae over depth were sampled. The lake with a deep food maximum was the high-mountain lake Oberer Arosasee (Arosa, Switzerland, Winder and Spaak, 2001). The lake without a deep food maximum was the lowland lake Schöhsee (Plön, Germany, Lampert, 1988).

In the Oberer Arosasee, POC samples were taken at 6 depths (0, 2.5, 5, 7.5, 10 and 12.5 m) every third week during the open water period from May 1998 to October 2000 and once under the ice cover in winter (for analytical method see Uehlinger et al., 1984). Phytoplankton samples were taken from the six depths from June to August 1998 every third week using a 5-L Schindler trap. In summer 1998 zooplankton was sampled weekly at mid-day and mid-night from three stations around the deepest part of the lake at 2.5 m intervals from 0 to 12.5 m depth using a duo-closing net with 95 mm mesh size (Bürgi, 1983). A total of 300 L per depth stratum was collected; samples per depth stratum were pooled.

In the Schöhsee, vertical profiles of POC were measured fortnightly from April until October 1998 from 1, 5 and 12 m depth (for analytical method see Uehlinger et al., 1984). From June until August 1998 phytoplankton samples were taken fortnightly at 1, 5 and 12 m depth using a 32-L Schindler trap. At the same dates, zooplankton was sampled from 1 to 12 m depth at 1-m interval at mid-day and once in June and July at mid-night using a 10-L Schindler trap.

In both lakes, temperature was recorded from the surface to the bottom at 1-meter intervals on each sampling occasion. For phytoplankton identification, 100-ml lake water from each depth stratum were fixed with Lugol's solution and analysed with the Utermöhl settling technique (Rott, 1981). Biovolumes were estimated from cell dimensions and geometry; cell size and shape distinguished edible from inedible algal cells (Infante, 1973; Porter, 1973; Conover and Mayzaud, 1984). Zooplankton samples were concentrated and preserved in 96 % ethanol. At least 100 individuals of adult daphnids (if possible) were counted from each depth.

Growth experiment under natural food conditions

Using *Daphnia* from both lakes, we conducted two growth experiments during the summer (when vertical migration is strongest) in the laboratory with lake seston. For the Oberer Arosasee experiment we used a clone of *Daphnia galeata*, and for the Schöhsee experiment a *D. galeata x hyaline* clone. The experiments were carried out in flow-through chambers (170 ml) similar to those described by Lampert et al. (1988), with a flow rate of 40 ml h^{-1} and constant temperature conditions (Oberer Arosasee 18 °C; Schöhsee 20 °C). Fresh water was collected from the lakes every morning: in the Oberer Arosasee, with a deep-water chlorophyll maximum, at 5 depths (1.3, 3.8, 6.3, 8.8 and 11.3 m) and in the Schöhsee, without a deep-water chlorophyll maximum, from 1, 5 and 12 m. The water was pre-filtered through a 30-µm mesh sieve, to remove larger zooplankton and inedible algae, and used to fill the reservoirs of the flow-through systems. These reservoirs were placed in the dark to avoid photosynthesis, and stirred continuously to prevent sedimentation.

Third brood neonates of mothers acclimated to standard conditions (12:12 light : dark photoperiod, 1 mg C L^{-1}) were collected within 12 hours after birth. At the start of the experiment, ten neonates were transferred to each of four pre-weighed aluminium weighing boats. The boats were dried overnight at 60 °C, cooled in a desiccator and weighed to the nearest 0.1 µg with an ultramicrobalance. This provided the initial dry weight per animal. Five neonates were placed in each flow-through vessels and provided with lake water (seston) from the different depths. In the Oberer Arosasee we used eight replicates per depth and in the Schöhsee three replicates per depth. After three days these animals were removed from the vessels and placed in pre-weighed aluminium boats, dried and weighed. All animals of a vessel were pooled to reduce measurement errors. Dry weights were converted into somatic growth rates per day using the formula

$$g_j = (\ln(W_3) - \ln(W_0)) / 3,$$

where W_0 is the mass of the animals at day zero, W_3 the mass at the end of the experiment and 3 is the duration of an experiment in days. Juvenile growth rate was used as a measure of fitness, as it is strongly correlated to the intrinsic rate of population increase (Lampert and Trubetskova, 1996). Juvenile growth rates were corrected for *in situ* temperatures, using the relation between temperature and developmental time determined by Vijverberg (1980), under the assumption that somatic growth rates scale with temperature in a similar way.

Results

Vertical profiles in the lakes

In the Oberer Arosasee, a distinct thermocline was absent and vertical temperature gradients were weak (Fig. 1); the lake is dimictic with a 6-month period of ice cover. POC accumulates in deep layers, especially during the

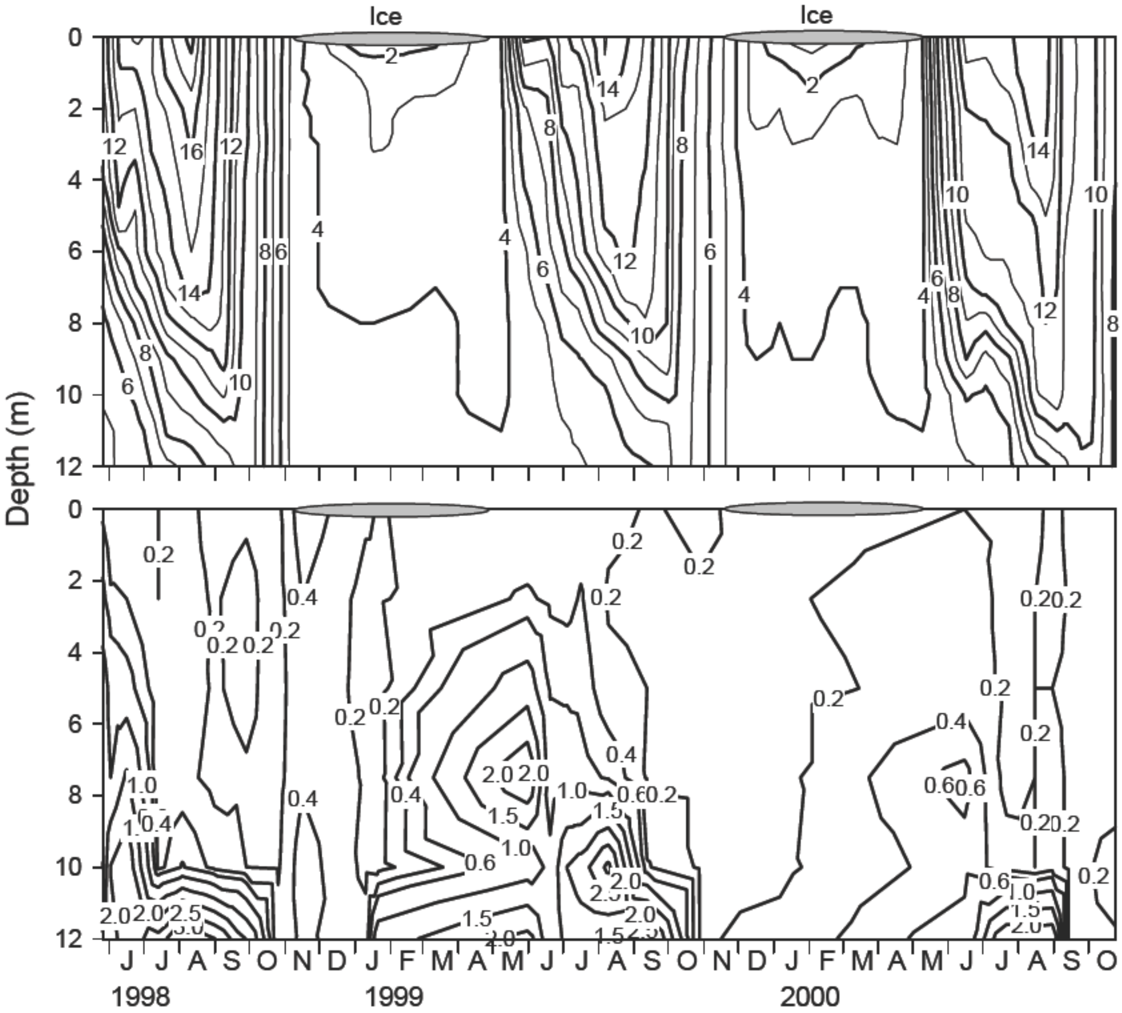

Figure 1. Isopleth plots of temperature (°C; top panel) and POC (mg L^{-1}; bottom panel) in the Oberer Arosasee from May 1998 to October 2000.

summer months (up to 3.6 mg L^{-1}). At this time, concentrations were low in surface waters (~0.2 mg L^{-1}). After the autumn turnover, POC was uniformly distributed throughout the water column (Fig. 1). The Schöhsee is a dimictic lake with a distinct thermocline during the summer months; thermocline depths increased from 8 m in May to 10 m in October (Fig. 2). POC concentrations were similar throughout the water column from April until October 1998 and between 0.7 and 0.4 mg L^{-1} (Fig. 2).

In the Oberer Arosasee, edible and inedible phytoplankton biomass increased with depth during the summer months (Fig. 3). During this period, *D. galeata* stayed in deep layers during the day and moved to the surface waters at night (Fig. 3). In the Schöhsee, edible phytoplankton biomass peaked slightly at 5 m depth and the inedible fraction increased with depth (Fig. 4). During the day, daphnids (mainly *Daphnia galeata x hyalina*) stayed in deeper strata and a part of the population moved upwards at night (Fig. 4).

Juvenile growth experiments

In the Oberer Arosasee, we measured considerable differences in somatic growth rates of *D. galeata* when raised on water taken from different depths

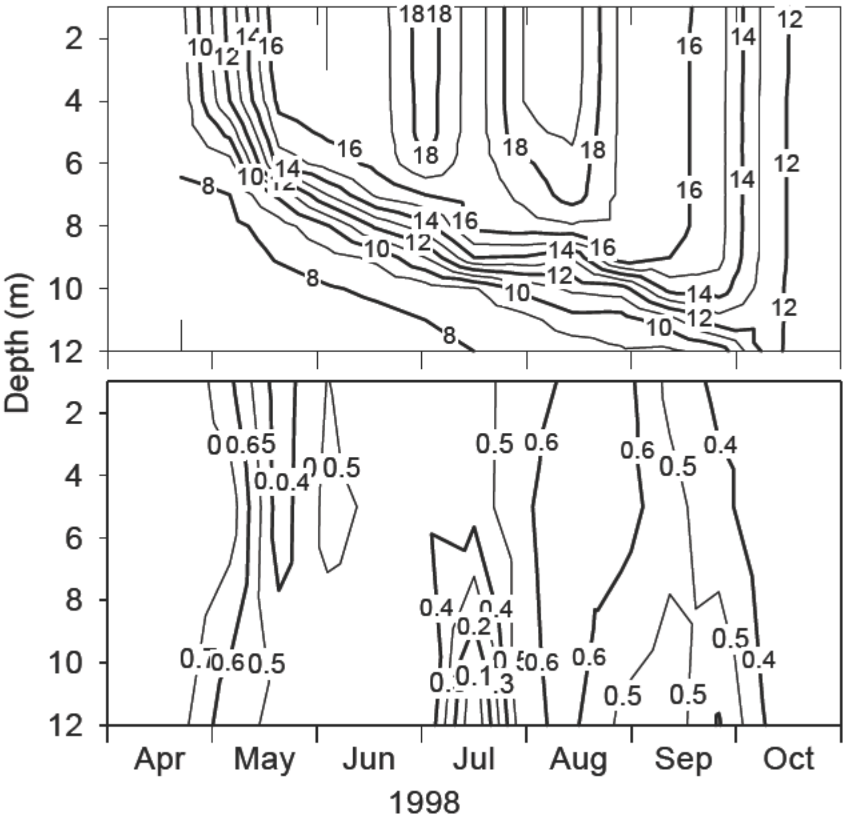

Figure 2. Isopleth plots of temperature (°C; top panel) and POC (mg L^{-1}; bottom panel) in the Schöhsee in 1998.

under constant temperature (18 °C) for both experiments in July, and we found a significant depth effect (Fig. 5, Table 1). At that time POC concentrations increased with depth and the temperature gradient was weak. Growth rate was strongly correlated with total POC ($r^2 = 0.83$, $P = 0.003$) and the POC fraction < 30 mm ($r^2 = 0.83$; $P = 0.002$). When we correct for the temperature differences in the different strata, the growth rates of the daphnids grown on seston from 8.8 and 11.3 m depths were still significantly higher than those on seston from the upper depths (Fig. 5). In the Schöhsee, growth conditions for daphnids were very similar among depths for the two dates in summer. We measured no significant effect of depth or date on growth rates (Fig. 6, Table 1). After temperature correction, growth rates on seston collected at 12 m depth were significantly lower (Tukey post-hoc comparison) than at 1 and 5 meters (Fig. 6).

Discussion

In this study we have shown that in summer juvenile growth rates of *Daphnia* were not necessarily lower when fed seston from deep-water depth strata, both in populations from lakes with and without deep-water chlorophyll

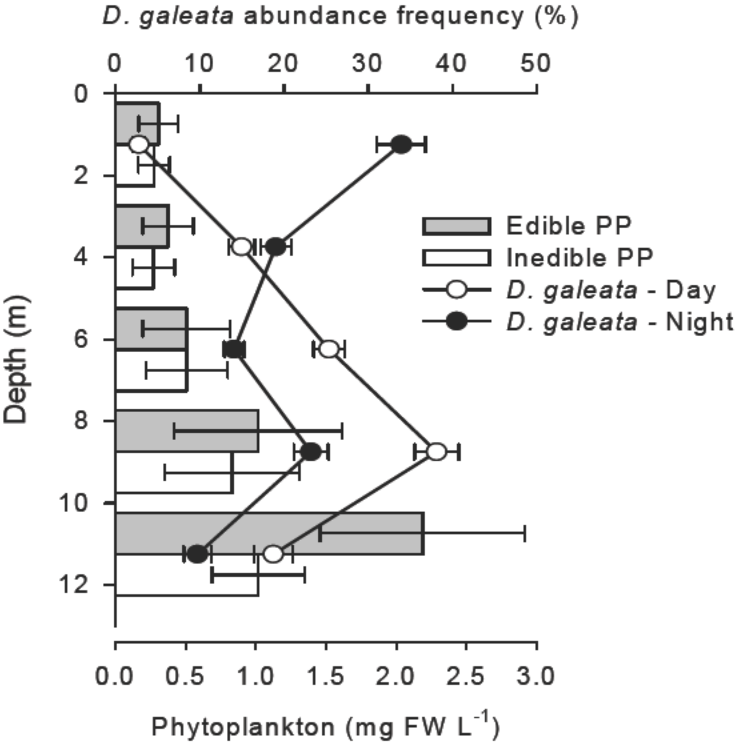

Figure 3. Vertical distribution of adult Daphnia galeata abundance frequency (%), and edible and inedible phytoplankton (PP) biomass (mg FW L^{-1}) in the Oberer Arosasee during the summer 1998 (June 23 – August 31). Error bars indicate standard errors.

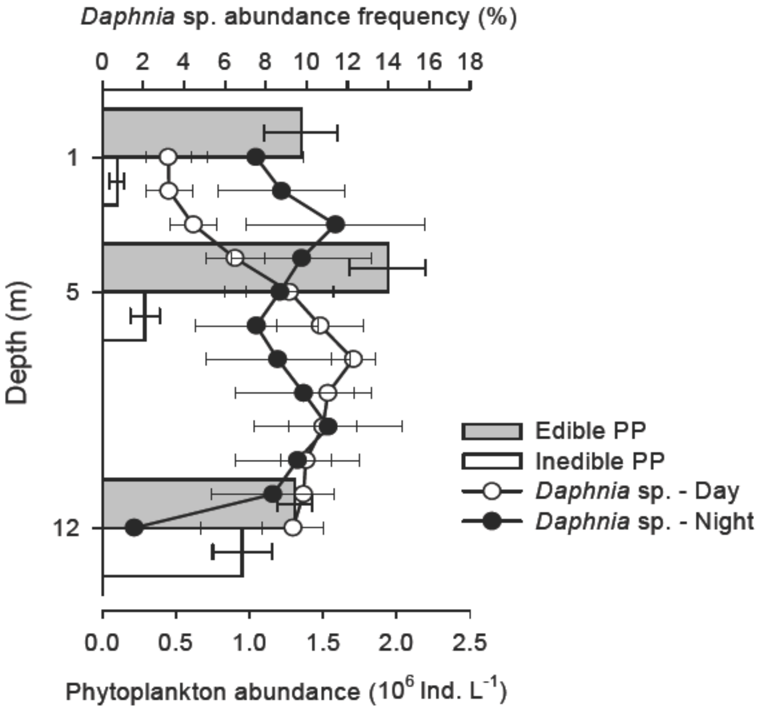

Figure 4. Vertical distribution of adult Daphnia sp. abundance frequency (%), and edible and inedible phytoplankton (PP) abundance (ind 10^6 L^{-1}) in the Schöhsee during the summer 1998 (June 3 – August 26). Error bars indicate standard errors.

maxima. Our results are in agreement with the study of Williamson et al. (1996), who also measured higher reproductive rates in the metalimnion compared to the epilimnion in a lake with a deep food maximum. These experiments provide evidence that under natural situations growing conditions are not necessarily worse in deeper strata compared to surface strata. In the Oberer Arosasee, deep-water food maxima were observed every summer over the three-year study (Fig. 1) and the edible and inedible phytoplankton biomass increased with depth (Fig. 3). Growth rates of *D. galeata* were significantly higher in deeper strata compared to surface waters (Fig. 5), suggesting that food conditions in the deeper strata were more than adequate. Quantitative food measurements (i.e. POC) explained a large part of the variation in *D. galeata* growth rate (~83 %). In the Schöhsee, without a deep-water food maximum (Figs. 2 and 4), growth rates of daphnids were not significantly different between depths (Fig. 6) and growth rates at 12 m were never lower during the growing season at standard temperature (Schöps 1999). Also in this lake, seasonal changes in POC concentration explained a significant part of the variation in *Daphnia* growth rate (Boersma et al., 2001).

The growth experiments were carried out at 18 or 20 °C and not at *in situ* temperatures. By computing the corrected growth rates we were able to estimate the effects of the temperature differences in the different strata. Comparisons between uncorrected and temperature corrected rates showed

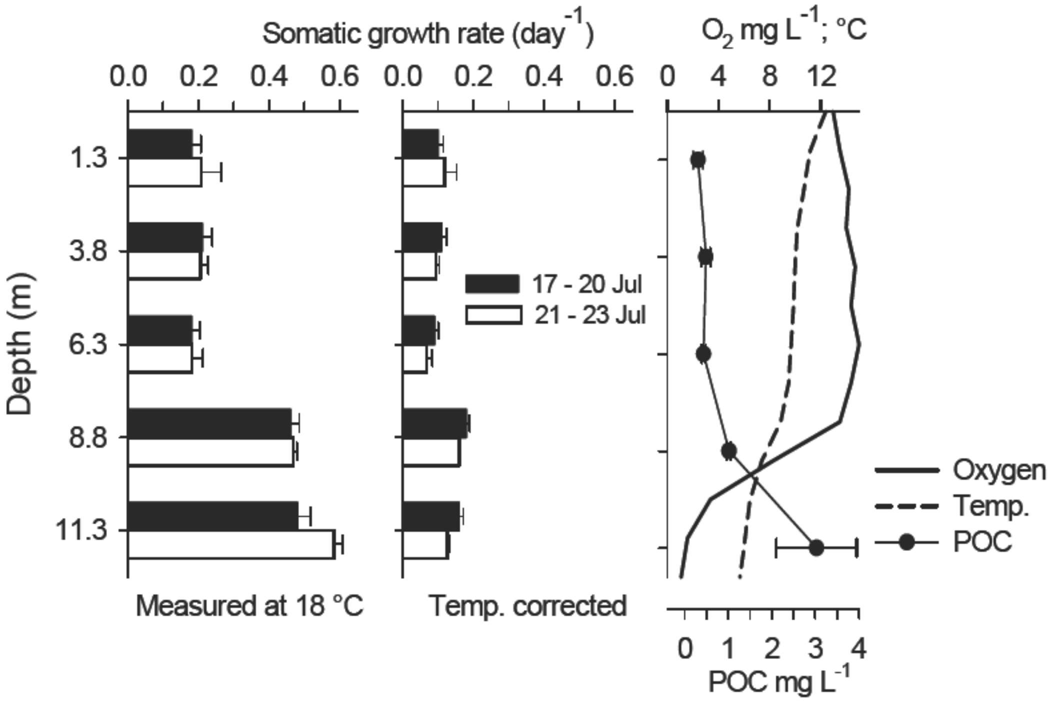

Figure 5. Sopmatic growth rates of *Daphnia galeata* cultured at 18 °C on lake seston collected from 5 different depths in the Oberer Arosasee in two periods in July 2001 (left panel). Growth rates are corrected for differences in temperature at the different depths in the middle panel. Vertical profiles of POC, temperature and oxygen are shown in the right panel. Error bars indicate standard errors.

that temperature indeed played an important role. In the Schöhsee, the temperature gradient was strong, and after the correction, growth rates were higher in the upper layers compared to the deep layer (Fig. 6). At night, a part of the *Daphnia* population migrated into the warmer surface waters (Fig. 4). In contrast, the Oberer Arosasee had a weak temperature gradient, and after temperature correction, the highest growth rates were still found in the deeper strata. According to the growth rates achieved on seston from the deeper strata in the Oberer Arosasee, daphnids should stay in deep water both day and night to maximise fitness. However, part of the *D. galeata* population migrated into the surface waters at night in this lake (Fig. 3). This upward migration was observed each summer during the three-year study (Chapter VI). This nocturnal upward migration in the Oberer Arosasee contradicts the hypothesis that migration occurs only when increased food levels at the surface make upward migration worthwhile, as suggested by Gliwicz and Pijanowska (1988). These authors showed that in lakes with fish, a weak temperature gradient and a high food concentration in deep waters that *Daphnia* stayed in deep waters both day and night. The upward

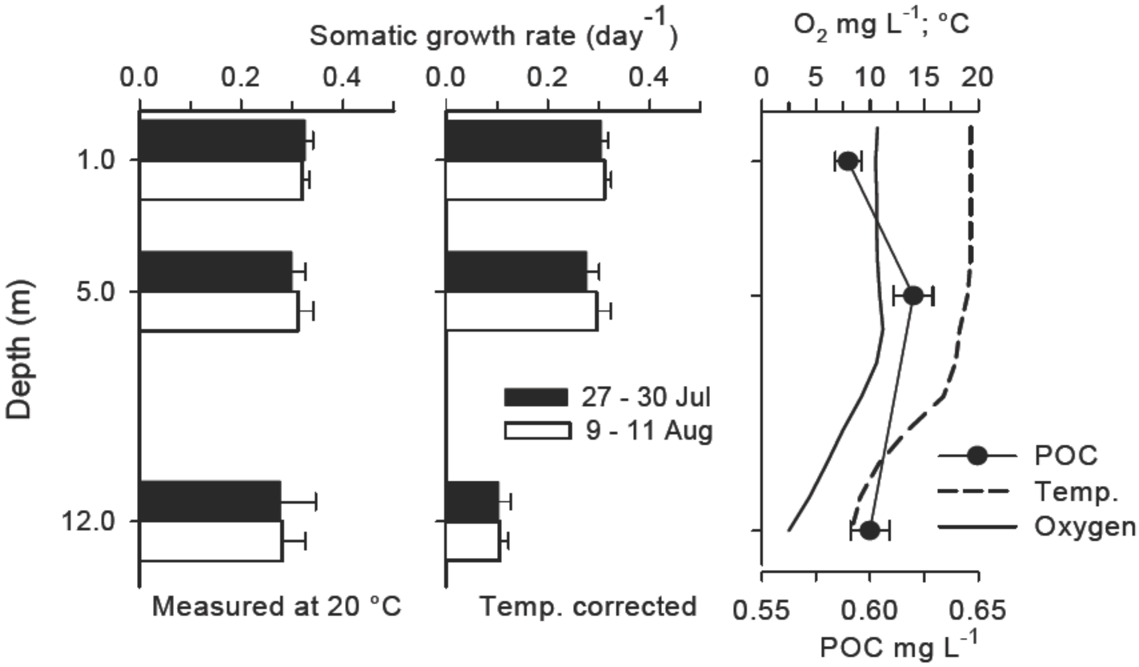

Figure 6. Somatic growth rates of *Daphnia galeata x hyaline* cultured at 20 °C on lake water collected from 3 different depths in the Schöhsee in two time periods in summer 1998 (left panel). Growth rates are corrected for differences in temperature at the different depths in the middle panel. Vertical profiles of POC, temperature and oxygen are shown in the right panel. Error bars indicate standard errors.

Table 1. Summary ANOVA table of growth rates of experimental animals as the dependent variable and date (random) and depth (fixed) as independent factors in the Oberer Arosasee and Schöhsee. Data are from 2 dates during the summer.

	Df	MS	df error	MS error	F	P
Oberer Arosasee						
Date	1	0.0161	73	0.0085	1.90	0.17
Depth	4	0.4510	73	0.0085	53.25	<0.001
Date x Depth	4	0.0072	73	0.0085	0.86	0.50
Schöhsee						
Date	1	0.0001	12	0.0046	0.03	0.88
Depth	2	0.0029	12	0.0046	0.64	0.54
Date x Depth	2	0.0001	12	0.0046	0.03	0.97

migration of *D. galeata* at night in the Oberer Arosasee might reflect avoidance of unknown costs of staying in the deep-water refuge. The intriguing question that remains is what are these costs and why do *D. galeata* move into surface waters at night if growing conditions are favourable in the deep layers?

Two methodological explanations need to be considered. First, we removed many of the inedible algae in our growth experiments by filtering the water to remove other zooplankters, hence, inedible algae could not interfere with feeding (Gliwicz, 1990). Therefore, it could be that we overestimated growth, especially at depths where the ratio between edible and inedible algae is low, as was the case in the Schöhsee at 12 m depth (Schöps, 1999). Secondly, to correct growth rates measured at laboratory temperatures with the ambient temperatures we used the formula from Vijverberg (1980). However, several temperature functions have been proposed to calculate egg development time of daphnids in relation to temperature, some of them are plotted in Figure 7 (Bottrell, 1975; Munro and White, 1975; Bottrell et al., 1976). Egg development time of *D. galeata* from the Oberer Arosasee measured in a laboratory experiment at 7 and 14 °C (S. Lass, unpublished results) was within the range of the other functions (Fig. 7). If we assume that the growth rates in the different depths need to be at least identical to make it worthwhile for the daphnids to migrate upwards at night, we can compute the temperature correction necessary to achieve this. This function of egg development time with temperature has been added to the ones shown in Figure 7, and it becomes clear immediately that this function is far outside the range of the other functions. Especially at higher temperature egg development time should be much faster compared to the other functions. In addition, Q_{10} of the hypothetical function was outside what have been measured in biological systems (Fig. 7 legend; Krogh, 1914). Therefore, it is very unlikely that the exact form of the temperature curve chosen here affected our results.

To achieve equal growth rates in the different depths, the temperature difference between the surface and deepest depth should be ~9 °C, with a steep temperature gradient (e.g. ~13 °C in the upper three depth strata and ~4 °C in the deeper strata). In the Oberer Arosasee, the average difference during the summer months between the surface and deepest depth is ~8 °C; however, the gradient is weak (Fig. 1). Nevertheless, the temperature differ-

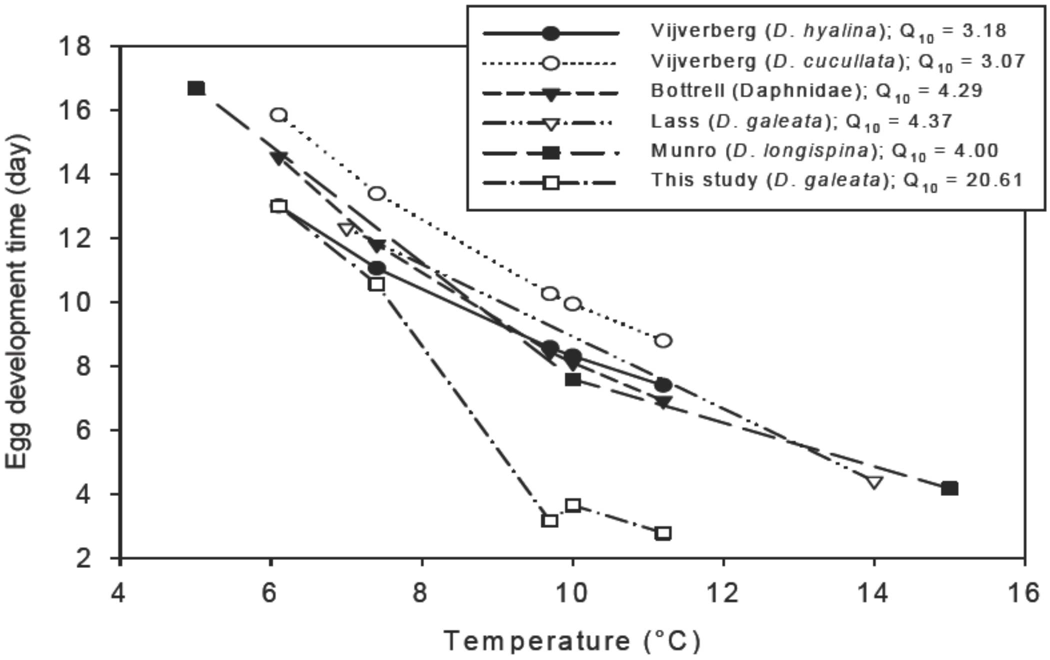

Figure 7. The duration of egg development at various temperatures for *Daphnia* spp. reported in the literature. Daphnidae (Bottrell et al., 1976); *D. galeata* (S. Lass, unpublished results), *D. longispina* (Munro and White, 1975); *D. cucullata* and *D. hyalina* (Vijverberg, 1980). Hypothetical egg development time of *D. galeata* from our experiment for equal growth rates in the different depth strata. For each function Q_{10} was calculated between the temperature range of 5 and 15 °C (for formula see Bottrell, 1975).

ence might be important to optimise fitness of the *D. galeata* population. Temperature explains greater than 80-90 % of the variation in embryonic egg development time of poikilotherms (Bottrell et al., 1976). The temperature in the Oberer Arosasee is always below temperature optima for growth rate and fecundity in *Daphnia* spp. (e.g. Geller, 1975; Orcutt and Porter, 1983; Yurista, 1999). Thus, the *D. galeata* population in the Oberer Arosasee may select the warmest waters to maximise fitness in the absent of light-dependent mortality risk, which are in surface waters at night.

Nocturnal migration into warmer water at night after feeding on benthic prey species was observed in larval fish species (Wurtsbaugh and Neverman, 1988). The upward migration promoted digestion, thereby allowing greater feeding and growth and resulted in three times faster growth than if they had remained in the cold hypolimnion. For *Daphnia*, Haney and Hall (1975) observed an increase in filtering rate up to tenfold at night. In contrast, Lampert and Taylor (1985) report no rhythmic feeding behaviour and no differences in filtration rates between day and night in *Daphnia*. Grazing experiments in the Oberer Arosasee indicated that *D. galeata* feed both day and night at all depths (M. Winder, unpublished data), suggesting that migration patterns can not be explained by diel rhythms in grazing activity. Feeding rates are linked to temperature and also to ambient food concentration (Beisner et al., 1997; Plath, 1999); filtration rates decrease at lower temperature and food availability. Due to the synergistic effect of food and temperature (Orcutt and Porter, 1984), we might have overestimated the growth rates in our experiment, especially for seston from the deep strata of the Oberer Arosasee.

A number of alternative reasons could exist for the observed vertical migration behaviour in the Oberer Arosasee. In the Oberer Arosasee, *Cyclops abyssorum*, the only predaceous zooplankter, may influence to the vertical migration behaviour of *D. galeata*. However, this copepod species also exhibits a nocturnal DVM behaviour with similar mean day and night depth as *D. galeata* (M. Winder, unpublished data). If *D. galeata* migrates to avoid predation pressure from *C. abyssorum*, it should have a different migration behaviour (Ohman et al., 1983). Avoidance of nocturnally predaceous invertebrates like *Chaoborous* may result in a reverse migration behaviour of the prey species (Neill, 1990); however, induction of DVM by copepods has not yet been observed.

In addition, low oxygen concentrations can restrict the vertical distribution of daphnids (Wright and Shapiro, 1990), although some species can counteract low oxygen concentration to a certain extent by producing haemoglobin (Sell, 1998). In the Oberer Arosasee, an anoxic layer develops below 10 m depth during the summer months. The anoxic area, however, did not prevent the daphnids from inhabiting the 10 - 12.5 m depth stratum, suggesting that they are highly tolerant to oxygen deficiency. Weider and Lampert (1985) observed that *D. pulex* species were able to regulate oxygen metabolism across a wide range of ambient oxygen concentrations, but below a critical oxygen concentration level of 3.5 mg L^{-1}, filtering and respiration rates in *D. pulex* decreased dramatically. A low oxygen layer may serve as a refuge from fish predation (Hanazato, 1992) in that fish are obligate aerobic animals. However, haemoglobin production requires energy and low oxygen concentrations are unfavourable for reproduction, thus influencing life-history traits such as a reduction in juvenile growth rates (Hanazato, 1995). The oxygen concentration in the Oberer Arosasee can explain, to a certain extent, the migration out of the deeper strata, but not the upward migration above 8 m depth, since above that layer oxygen concentrations and saturation were always above 8 mg L^{-1} and 85 %, respectively, during summer (Fig. 5).

In conclusion, our growth experiments showed that food availability in deep waters can be as good as in surface strata in lakes with and without deep-water chlorophyll maxima. Therefore, temperature might be the main cost for staying in deep refuge in lakes with a steep temperature gradient. However, also in a lake with a weak temperature gradient but overall low temperatures daphnids migrated upwards at night and may benefit from warmer temperatures to optimise fitness in the absence of light-dependent mortality risks. The main cause for this phenomenon still needs to be clarified.

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Chapter VI

Diel vertical migration—not a predator avoidance strategy in high-mountain lakes?

with P. Spaak, W. Mooij and H. R. Bürgi

Abstract

Several hypotheses have been put forward to explain the adaptive significance of diel vertical migration (DVM) behaviour in zooplankton and it is now generally accepted that DVM is a predator avoidance strategy in which species trade-off reduced reproductive output for lower light-dependent mortality. However, in lakes with subsurface food maxima, optimal conditions of temperature and food are uncoupled and zooplankton should allocate their time at different depths depending on the temperature gradient. Seasonal migration patterns of *Daphnia galeata* in a Swiss high-mountain lake (Oberer Arosasee) with a deep food maximum showed that both adults and juveniles exhibit DVM behaviour almost throughout the year. Daphnids did not increase migration amplitude when fish biomass or kairomone concentration was altered, neither in a fish stocking field experiment nor in *in situ* enclosures. In a large indoor mesocosm experiment that mimicked lake summer conditions, *D. galeata* from the Oberer Arosasee increased mean night depth when fish were added and did not migrate in the absence of fish. This behaviour suggests that the *D. galeata* population of this high-mountain lake responds to the presence of fish and migrates to deeper colder water. Our results suggest that the major benefit of night-time movement into surface waters of daphnids in the lake was an acceleration of embryo development due to warmer temperatures, but not a feeding gain. Whereas the day depths are determined when the combination of food and temperature is optimal, UVR may determined the timing of migration, since the time spent in surface and deeper strata is strongly synchronised with light intensity. Our results indicate that the migration can be explained by phototactic reaction and fish chemicals are not necessarily involved.

Introduction

Many freshwater and marine zooplankton reside in deep, dark water layers during the day and return to the surface at night. Whereas the proximate cause for this diel vertical migration (DVM) behaviour is a phototactic reaction to relative changes in light intensity (Ringelberg, 1999), several hypotheses have been proposed to explain the adaptive significance of DVM (e.g. metabolic and demographic advantages, energy conservation and predator avoidance, for a review see Lampert et al., 1988; Lampert, 1993). None of the metabolic advantage hypotheses have been substantiated by experimental studies (Orcutt and Porter, 1983; Stich and Lampert, 1984; Lampert, 1988). The predator avoidance hypothesis, avoiding surface waters during the day to reduce predation from visual planktivores such as fish, has strong empirical support (Lampert, 1993). This hypothesis explains diverse phenomena, including increased migratory amplitude with increased body size, colour and water transparency (Wright et al., 1980; Dodson, 1990), as well as seasonal migration patterns in which peak migration amplitudes often coincide with periods of most intense predator biomass (Bollens and Frost, 1989; Stich, 1989; Ringelberg et al., 1991b). The strongest evidence for the predator avoidance hypothesis can be attributed to the inducible and reversible DVM behaviour when prey species are exposed to potential predators or predator-specific chemical cues—kairomones (e.g. Dodson, 1988; Forward, 1993; Loose et al., 1993; De Meester and Cousyn, 1997). In a laboratory experiment, Loose (1993a) observed that the amount of fish present and hence kairomone concentration in the water determines the strength of migration amplitude in a *Daphnia* clone.

In addition, Hairston (1980) proposed that DVM in zooplankton might have evolved as a mechanism to avoid photodamage. Recent experiments have shown that ultraviolet radiation (UVR) avoidance is an additional factor that induces the daytime downward migration in *Daphnia* (Hessen, 1994; Leech and Williamson, 2001; Rhode et al., 2001). UVR may explain why zooplankton migrates vertically in arctic lakes during the summer in the absence of fish predation (Williamson et al., 2001). The deleterious effect of UVR, however, seems to be limited to clear or shallow waters, restricting this hypothesis to vertical migration patterns under specific conditions.

Other factors, like food availability, and therefore the nutritional status of animals, can modify the extent by which zooplankton respond to the presence of predator kairomones. Migration often ceases when food is limiting (Huntley and Brooks, 1982; Johnsen and Jakobsen, 1987) and starved animals respond much less to changes in light intensity than well-fed animals (Van Gool and Ringelberg, 1995). Plankton stay in deeper water during the day and ascend to surface waters at night to benefit from increased food concentration and higher temperatures. In filter-feeding plankton, higher food availability increases clutch size (Lampert, 1978) and higher temperatures increase the rate of development (Bottrell et al., 1976).

There are large demographic costs involved when swimming out of surface water layers with warmer temperatures and high food concentrations. This explains why simply staying deep during both day and night is not an evolutionarily stable strategy (Gabriel and Thomas, 1988). Costs due to spending half of the day in suboptimal environmental conditions are high because temperature and food availability are generally low at the day depth refuge, resulting in a prolonged egg development time and lower egg production due to cold and nutrient-poor waters, and thus, a lowered birth rate (Orcutt and Porter, 1984; Ringelberg et al., 1991b; Loose and Dawidowicz, 1994). Metabolic costs due to temperature differences are pronounced and may account for reduced reproductive output and fitness of migrating populations (Stich and Lampert, 1984; Dawidowicz and Loose, 1992b). However, food availability is not always highest in surface waters and deep-water food maxima are well documented in various lakes (Fee, 1976; Williamson et al., 1996). In lakes with high food concentrations in deep waters and weak temperature gradients, Gliwicz and Pijanowska (1988) showed that *Daphnia* did not migrate, but remained in deep waters day and night. In contrast, Williamson et al. (1996), who investigated a lake with high chlorophyll concentrations in the metalimnion and upper hypolimnion and a steep temperature gradient, observed that part of the *Daphnia* and *Diaptomus* population returned to the food-poor epilimnion at night. Different temperature gradients between the lakes studied by these authors, all of which contained fish, may account for the different migration patterns (Williamson et al., 1996).

Whereas in stratified lakes surface waters are always warmer (except under ice cover), the vertical gradient of food may change considerably. Deep food maxima result in a trade-off between rapid development but low energy input in surface waters and slow development but high energy input in deep layers. The behavioural response of zooplankton to deep algal maxima remains poorly understood. If food maxima are in deep-water layers, a model developed by Lampert et al. (submitted) predicts that herbivorous zooplankton should allocate the time spent in the deeper strata according to the temperature gradient and ascend to warmer water to optimise their fitness, even if fish predation pressure is low. High-mountain lakes often fulfil this criterion of deep-water algal maxima (Tilzer and Schartz, 1976) and are therefore suitable environments to answer questions concerning tradeoffs between food and temperature. In high-mountain lakes, deep-water algal maxima are attributed to high nutrient availability and reduced UVR in deep layers (Tilzer and Schartz, 1976). Salmonids are often the dominant fish species in high-mountain lakes, feeding mainly on benthic invertebrates and less on plankton (Fitzmaurice, 1979; Cavalli et al., 1998). Thus, to some extent the effect of fish predation and fish kairomone concentration is uncoupled in these lakes.

The objective of this study was to investigate the DVM behaviour of *Daphnia* in relation to vertical changes in temperature and food distributions and changing fish biomass in an alpine lake. Field observations were combined with *in situ* and laboratory enclosure experiments. Our study investigated trade-offs between fitness parameters in the context of DVM. Additionally, we used a model to predict the optimal depth that would maximise fitness for *Daphnia* under prevailing conditions. In particular, we assess the following hypotheses: 1) *Daphnia* from a high-mountain lake will react to fish kairomones with DVM, although predation risk is low. 2) The presence of a deep chlorophyll maximum will increase the migration amplitude of *Daphnia*. 3) The mean depth of the *Daphnia* population (day and night) is expected to be at the depth where the highest birth rates can be realised under predator free conditions.

Material and Methods

Study area

The study was performed in a dimictic high-mountain lake, Oberer Arosasee, Switzerland, located in the catchment of the River Rhine at an altitude of 1,734 m a.s.l. It is a small (surface area, 7.1 ha), relatively deep ($\text{depth}_{\text{max}}$ =

13 m, depth$_{\mathrm{mean}}$ = 7.3 m) oligotrophic lake with a period of ice cover lasting about 6 months. During the summer and winter an anoxic zone (< 0.5 mg oxygen L^{-1}) develops below 11 m. The crustacean zooplankton community consists of the herbivorous species *Daphnia galeata*, *Eudiaptomus gracilis*, *Bosmina longirostris* and the omnivorous *Cyclops abyssorum*. The fish community in the lake is dominated by salmonids, especially brown trout (*Salmo trutta*), charr (*Salvelinus alpinus*), and fewer rainbow trout (*Oncorhynchus mykiss*) and by minnow (*Phoxinus phoxinus*). Four times during July and August of each year ~110 kg adult brown trout and charr (> 250 mm total length) were stocked in the lake as game fish.

Field methods

During the open water period the vertical distribution of the zooplankton in Oberer Arosasee was sampled once a week in 1998, fortnightly in 1999 and monthly in 2000. During the ice cover period, samples were taken twice in 1999 and five times in 2000. In addition, zooplankton was sampled 3 or 4 days before and after fish stocking in 1998 and 1999 (total 7 - 8 observations per event). Samples were taken at mid-day (11:00 – 14:00 h) and mid-night (23:00 – 1:00 h) from three stations around the deepest part of the lake at 2.5 m intervals from 0 to 12.5 m depth using a duo-closing net (95 mm mesh size; (Bürgi, 1983). A total of 300 L per depth stratum was collected. Samples per depth stratum were pooled, concentrated and preserved in 96 % ethanol. On each sampling date, temperature was measured at 1-m intervals; chlorophyll *a*, DOC and POC were measured at 6 depths (2.5-m intervals) in 1998 and at 12 depths in 1999/2000 (for method see Uehlinger et al., 1984; Murray et al., 1986). Secchi depth was estimated on every sample date. Photosynthetic active radiation (PAR) was measured fortnightly in 1999 using a quantum solar irradiometer (Lamda Corp). An attenuation coefficient (K_{d320}) was estimated from average DOC concentrations between 0 and 5 m depth (Morris et al., 1995).

From every depth stratum, at least 100 *Daphnia* individuals per development stage (i.e. adult female, juvenile and male) were counted if available in the sample. Mean depth of each zooplankton species was determined on each sampling date by multiplying the number of individuals per stratum by the average depth of that stratum. These values were summed and divided by the total number of individuals counted in all strata.

Lake enclosure experiment

We installed 6 polyethylene tubes (1 m diameter, 10 m deep, volume 7,850 L) in the lake in August 2000. The tubes were open at the surface and closed with a net (200 mm mesh) at the bottom to exclude fish. The bottom of the tubes was below the thermocline, hence reducing water exchange. During installation, the tubes were slowly lowered into the lake, thereby enclosing the natural plankton community. Three replicate enclosures, with and without fish, were installed in a randomised block design. In the three fish treatments, fish presence was manipulated by enclosing 4 juvenile brown trout (~70 mm total length) in cages placed at 2, 6 and 8 m depths. The enclosures remained *in situ* from 14 – 30 August; the experiment was ended when periphyton on the walls of the enclosures began to cause visible shading. Enclosures and the lake were sampled for zooplankton abundance at 5-day intervals with a 5-L Schindler trap at 1-m intervals from the surface to 10 m depth. Temperature, oxygen, transparency and pH were recorded on days 2, 4 and 11.

Plankton Tower experiment

To study the influence of kairomones on DVM of *Daphnia galeata* from the Oberer Arosasee under controlled conditions, a large-scale experiment was conducted in the plankton towers at the Max-Planck-Institute in Plön, Germany (11.2 m high, 0.86 m diameter, Lampert and Loose, 1992) under long day light conditions (16 h light, 8 h dark). The summer conditions in the Oberer Arosasee were mimicked in the two towers, especially the deep chlorophyll maximum and weak temperature gradient. The food maximum was established at 6 – 11 m depth by adding the unicellular alga *Scenedesmus acutus* daily into the hypolimnion to a final concentration of 0.8 mg C L^{-1}. Both towers were stocked with a mixed *D. galeata* population from the Oberer Arosasee consisting of 12 genotypes that were isolated from the lake in spring 2001 and grown as clonal populations in the laboratory.

Daphnids were acclimated to the experimental temperature, light and food conditions for 10 days before sampling started. From day 1 to 10 both towers received the same treatment, i.e. without the presence of fish. Thereafter (day 12 – 16) a fish treatment was applied to one tower by enclosing 2 individuals of *Leuciscus idus* in each of two cages, one placed at 1.5 and one at 4 m depth. From day 17 – 21 the fish were moved into the cages of the other tower. Zooplankton samples were taken 10 h after initiation of day-time conditions and 3 h after initiation of night-time conditions. *Daphnia* were collected simultaneously in both towers using pumps (60 L per depth) and flow-through traps (Lampert and Loose, 1992) at 11 depths (0.6, 2, 3, 4.5, 5, 5.5, 6, 7, 7, 8, 9 and 10 m). At each depth, at least 100 daphnid individuals per stage (i. e. adult female, juvenile and male) were counted (if available) and clutch size was determined every second sampling day.

After 31 days part of the water was removed from the bottom (the lower 2 m) and refilled at the top to lower the depth of the food maximum. A new food maximum was established at 8 – 11 meters, replenished daily and the vertical distribution of daphnids (day and night) was determined for another 3 days with fish treatment in one tower and no fish in the other tower.

Modelling the fitness of Daphnia

We used a simple model to calculate the expected fitness conditions in the water column related to the reproductive output, which incorporates food-to-egg conversions and temperature-to-development time conversions. For the tower experiment, we used the food-fecundity relationship for *D. galeata* measured on a diet of *Scenedesmus* (Boersma and Vijverberg, 1995) for conversion of food concentration to egg numbers. We calculated birth rates b according to the Edmondson-Paloheimo formula (Paloheimo, 1974)

$$b = \ln (E + 1) / D$$

where E is the per capita egg ratio and D is the egg development time, calculated as

$$\ln D = \mathrm{LN}(A) - B * \mathrm{LN}(T^2)$$

where A and B are regression parameters and T is the mean temperature (°C) of the corresponding depth (Spaak and Hoekstra, 1997). D is a function of temperature and E is a function of food concentration. Death rate was set to zero. For the lake, growth rate was estimated from a life-history experiment with daphnids raised on natural seston from different depths (Chapter V) and corrected for lake temperature.

Statistical analysis

In the Oberer Arosasee significant differences in mean depth before and after the fish stocking events were analysed using one-way ANOVA. In the enclosure and tower experiments, the vertical distributions were analysed using principal components analyses based on the sample covariance matrix followed by an analysis of variance on the principal component scores to detect significant differences between treatments (Manly, 1997). We tested the effects Fish (present or absent), Time (day or night) and Food (high concentrations between 5.5 – 11m and between 8 – 11 m) on the vertical distribution of daphnids.

Results

Vertical distribution patterns in the lake

During the summer months a weak temperature gradient developed with a mean epilimnion temperature of 14 °C and a hypolimnion temperature of 7 °C (Fig. 1). Between ice break-up and autumn turnover, chlorophyll *a* concentrations always were higher in deeper layers and the gradient between

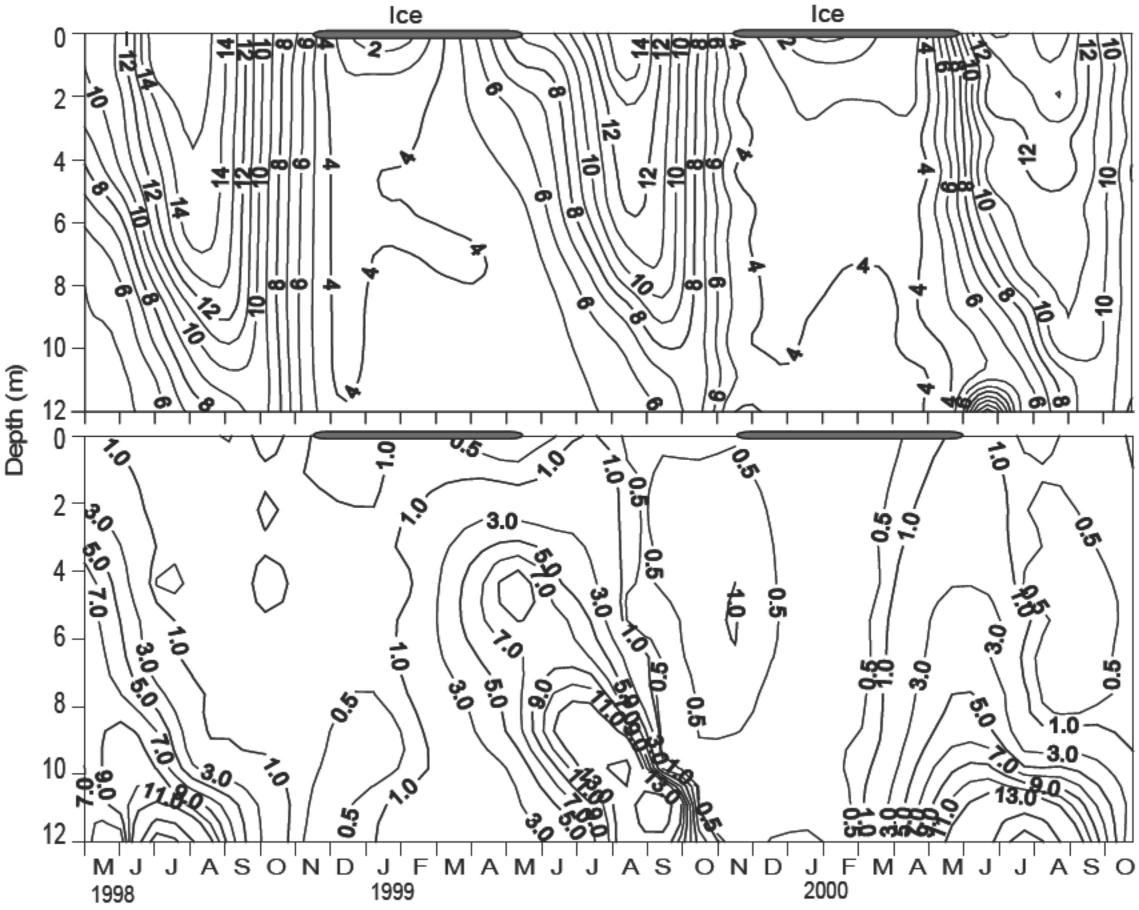

Figure 1. Temperature (°C; upper panel) and chlorophyll *a* (mg L^{-1}; lower panel) isopleths from May 1998 until October 2000 in the Oberer Arosasee.

upper and lower strata increased monthly (Fig. 1). During the summer months, chlorophyll *a* concentrations were below 1 mg L^{-1} in the upper 9 m and peaked in the deep strata (10 – 12.5 m); Secchi depth transparency varied between 2.9 and 12.0 m (data not shown). After autumn turnover and under the ice cover chlorophyll *a* was below 1 mg L^{-1} throughout the water column. This trend was repeated during the three years of observation. Juveniles and adults of *D. galeata* performed a daily migration almost throughout the whole three-year sampling period (Fig. 2); maximum migration amplitudes of adults and juveniles were 5.7 and 4.4 m, respectively. The distribution patterns indicate a seasonal trend with increasing mean day and night depths towards autumn for both adult and juvenile daphnids. Before and after the fish stocking, mean day depths ($F_{(1, 45)} = 0.22$; $P = 0.64$) and night depths ($F_{(1, 41)} = 0.001$; $P = 0.98$) as well as the migration amplitude ($F_{(1, 41)} = 0.088$; $P = 0.77$) of adult *D. galeata* were not significantly different (Table 1).

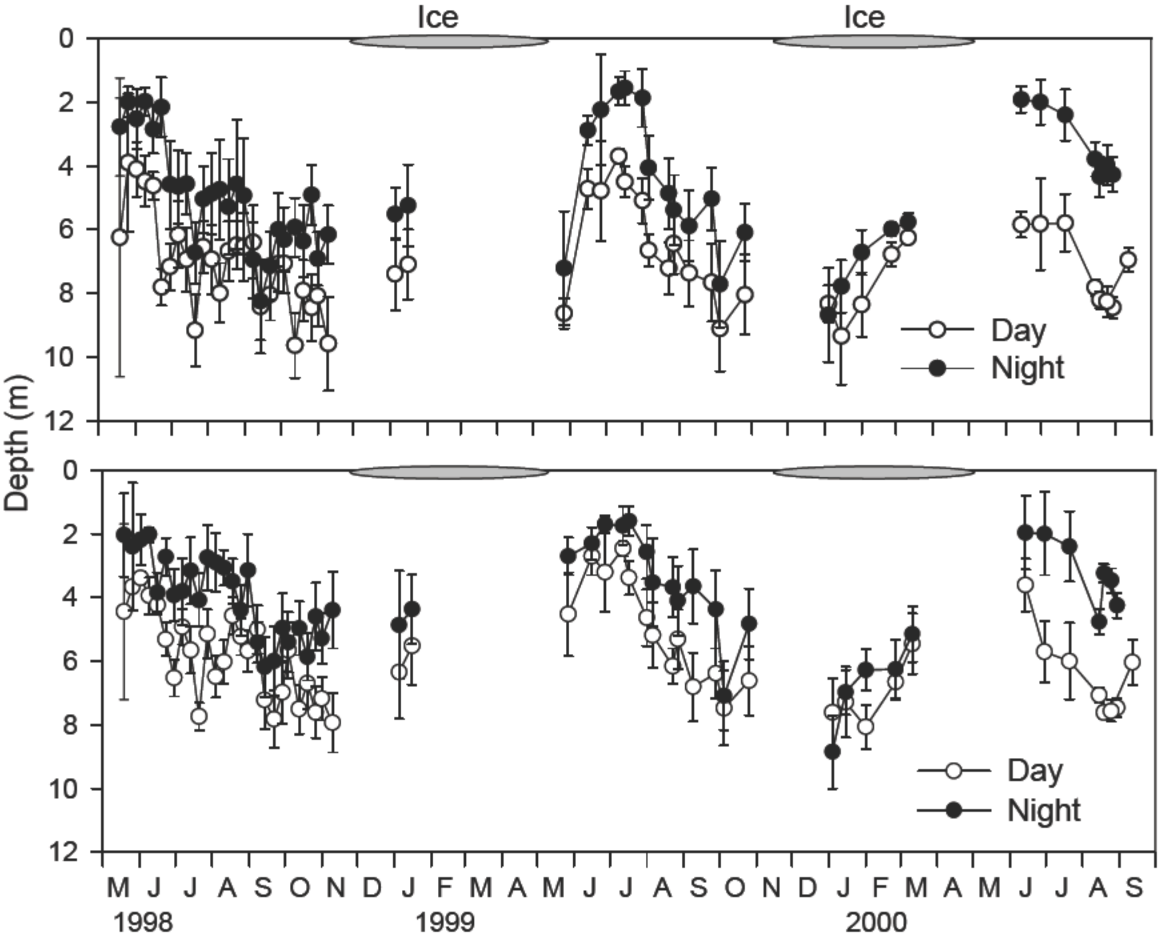

Figure 2. Mean day and night depths of adult (upper panel) and juvenile (lower panel) *Daphnia galeata* from May 1998 until September 2000 in the Oberer Arosasee. Error bars indicate 95 % CL.

Table 1. Average day and night mean depth (MD; m) and migration amplitude (m) of adult *Daphnia galeata* before and after of each fish stocking (FS) event in 1998 and 1999 in the Oberer Arosasee; n = number of observation; ± 95 % C.L.

		MD – Day		MD – Night		Amplitude	
Date	n	before FS	after FS	before	after FS	before FS	after FS
28 Jun – 3 Jul 1998	6	7.3 ± 0.6	7.7 ± 1.3	4.1 ± 1.3	4.9 ± 1.1	3.3 ± 0.7	2.8 ± 1.2
13 – 18 Jul 1998	6	8.0 ± 1.0	8.5 ± 1.3	4.8 ± 1.2	6.7 ± 1.0	3.2 ± 0.9	1.8 ± 0.8
29 Jul – 3 Aug 1998	6	8.1 ± 1.1	7.6 ± 1.1	6.3 ± 1.1	5.4 ± 1.2	1.8 ± 1.0	2.2 ± 1.2
27 Jun – 4 Jul 1999	8	4.5 ± 0.5	4.2 ± 0.3	2.3 ± 0.5	1.8 ± 0.3	2.2 ± 0.6	2.4 ±0.2
12 – 18 Jul 1999	7	3.9 ± 0.2	4.4 ± 0.5	2.0 ± 0.5	1.6 ± 0.6	1.9 ± 0.4	2.8 ± 0.3
2 – 7 Aug 1999	6	5.6 ± 0.6	6.7 ± 0.5	2.5 ± 1.3	3.5 ± 1.2	3.1 ± 0.9	3.1 ± 0.8
23 – 28 Aug 1999	6	7.6 ± 09	6.5 ± 0.9	5.9 ± 1.1	5.7 ± 1.0	1.6 ± 0.9	1.2 ± 0.2

Enclosure experiment

During the experiment the vertical temperature profile of the enclosures and the lake were similar; POC was higher in the enclosures than in the lake, but did not vary significantly with depth (Fig. 3). Oxygen concentration decreased from the surface to 10 m depth with values between 11.0 – 1.4 mg L^{-1} in the lake and 8.9 – 2.8 mg L^{-1} in all enclosures. The presence of fish in the enclosures had no significant effect on the vertical distribution of adult daphnids ($F_{(11, 34)} = 0.35$; $P = 0.95$; Fig. 3). Average mean day depths in all enclosures were around 6.8 m. At night, daphnids were evenly distributed throughout the water column with mean depths of around 5 m. Time (day, night) significantly effected ($F_{(11, 34)} = 16.81$; $P < 0.001$) the vertical distribution pattern. In the lake, adult daphnids had a pronounced daily vertical migration ($F_{(4, 4)} = 175.6$; $P = < 0.001$; Fig. 3), with a mean day depth of 8.2 m and a mean night depth of 4.1 m, and thus a higher migration amplitude. Temperatures were around 11 °C and 13 °C at the mean day and night depths (Fig. 2). Juvenile daphnids did not react to the presence of fish in the enclosures ($F_{(10, 32)} = 0.399$; $P = 0.94$; data not shown). However, vertical distribution patterns of juveniles were significantly different between day and night in the enclosures ($F_{(10, 32)} = 18.99$; $P < 0.001$) with a mean day depth of 6.6 m and a night depth of 4.2 m.

DVM correlation with environmental parameters

Mean day and night depths of adult and juvenile daphnids in the lake correlated significantly with temperature and chlorophyll *a* gradients in the water

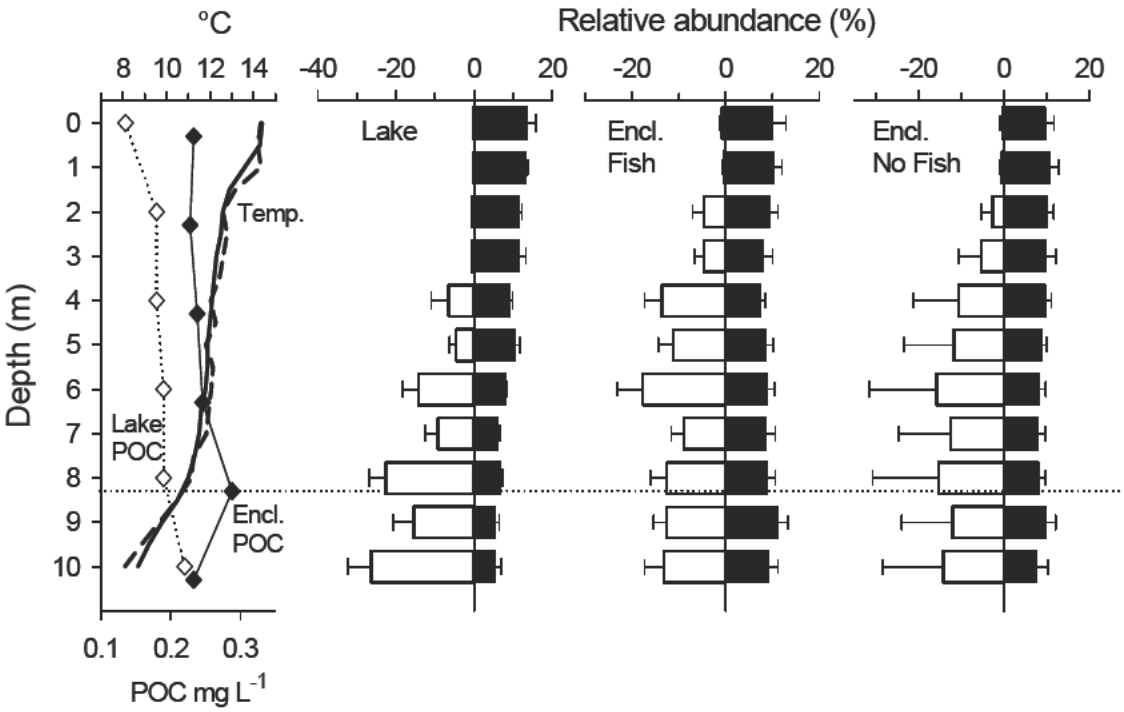

Figure 3. Average vertical distribution of temperature (lake solid line and enclosure dashed line) and POC in the lake and enclosures and of adult *Daphnia galeata* during day (open bars) and night (filled bars) in the lake and in the enclosures with and without fish (n = 4). Error bars indicate standard errors.

column of the Oberer Arosasee (Fig. 4; Table 2). Mean day- and night-depth of daphnids decreased, when the temperature difference between the upper (0 – 4 m) and lower (4 – 12 m) strata increased. In addition, migration amplitude of adults and juveniles significantly increased with increasing temperature gradients in the water column. Also the migration amplitude of adult daphnids correlated significantly with chlorophyll *a* gradients and the amplitude decreased when food was more homogenously distributed throughout the water column (Fig. 4; Table 2). There was a strong positive linear correlation between mean day depths of adult and juvenile *D. galeata* with Secchi disc transparency; but migration amplitude did not correlate with Secchi depth (Fig. 4; Table 2). The attenuation depth of UV_{320} did not correlate with mean depth of either adults or juveniles (Table 2).

Tower experiment

Most adult *D. galeata* females resided near the thermocline at the edge of increasing food concentration (5 – 5.5 m depth) during both day and night in the absence of fish kairomones (Figs. 5 and 6). The daytime vertical distribution of adults was significantly influenced by the presence of fish chemicals (Figs. 5 and 6; Table 3). The animals migrated into deeper strata during

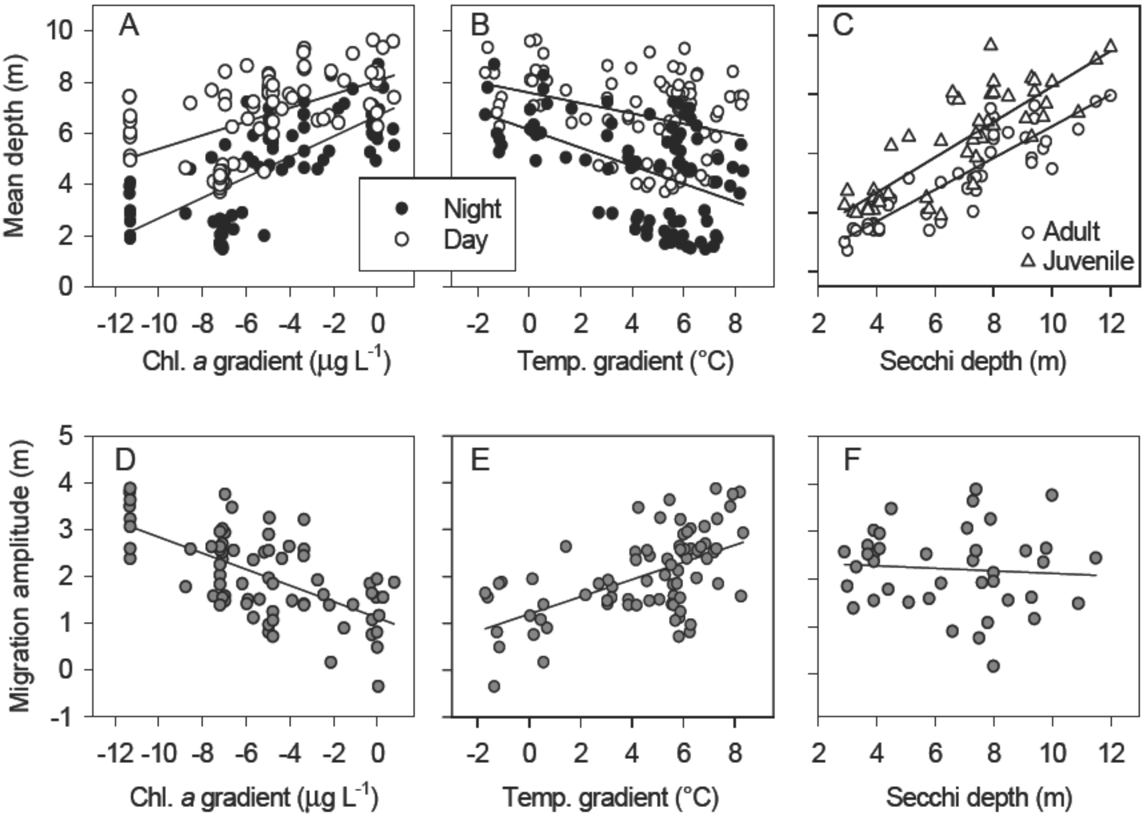

Figure 4. Relations between chlorophyll *a* (Chl. *a*) gradient (A) and temperature gradient (B) with mean depth (day and night) of adult *Daphnia galeata* in the Oberer Arosasee. Secchi disc transparency with mean day depths of adult and juvenile *D. galeata* (C). Relations between chlorophyll *a* gradient (D), temperature gradient (E) and Secchi disc transparency (F) with the migration amplitude of adult *D. galeata*. Temperature and chlorophyll *a* gradients result from difference between the upper (0 - 4 m) and lower (4 - 12 m) layers in the Oberer Arosasee. Given are dates from 1998 and 1999; for regression statistics see Table 2.

the day, residing at temperatures between 8 and 10 °C and returning to the thermocline depth (5 – 5.5 m) at night-time. This migration was reversible after fish were removed and added to the other tower (data not shown). After maximum food concentration was lowered to between 9 and 11 m, the main part of the adult population in the fish treatment followed the food and stayed at 8 m depth where temperature was around 8 °C. At night, some *D. galeata* moved upwards and around 25 % remained at their day-depth (Figs. 5 and 6; Table 3). A smaller part of the population in the non-fish treatment followed the food downwards and remained there day and night. In contrast, juveniles and males did not respond to fish chemicals or food by changing their vertical positions in the towers (Fig. 6; Table 3).

Table 2. Regression analyses of adult and juvenile *Daphnia galeata* mean depth and migration amplitude in 1998 and 1999 in the Oberer Arosasee on environmental independent variables. T = time, D = daytime, N = night-time, n = number of analyses, r = coefficient of determination, ns = not significant.

		Adults			Juveniles		
	T	n	r	P	n	r	P
Mean depth (m)							
d Chl. *a* (μg L^{-1})[1]	D	82	-0.53	<0.0001	82	-0.56	<0.0001
	N	82	-0.67	<0.0001	82	-0.60	<0.0001
d Temp. (°C)[2]	D	84	-0.34	<0.002	84	-0.42	<0.0001
	N	84	-0.50	<0.0001	84	-0.60	<0.0001
Secchi depth (m)	D	47	0.85	<0.0001	47	0.85	<0.0001
UV Z1%(m)[3]	D	16	-0.04	ns	16	-0.15	ns
Migration amplitude (m)							
d Chl. *a* (μg L^{-1})[1]		76	-0.64	<0.0001	82	-0.10	ns
d Temp. (°C)[2]		77	0.57	<0.0001	84	0.32	0.003
Secchi depth (m)		41	0.08	ns	45	0.40	0.006

[1] Chlorophyll *a* difference between the upper (0 – 4 m) and lower (4 – 12 m) strata.
[2] Temperature difference between the upper (0 – 4 m) and lower (4 – 12 m) strata.
[3] The depth to which 1 % of the incident 320-nm surface irradiance penetrates.

Discussion

In this study, we observed DVM in the *Daphnia galeata* population of the high-mountain lake Oberer Arosasee throughout most of the year during all three years of the study (Fig. 2). The migration amplitude varied over the season; nevertheless, during the day daphnids stayed always in deeper strata and migrated to shallower depths at night, except for a few dates. This is in contrast to many studies that have documented DVM behaviour only during the summer months when fish predation pressure is high (e.g. Stich, 1989; Ringelberg et al., 1991a; Field and Prepas, 1997). It is likely that the uncoupled food and temperature optima in the Oberer Arosasee (Fig. 1) cause the continual migration behaviour of daphnids. The subsurface food maximum results in a trade-off between high-energy availability and slow development rate in deep cold layers. The day depths of daphnids are determined in such a way that the combination of food and temperature is optimal, whereas at night, daphnids moved into warmer, food-poor surface layers. The fact that the migration pattern of daphnids in the lake is synchronised

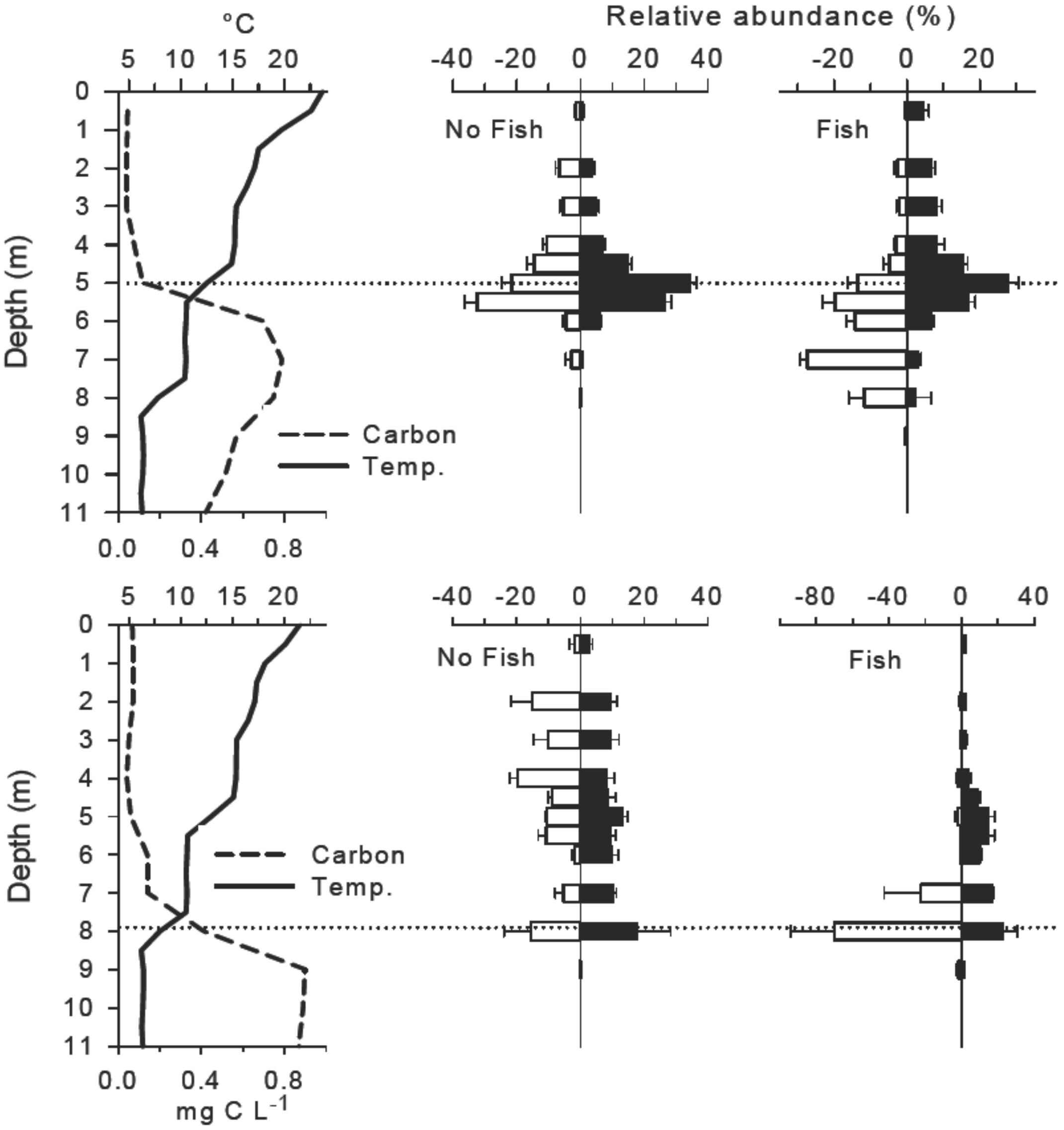

Figure 5. Mean values of carbon and temperature distribution in both plankton towers over the duration of the experiment and average vertical distribution of adult *Daphnia galeata* during day (open bars) and night (filled bars) in the absence and presence of fish (n = 4 x 2 towers) with food maxima below 5.5 m (top panel) and food maxima below 8 m (n = 3 x 1 tower; bottom panel). The dotted line indicates depth of the thermocline; error bars indicate standard errors.

with changes in light intensity, i.e. with dawn and dusk, suggests that a light-dependent mortality factor (UVR, visual hunters) has to be involved in their vertical dial distribution.

The harmful effect of sunlight was one of the first hypothesis put forward to explain the adaptive significance of DVM (Huntsman, 1924; Hutchinson, 1967) and recently is has been confirmed experimentally that UVR alters vertical movement in *Daphnia*, including juveniles (Leech and Williamson, 2001; Rhode et al., 2001). The hazardous effect of UVR on

Table 3. Tower experiment. Results of three-way ANOVAs to test for the effect of Time (day, night), Fish factor (yes, nor), Food (high concentration from 5.5 – 11 m, and from 8 – 11 m) and their interactions on the factor scores resulting from PCA analysis from the vertical distribution of adult and juvenile Daphnia galeata.

	Adults				Juveniles			
	df	MS	F	P	df	MS	F	P
Time	1	4.89	15.31	<0.001	1	0.481	0.53	0.47
Fish**f**actor	1	7.04	22.03	<0.001	1	0.256	0.28	0.59
Food	1	38.44	120.29	<0.001	1	1.642	1.8	0.18
T x Ff	1	4.37	13.69	<0.001	1	0.030	0.03	0.86
T x F	1	1.55	4.84	0.031	1	1.210	1.32	0.25
Ff x F	1	4.05	12.69	<0.001	1	2.798	3.06	0.08
T x Ff x F	1	3.55	3.55	0.001	1	0.302	0.33	0.57
Error	73	0.32			73	0.910		

zooplankton is especially pronounced during summer in freshwaters at high altitude or latitude (e.g. Siebeck et al., 1994; Cabrera et al., 1997; Zagarese et al., 1998; Williamson et al., 2001). Furthermore, Williamson et al. (2001) observed diel migrations of *Cyclops* and *Daphnia* to deeper waters during the day in fishless arctic lakes, as did Pennak (1944) in Colorado mountain lakes. A UVR life history experiment in the Oberer Arosasee indicated that daphnids did not reach maturity at the surface when exposed to full solar radiation (Chapter VII, Winder and Spaak, in press). Therefore, only subsurface strata remain an effective refuge for small and large zooplankton during daylight in this high-mountain lake. Interestingly, the remaining crustacean plankton (*B. longispina, E. gracilis*, *C. abyssorum*, nauplia) also avoided surface waters during daytime (M. Winder, personal observation). High UVR at the surface may account for the downward migration in juvenile daphnids, because in the absence of UVR (tower experiment) juvenile daphnids did not performed DVM and showed no reaction to fish chemicals. However, the deleterious effects of UVR cannot account for the downward migration to deeper strata, since the UVR is mainly absorbed in the upper 2 m and mean day depth of adults and juveniles do not correlate with the attenuation depth of UV irradiance (Table 2). Even though UVR is not important in determining day depth, it probably does determine the timing of migration, i.e. its synchronisation with dawn and dusk.

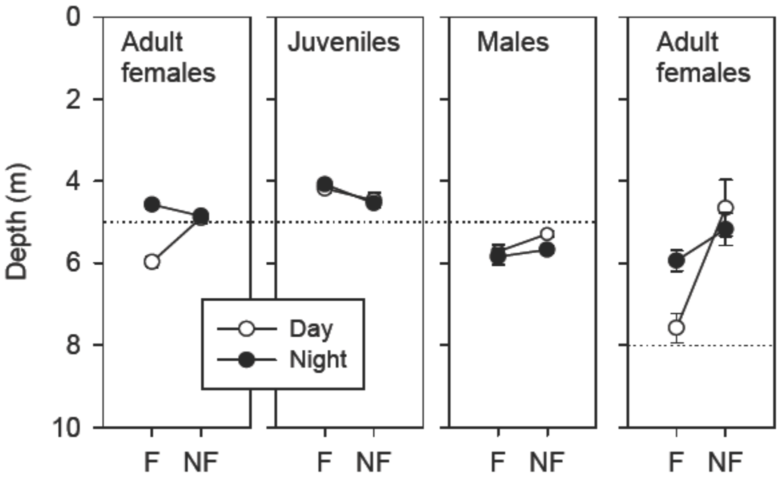

Figure 6. Daphnia galeata mean day and night depths (with standard error; when error bars are not visible, they are within the range of plotted points) for adult females, juveniles and males in the plankton towers for the fish (F) and no fish treatments (NF) at food maxima between 5.5 and 11 m depth. The right panel shows mean depths of adult females with high food concentration between 8 and 11 m. Dotted lines indicate depth below which food increased.

Vertical distribution patterns of daphnids before and after fish stocking in the Oberer Arosasee and the field enclosure experiment with manipulated fish biomass indicated that daphnids did not respond to changing fish biomass (Table 1, Fig. 3). In addition, zooplankton population demographics from the Oberer Arosasee showed that fish predation on daphnids was low and the size distribution of *D. galeata* did not change as expected under positive size-selective predation (Chapter III, Winder et al., submitted). Nevertheless, since the size of the *D. galeata* population is rather small (max. size of 1.9 mm, size at maturity of 1.6 mm), the impact of fish predation on large-sized daphnids or a life-history response of daphnids to reproduce at a smaller size cannot be excluded. Our results indicated that besides the decoupling of food and temperature, the actual fish predation pressure and kairomone concentration also are uncoupled in this lake. Experimental studies have shown that there is genetic differentiation in depth selection behaviour among lake *Daphnia* (De Meester and Weider, 1999), including some clones exhibiting a weak response to fish chemical cues. Therefore, it was of interest to investigate whether this high-mountain *D. galeata* population reacts to fish mediated cues at all. In the tower experiment, where we mimicked summer conditions of the Oberer Arosasee, the *D. galeata* population remained around the thermocline both day and night where food concentration increased, in the absence of fish kairomones (Figs. 5 and 6). This

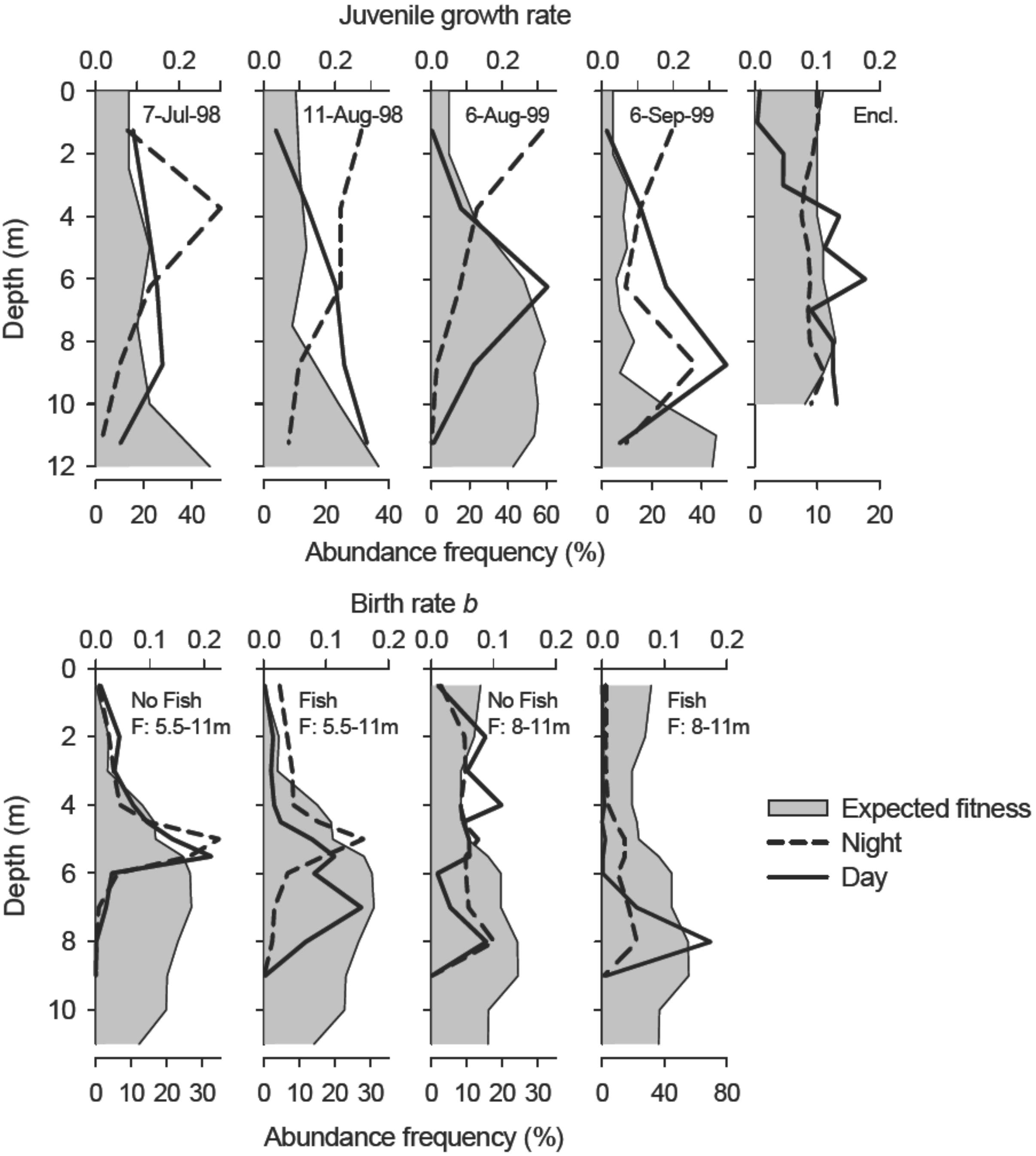

Figure 7. Expected fitness in the water column based on juvenile growth rates (day^{-1}) and birth rates (day^{-1}) of Daphnia galeata estimated from the ambient POC and temperature measurements, together with D. galeata abundance frequency distribution during day and night. The upper panel shows situations in the Oberer Arosasee during the summers of 1998 and 1999 and in the enclosure (August 2000) using juvenile growth rate as the fitness parameter. The lower panel shows the situation in the plankton tower both with and without fish with high food concentration (F) from 5.5 – 11 m and from 8 - 11 m depth using empirical birth rate estimates.

is in agreement with data on the lake, at least with respect to day depth. However, this *D. galeata* population in the tower experiment did respond to fish kairomones by migrating deeper into cold habitats during the day. Exchanging the fish between the towers reversed this response.

Since the same clones are involved, the contrasting behaviour in the lake and the tower experiments suggests that there must be a difference in a proximate environmental factor between the lake and towers. In the lake, the high chlorophyll or POC concentrations may not be an adequate indicator of the food availability for daphnids (Boersma et al., 2001) and reduced food quality in deep strata could explain the nocturnal ascent. However, when daphnids from the Oberer Arosasee were raised on seston taken from different depth strata of the lake, growth conditions were better in deep strata, even after correction for the ambient temperature. In addition, oxygen and invertebrate predation do not explain the migration to shallow night depths in the lake (Chapter V). It is likely that in the lake the lower maximum temperature and weaker vertical temperature gradient, compared to the towers, forced the daphnids to move upward under mortality-save conditions. Orcutt and Porter (1983) found that egg development rate in *D. parvula* was approximately four times slower at 5 °C compared to 15 °C (~20 days versus ~4 days). Further, these authors observed that fecundity parameters (i.e. number of broods, brood size) showed optima at 15 °C. This suggests that in order to maximise fitness, *D. galeata* may migrate into surface waters in the lake where temperature is around 14 °C, whereas in the towers, the ambient temperature above the thermocline was in the same range. In the Oberer Arosasee, the demographic advantages of temperature alone could account for the nocturnal upward migration of *D. galeata*. The different responses to the different temperature regimes may be a strategy to optimise fitness.

Modelling the expected fitness distribution in the water column, according to empirical estimates of population growth rates, demonstrated that the effect of food on birth rate or somatic growth rate is dominant, whereas the temperature effect is minimal. However, the migration behaviour of daphnids suggests that the temperature effect may be stronger in determining the vertical migration then expected from our assessment in Figure 7. Under predator-free conditions, migrating daphnids were indeed observed to ascend into warmer low-food waters at night. This behaviour supports the hypothesis that the thermal gradient of the water column is the major cost of

DVM (Loose and Dawidowicz, 1994). Life-history experiments with varying temperature and food conditions have demonstrated that migrating populations have lower growth rates than non-migrating populations and that maximum fitness is achieved by remaining in surface waters, in the absence of planktivores fishes (Orcutt and Porter, 1983; Ohman, 1990; Dawidowicz and Loose, 1992a).

It is of interest to ask why the *D. galeata* population did not react to fish manipulation in the field (i.e. fish stocking experiment, enclosure experiment), but showed a rapid response (within a day) to fish kairomones in the plankton towers. Other field studies have shown that *Daphnia* increase DVM behaviour when fish predation intensity increased (e.g. Dorazio et al., 1987; Dini and Carpenter, 1992). All of these studies showed a relatively rapid response, indicating an induced behavioural response to the presence of potential predators (Dodson, 1988). In the Oberer Arosasee, the stocked fish biomass might have been too low or the kairomone concentration in the lake may always be above a threshold level such that the stimulus is constant. The fish population consists of salmonids that feed primarily on benthic invertebrates (Elliot, 1994); however, diet analysis showed that trout do indeed prey upon daphnids (M. Winder, unpublished data). It is not clear if daphnids can differentiate between kairomones of different fish species; however, many fishes, even benthic feeders, have been shown to evoke a behavioural reaction in *Daphnia* (Loose, 1993b; Von Elert and Loose, 1996). In the enclosure experiment, low temperatures (mean 12 °C) might have slowed the degradation of fish kairomones in the enclosures without fish. However, Loose (1993a) showed in an experiment at 20 °C that daphnids changed their migration behaviour within 24 hrs when fish were removed due to rapid degradation of the chemical substance (Loose et al., 1993). Therefore, we assume that the kairomone concentration at least decreased significantly during the experiment. Other *in situ* enclosure experiments have shown that zooplankton species changed their migration behaviour depending on the presence or absence of predators within a few days, when lake water that contained kairomones was used to fill the tanks (Bollens and Frost, 1989; Leibold, 1990; Dini and Carpenter, 1992). Until the chemical structure of the fish kairomone is not identified, we can only speculate about kairomone concentrations in the field. Nevertheless, if fish chemicals had mediated the vertical distribution of daphnids in the enclosures, we would have at least expected an increased mean day depth in the fish enclosures or a decrease in the non-fish enclosures. However, mean day depth remained the same during the experiment in the enclosure with and without fish (Fig. 3).

Our field observations suggested that the uncoupled optima of food (energy gain) and temperature (development) stimulated the up and down movement in *Daphnia*. Daphnids stayed closer to the surface during the day and night, when the temperature gradient between the upper and lower strata increased (Fig. 4) and the migration amplitude increased with increasing temperature gradients. Since temperature and chlorophyll *a* gradients changed in a consistent way, the same patterns were observed with chlorophyll *a* gradients. Depth selection behaviour in daphnids was strongly determined by both the temperature and food gradient. The synchronous migration at dawn and dusk, however, indicates that a light-dependent trigger is related to the diel migration behaviour. Thus, food and temperature are not so much the driving forces but rather modulate the actual depth at which the animals stop migrating. In the Oberer Arosasee, Secchi depth explained a significant proportion of the mean day depths, both in juvenile and adult daphnids (Fig. 4; Table 2); however, there was no relationship between migration amplitude and water transparency. The predator-avoidance scenario suggests that migration intensity is proportional to water clarity, which is proportional to Secchi depth (Dodson, 1990). Therefore, the migration amplitude observed in this lake cannot be explained by predator avoidance. In laboratory experiments, it has been shown that *Daphnia* react to increases in light intensity with a downward movement and to decreases in light intensity with upward swimming (Ringelberg, 1999), while fish kairomones enhance the migration behaviour (Loose, 1993b). Modelling vertical migration, Ringelberg (1993) estimated migration amplitude of approximately 2 m without the effect of fish kairomones and accelerating rates of light change.

To conclude, in the Oberer Arosasee tradeoffs among food and temperature evolved, especially during the summer months, and daphnids migrate upward, out of food rich environments at night. Food and temperature modulate the actual depth, at which the animals stop migrating, whereas UVR determines the timing of migration, i.e. its synchronisation with dawn and dusk. Although this population of daphnids responded to fish kairomones in the tower experiment, there was no evidence of such a reaction in the field. Therefore, the migration can be explained by phototactic reaction and might result without the enhancing effect of fish kairomones. Our results suggest that the major benefit of night-time movement into surface waters is an acceleration of embryo development due to warmer temperatures, but not a feeding gain.

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Chapter VII

Effects of natural UV radiation on the life history of *Daphnia* in a high-mountain lake

with P. Spaak; Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie, in press

Abstract

The hazardous effect of UV radiation (UVR) on zooplankton is especially pronounced in freshwaters at high altitude or latitude. In an *in situ* experiment of a high-mountain lake we investigated the effects of natural UVR on the survival and life histories of newborn *Daphnia galeata*. Both UV-A and UV-B strongly affected survival and life history of daphnids. At the surface, daphnids did not reach maturity. At 100-cm depth daphnids under UV stress had higher age at maturity, lower size at maturity and smaller clutch sizes. The deleterious UVR effects on daphnids decreased with increasing depth, therefore, downward diurnal migration provides effective protection during high radiation input.

Introduction

Several mechanisms have been suggested regarding how zooplankton avoid or protect themselves from the hazardous effects of ultraviolet radiation (UVR, 290 – 400 nm) in near-surface waters. The production of photoprotective pigments is one possible defence mechanism (De Meester and Beenaerts, 1993). In cladocerans the cuticular melanin pigmentation directly absorbs UVR and increases survival (Hebert and Emery, 1990), whereas in copepods the protective function of carotenoids is well known (Ringelberg et al., 1984). Carotenoids may also be important in protecting eggs and progeny of daphnids (Hessen, 1994).

Although there is evidence that diel vertical migration (DVM) of zooplankton is primarily a predator avoidance strategy (Lampert, 1989), DVM also may have evolved as an UVR avoidance mechanism (Hairston, 1976; Siebeck and Böhm, 1994). For example, Hessen (1994) showed that *Daphnia* exhibited an immediate downward migration in response to UVR. However, because of the rapid attenuation with depth the amplitude of UVR-induced migration in *Daphnia* is suggested to be relatively small compared to the predator-induced migration into the hypolimnion (Ringelberg, 1999). In lakes with high fish predation pressure, daphnids stay deeper during the day than the depth where UVR has a significant effect on mortality (Zagarese et al., 1994). However, juvenile daphnids were shown to migrate less and often remain in near surface waters during the day, where an UVR risk exists (Ringelberg et al., 1991).

In daphnids, the harmful effect of artificial and natural UVR on the survival and brood size of adults has been well demonstrated (e.g. Zellmer, 1995). The effects have been found to be species and genotype specific; the specific UVR tolerance is based on the differing capacities to recover (e.g. photreactivation) from UVR-induced damage (Siebeck and Böhm, 1991). However, little is known on how UVR impacts newborns and their life history under natural radiation conditions. This study was designed to investigate the effects of natural UVR on the survival and life histories of newborn *Daphnia galeata* in a high-mountain lake. The *D. galeata* population migrates throughout nearly the entire year in this lake. Further, an earlier study showed that the presence of fish does not influence their migration amplitude (Chapter VI). Therefore, it is of interest to investigate how UVR influence daphnids, survival and reproductive success in the surface layer, and if UVR may induce downward migration during daytime.

Materials and methods

We performed our experiment during August 2000 in the Oberer Arosasee (mean depth, 7.3 m; chlorophyll *a*, 3.4 µg l^{-1}; DOC, 1.5 mg l^{-1}), situated at 1734 m a.s.l. in the Central Alps, Switzerland (46°13′N, 09° 41′E). The fish community in the lake consists of native species (brown trout, minnow) and introduced salmonid fishes. The experiment started on a cloudless day, and this cloudless weather lasted for the first 15 days of the 18-day experiment. Irradiation spectra (range 280 - 700 nm) were measured using a Macam SD104A/B-Cos spectroradiometer for UV-B and UV-A radiation and a quantum solar irradiometer (Lamda Corp) for PAR.

We used a *D. galeata* clone originating from the Oberer Arosasee that had been cultured for several generations in the laboratory without UV-exposure. In the laboratory, mothers and grandmothers of the experimental animals were raised at a 12:12h LD cycle, in 18 °C filtered (0.45 µm) lake water, which was changed daily. Chemostat-grown *Scenedesmus obliquus* was used as food at a concentration of 1 mg C l^{-1}.

To create different levels of radiation we used five different treatments: (1) UVR plus PAR (i.e. full-sunlight) with Quartz bottles (100 % transmittance at 320 nm); (2) UVR plus PAR with Duran G 20 (Scott, Germany) bottles (64 % transmittance at 320 nm); (3) UV-A plus PAR using overhead foils (Xerox, Type C) to exclude UV-B (43 % transmittance at 320 nm); (4) PAR using overhead foils plus plexiglass lids (Röhm, Germany) to exclude UVR (71 % transmittance at 405 nm); and (5) a dark control (i.e. bottles wrapped with aluminium foil). Quartz and Duran bottles (100 ml) were used for the total solar radiation exposures (treatments 1 and 2); for the other treatments only Duran bottles were used. For each treatment 8 replicate bottles were filled with filtered (20 µm) lake water. We added cultured *Scenedesmus obliquus* to a final carbon concentration of 1.5 mg l^{-1} and stocked the bottles with 5 newborn *D. galeata* collected within 12 h of birth. The bottles were incubated at two different depths (10 cm and 100 cm), corresponding to 63 and 5 % of the integrated UV-B and 65 and 15 %

of the integrated UV-A irradiance at the surface (Fig. 1). This design resulted in 5 (treatments) x 2 (depths) x 8 (replicates) = 80 experimental bottles. The bottles were incubated in the lake horizontally; the temperature was ~15.8 °C at both incubation depths. Each day, we changed water and food, recorded survival and number of eggs. The length of daphnids was measured when they had their first brood.

Kaplan-Meier Analysis was used for the survival function; treatments were compared using the log-rank test in STATISTICA. The percentage survival values were arcsine square-root transformed to normalise their distribution (Sokal and Rohlf, 1995). Significance between depth and treatments was tested using two-way analyses of variance followed by Tukeys post-hoc comparison test.

Results and discussion

The survival rate of newborn *D. galeata* in the Oberer Arosasee was adversely affected by natural UV-B and UV-A radiation (Fig. 2). High mortality was also found at 100-cm depth, corresponding to the depth where only

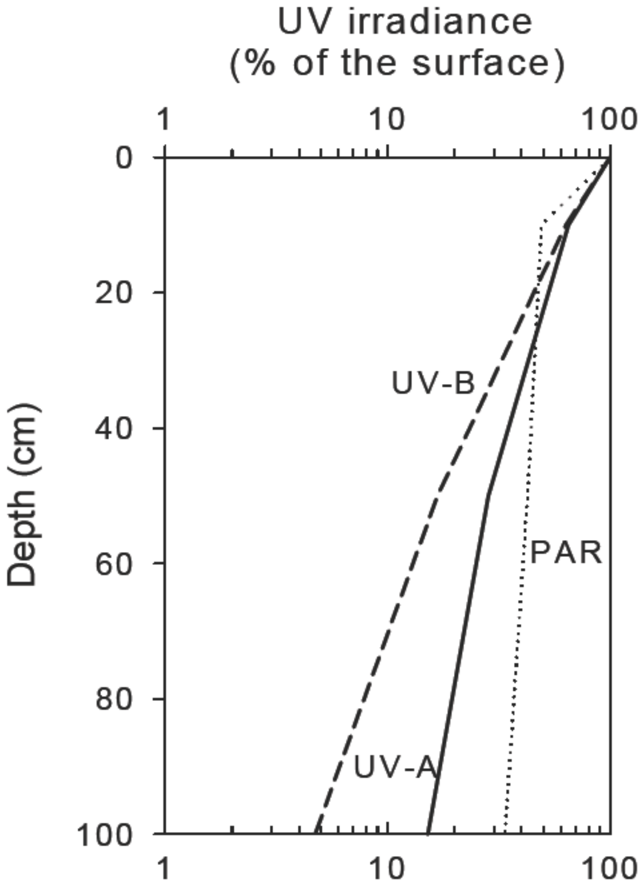

Figure 1. Vertical profile of the relative UV-A, UV-B and PAR irradiance at noon in the Oberer Arosasee in August.

5 and 15% of the surface UV-B and UV-A radiation, respectively, penetrated (Figs. 1 and 2). The survival rate for both UVR treatments differed significantly from the PAR and control treatments (log-rank test, $p < 0.001$) at both depths, indicating a strong effect not only of UV-B but also of UV-A radiation. Biological damage and increased mortality of UV-A radiation also has been shown in other aquatic organisms, such as viruses, heterotrophic flagellates and benthic diatoms as well as in the copepod *Boeckella gracilipes* (Suttle and Chen, 1992; Bothwell et al., 1994; Sommaruga et al., 1996; Tartarotti et al., 2000). In contrast, another population of the latter species and the rotifer *Keratella taurocephala* have been shown to be UVR resistant (Williamson et al., 1994; Cabrera et al., 1997). The difference in survival

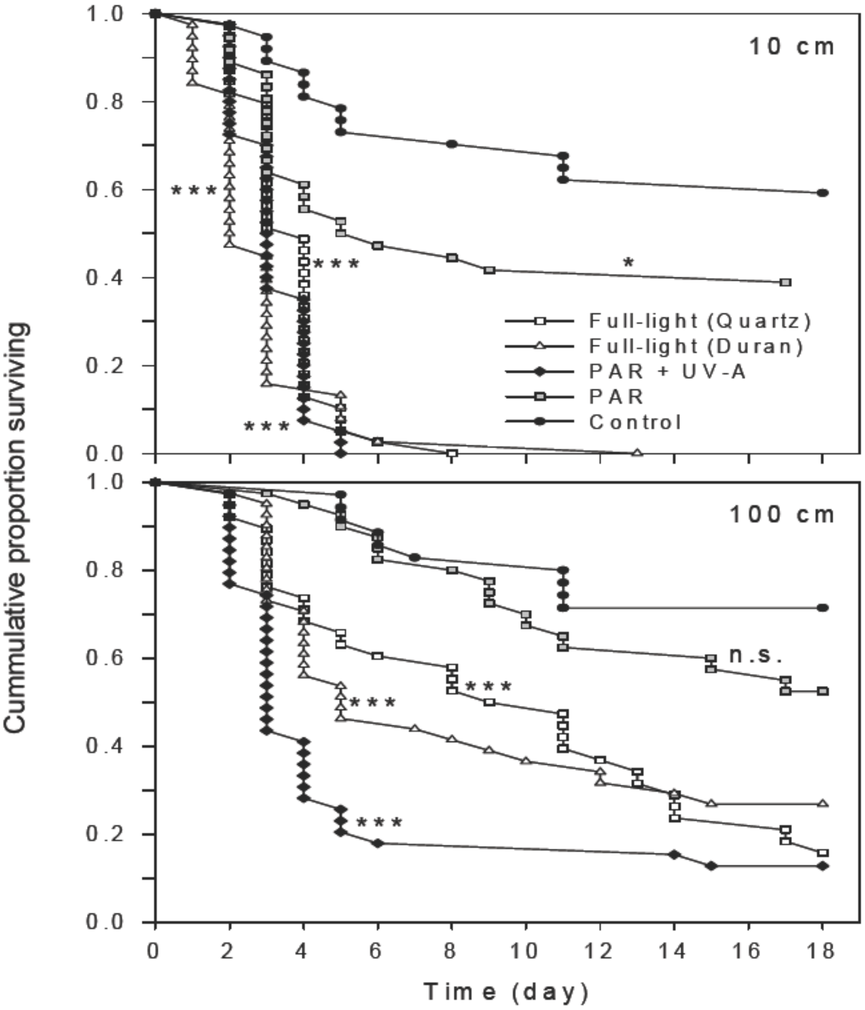

Figure 2. Cumulative surviving proportion of *Daphnia galeata* in different treatments at 10-cm and 100-cm depths using Kaplan-Meier Analysis function. Log-rank test was used to test for significant differences between the control and the other treatments at each depth (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

rate between the two depths was statistically significant in the full-sunlight (log-rank test, $p < 0.01$) and UV-A plus PAR (log-rank test, $p < 0.05$) treatments, but not in the other treatments. All exposed individuals died within 8 days in both UVR treatments at the surface, whereas approximately 20 % survived the total exposure period (18 days) at 100-cm depth. Between day 3 and 5, the mortality rate in the UV-A plus PAR treatment was unexpectedly high at 100-cm depth. This might be caused by an experimental error and not by UV-A radiation. *Daphnia galeata* in the Quartz and Duran bottles showed similar survival rates at both depths (log-rank test, $p > 0.05$) in the full-sunlight treatment.

After the first 2 days of exposure, mortality increased rapidly at both depths in the UVR treatments, suggesting that the UV-sensitive life stages in *D. galeata* were after the second day of exposure. However, Siebeck &

Table 1. Results of two-way ANOVAs for the survival and life history characters of *Daphnia galeata*. Depths and treatment (control, full-sunlight, UV-A plus PAR, PAR) were used as factors. Significant ($P < 0.05$) reactions are indicated with bold P-values.

Trait	Source	*df*	MS	F	P
Survival after 3 days	Depth	1	3.851	16.335	**<0.001**
	Treatment	4	1.808	7.671	**<0.001**
	D x Treat.	4	0.359	1.523	0.205
	Error	70	0.236		
Survival at maturity	Depth	1	2.633	16.710	**<0.001**
	Treatment	4	2.208	14.010	**<0.001**
	D x Treat.	4	0.026	0.168	0.954
	Error	70	0.158		
Age at maturity	Depth	1	0.612	0.135	0.716
	Treatment	1	4.148	9.189	**0.006**
	D x Treat.	1	0.203	0.451	0.508
	Error	24	0.451		
Size at maturity	Depth	1	0.003	0.586	0.451
	Treatment	1	0.164	36.004	**<0.001**
	D x Treat.	1	0.000	0.098	0.758
	Error	24	0.005	0.005	
No. eggs at maturity	Depth	1	2.941	2.361	0.137
	Treatment	1	10.966	8.805	**0.007**
	D x Treat.	1	2.953	2.371	0.137
	Error	24	1.245		

Böhm (1994) showed that all adult *D. galeata* died within 6 hours when exposed to full-sunlight at water surface at a comparable latitude. The longer survival rate of newborns found in this study could be due to the photo-protective function of carotinoids, which are restricted in cladocerans to eggs and early life stages (Hessen, 1993).

The mortality rate in the PAR treatment also was relatively high (60 % at 10-cm and 40 % at 100-cm depth, Fig. 2); the PAR treatment was weakly different from the dark control at 10-cm (log-rank test, $p < 0.05$) and not significantly different at 100-cm depth (log-rank test, $p > 0.05$). Between the two depths, the exposure of daphnids to PAR only and daphnids in the dark control, showed no significant differences in mortality (log-rank test, $p > 0.05$).

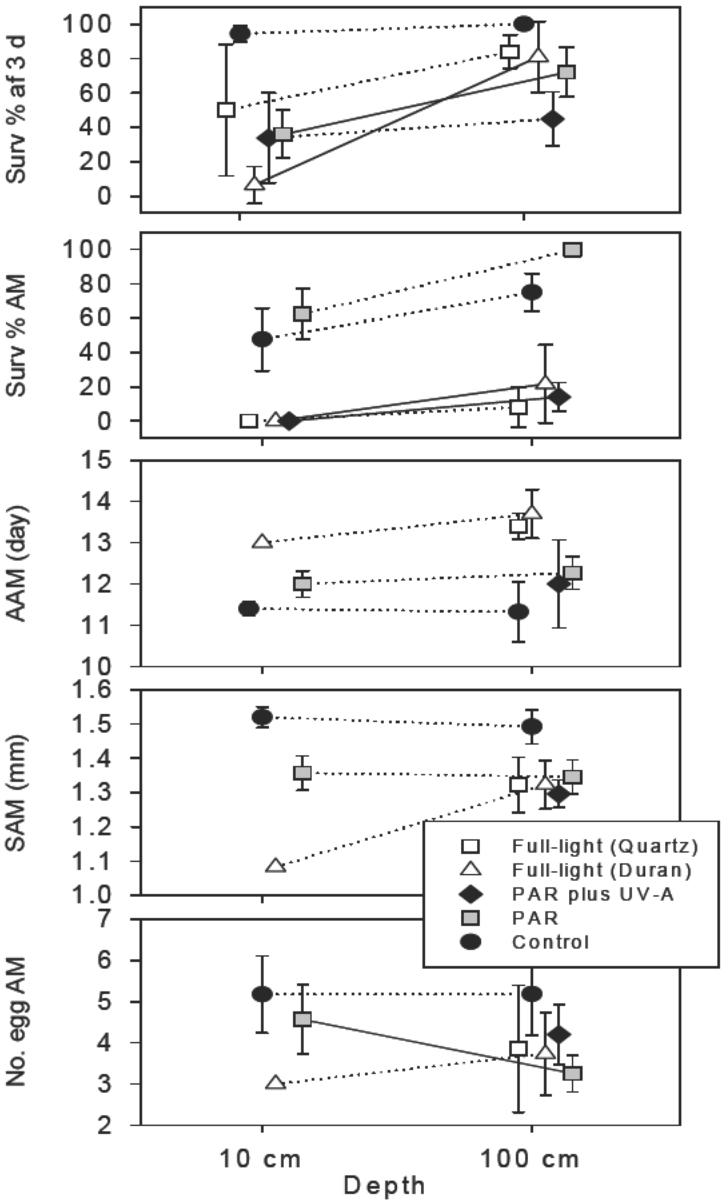

Figure 3. Reaction norms of Daphnia galeata for 5 different treatments at 10-cm and 100-cm depths. Significant differences (ANOVA) between the two depths are indicated with solid lines. Error bars indicate 95 % confidence intervals. Sur% af 3 d = survival percent after 3 days of exposure, Sur % AM = survival percent at maturity, AAM = age at maturity, SAM = size at maturity, No. egg AM = number of eggs at maturity.

In our experiment, we found no significant interaction between depth and treatment, contrary to expectations (Table 1). However, depth had a significant effect on the survival of newborns from the third day of exposure until maturity, suggesting that downward migration during daytime is important for daphnids to escape from the hazardous UVR in the surface layers. All of the investigated traits showed significant treatment effects (Table 1). The survival rate after 3 days of exposure increased significantly at 100-cm depth compared to the surface layer in the full-sunlight (Duran) and PAR treatments (Fig. 3), whereas the survival rate at maturity was significantly higher only in the full-sunlight with Duran bottles and UV-A plus PAR treatments. For age and size at maturity the different treatments showed no significant response at the different depths, but almost all daphnids exposed to UVR died before reaching maturity. At both incubation depths, daphnids under UVR stress showed greater age and lower size at maturity at both depths, as well as lower egg number at first reproduction at the surface (Fig. 3). At 100-cm depth the egg number at first reproduction showed no clear differences among treatments. Thus, reproduction may be affected mainly at the water's surface. This agrees well with the results of Zellmer (1998), who found that daphnids reproduction was affected mainly in the upper water column, as well as with studies from other zooplankton species (Williamson et al., 1994). Our results indicate that the surface layer in this high-mountain lake is not 'safe' for juvenile *D. galeata* due to UVR. Therefore, the avoidance of UVR may be at least a partial explanation for the observed DVM pattern.

Conclusions

In this study we showed that both UV-B and UV-A radiation strongly affected the survival of newborns of *D. galeata* at the surface in a high-mountain lake. The deleterious effects decreased with increasing depth. About 83 % of the newborns survived the first 2 days of the *in situ* exposure; the most sensitive life history stages were between an age of 3 to 5 days. Furthermore, daphnids under UVR stress had higher age at maturity and lower size at maturity as well as smaller clutch sizes. The high sensitivity of *D. galeata* to solar UVR reduced its ability to live and reproduce near the surface. Since at 100-cm depth UVR had a less harmful effect on survival and life-history traits of *D. galeata*, we conclude that downward migration provides effective protection during high radiation input.

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Chapter VIII

Synthesis

The ability of an organism to cope with the abiotic and biotic environment, i.e. fluctuating temperature, high solar radiation, predation and competition, determines in part its distribution and evolutionary success. The central question of this thesis is how zooplankton species inhabiting high-mountain lakes respond to changing environmental conditions. In *Chapter II*, I addressed the questions of how zooplankton structure has been altered during the last century in Swiss high-mountain lakes and investigated the present genetic variation of *Daphnia*. In *Chapters III* to *VII*, I studied one high-mountain lake system more intensively and investigated how abiotic (i.e. vertical temperature gradients, ultraviolet radiation) and biotic (i.e. predation, competition, vertical food distribution) demands influence the phyto- and zooplankton population dynamics, as well as the seasonal condition, behaviour and life history of zooplankton. In particular, I focused on the cladoceran *Daphnia*, an ecologically important taxon of grazers in lake plankton systems.

High-mountain lakes—a challenge for zooplankton?

Natural and anthropogenic impacts strongly influence the Alpine region, including high-mountain lakes. Various studies have shown that fish introduction into fish-free alpine lakes drastically affected the zooplankton composition. In *Chapter II* of this thesis, we focused on how human activities, especially fish stocking, changed the zooplankton composition in Swiss high-mountain lakes. Surprisingly, re-sampling of Swiss high-mountain lakes indicated that the zooplankton composition did not change much compared to ~100 years ago, even though the human influence in high-mountain lakes increased drastically during this period. However, we do not know how fish introduction altered the overall zooplankton community because fish introduction occurred in these lakes long before zooplankton data were available. Palaeoecological studies from freshwater organisms in Swiss lowland lakes demonstrate that the major changes were evident by the end of the 19th century (Lotter et al., 1998) and were probably due to increasing eutrophication. Thus, palaeoecological analyses of aquatic organisms in high-mountain lakes would help to reconstruct the overall change in the zooplankton community structure. Further, our sampling using a single-survey approach probably failed to document the presence of some rare taxa. But inclusion of these rare taxa as a result of a more intensive sampling regime would likely have had little effect on the overall results. In high-mountain lakes, the growing season is short, allowing only a single generation for many taxa. As a result, planktonic crustacean species composition perhaps changes little over the course of the summer.

As many zooplankton species produce resting stages that may remain viable in a dormant state for many years, there might be a potential for recovery of zooplankton in high-mountain lakes once returned to a fishless condition. A study of lakes in the Sierra Nevada Mountains showed that most common taxa recovered after trout disappeared (Knapp et al., 2001). These lakes had harboured fish populations for around 29 years. In alpine lakes of the Canadian Rocky Mountains, resting eggs of calanoid copepods remained viable for at least 15—20 years (Parker et al., 1996), and >100 year old eggs of another calanoid species have been hatched from small lakes in Rhode Island (Hairston et al., 1995). Similarly, resting eggs of *Daphnia* can remain viable for ~40 year (Cáceres, 1998). However, zooplankton egg bank viability declines with time, and thus, with the duration of fish occupation. This suggests that the possibility for a viable egg bank in European high-mountain lakes is low because of the relatively long period of fish stocking.

Integrating the trophic and chemical network

Typical food web models consider only the direct effects of predators on prey numbers. However, it is well known from an evolutionary perspective that predators also interact strongly with their prey by altering prey behaviour, morphology and life histories. For example, prey may avoid predators by shifting habitat use, reducing feeding rates or changing their diel activity pattern (Sih, 1987). Prey species across a wide range of taxa show a plastic response to chemical cues from a potential predator that reduce their risk in the presence of predators (e.g. DeWitt, 1998). The increased probability of survival for an individual prey organism may have population- and even system-wide consequences.

Recent studies illustrate that the dynamics in food webs may not be predictable solely from isolated predator-prey interaction studies since those neglect plastic responses to chemical information. The results of this thesis suggest that chemical mediated cues from fish are essential as a predator avoidance mechanism for planktonic organisms. Antipredator-avoidance strategies, like diel vertical migration (DVM), are important for maintaining coexistence of fish and large-sized zooplankton like *Daphnia*. Moreover, DVM of zooplankton affects the resource availability for planktivorous fish as well as the grazing pressure on phytoplankton and in turn indirectly the dynamics and structure of populations. Also, planktonic algae are not defenceless food particles, easily harvested by herbivorous species, but produce grazing resistant structures (e.g. larger size, spines, production of toxins; Hessen and Van Donk, 1993). Such adaptive, antiherbivore strategies reduce algal edibility, which results in lower growth rates of herbivorous species. Figure 1 illustrates the trophic and chemical network with defence mechanisms of known traits in *Daphnia*

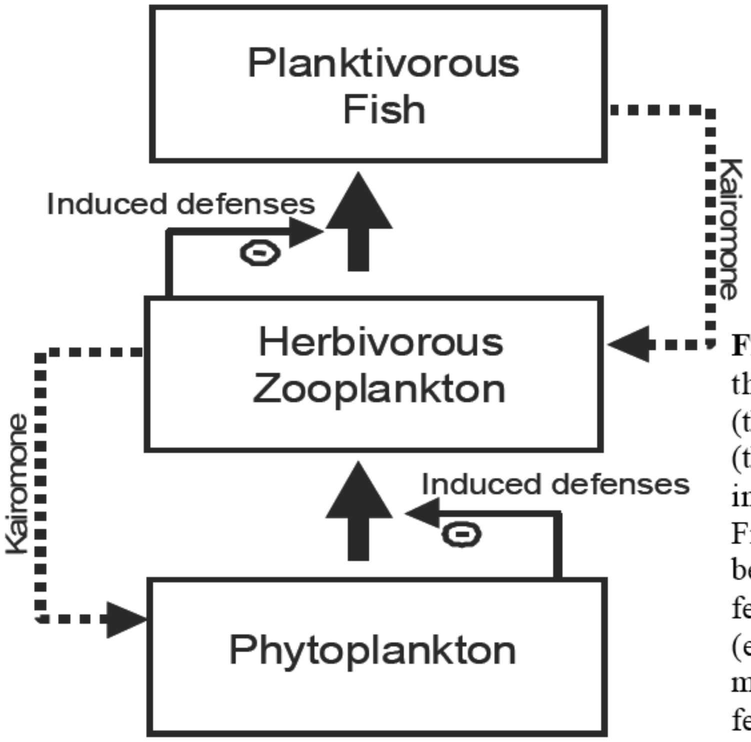

Figure 1. Major interactions of the aquatic trophic cascade (thick lines) and of information (thin lines) which is carried by infochemicals (broken lines). Fish infochemicals may induce behavioural and life-history defences in *Daphnia*. Zooplankton (e.g. *Daphnia*) infochemicals may induce morphological defences in algae.

and algae. In the presence of fish kairomones *Daphnia* may change their behaviour and/or life history in such a way that fish less easily detects them. Zooplankton kairomones may induce the formation of colonies or spines in algae, which reduce algal edibility. These inducible responses may change biomass of the trophic levels.

Such cascading effects are known in streams. For example, the freshwater snail *Physella* changed habitat as a response to predation risk, which affected their grazing activity and, in turn, led to increased biomass of periphytic algae (Turner, 1996). A few experimental studies have shown how behavioural optimisation of predators and prey can influence food web dynamics (e.g. Turner and Mittelbach, 1990; Chase, 1999). Several aspects need further investigation to move from studies on the individual level to those addressing population and community processes. Identifying the system consequences of DVM should be a goal in future work. Knowledge of the compounds responsible for chemical signals may improve our ability to design meaningful experiments, and thus should be a major focus of future studies. For my study it would have been profitable if the natural concentration of fish kairomones could have been measured, but we could only speculate about its concentration based on changing fish biomass. With knowledge about the chemical composition of kairomones, we might also understand why predators cannot avoid advertising their presence, thus inducing anti-predator defences by their prey.

Unfortunately, we were not able to measure the fish biomass in the Oberer Arosasee or to investigate fish diets. From the amount of fish introduced we had a rough estimation of changing fish biomass. However, nothing is known of the fish population structure in this lake. Hundreds of adult salmonids are stocked each year, however nothing is known about their reproduction success. Estimates of juvenile fish biomass would have been especially useful, because juvenile stages of almost all fish are planktivorous. Analysis of the zooplankton population structure revealed only indirect assumptions about the magnitude of fish predation pressure on zooplankton.

Chemical communication

Numerous examples of chemically induced phenotypic changes of aquatic organisms have been reported in both lentic and lotic systems, stimulating an increased interest in phenotypic plasticity (Tollrian and Harvell, 1999). However, this should not lead to the impression that we expect all prey to evolve inducible defences. It still seems that species with inducible defences represent the minority. This view might change with the increasing number of species observed forming cryptic defences (e.g. resource allocation shifts). In addition, we are just becoming aware of how anthropogenic chemicals (e.g. heavy metals, insecticides) contaminating the natural environment can affect fine-tuned chemical communication in aquatic organisms (Hanazato, 1998). Even quite low concentrations of anthropogenically-manufactured chemicals might interfere with the chemical communication between organisms. The field of chemical communication in aquatic systems has doubtless the potential to produce many interesting results in the future.

Behavioural plasticity

Within the behavioural repertoire of zooplankton, DVM is perhaps the most broadly distributed trait, occurring in diverse animal phyla, widespread geographic locales, and in marine and freshwater habitats. DVM behaviour of *D. galeata* is a central theme in this thesis. A number of scientists have puzzled about '*The why and when of up and down*' (Enright, 1979). Historically, there have been two lines of investigation to explain DVM. Initially, research focused on the physiological processes that make possible the performance of the behaviour, so-called 'proximate' causes. More recently, research has focused on a search for the evolutionary mechanisms that drive the selection of this behavioural trait. A widely accepted explanation for the ultimate cause of DVM is the 'predator-avoidance' hypothesis. In addition, it has been proposed that DVM behaviour is an inducible response, mediated by organic substances released by predators.

Trade-offs and the adaptive significance of DVM

The adaptive significance of DVM can be understood from the perspective of a trade-off between reduced reproductive output and reduction of light-dependent mortality risk. In the Oberer Arosasee, however, temperature and food optima were uncoupled due to deep food maxima; therefore, tempera-

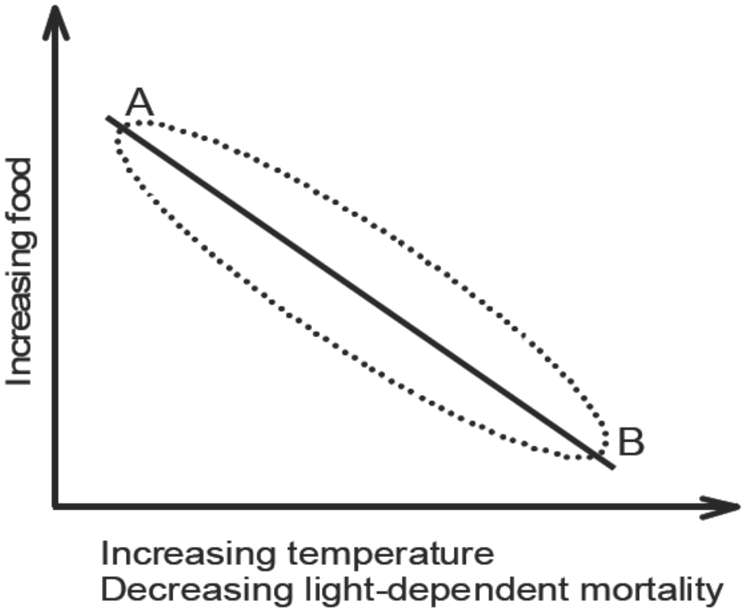

Figure 2. Optimal conditions in the Oberer Arosasee. Trade-off between light-dependent mortality risk and temperature in the surface waters and energetic gain in deep strata. The line indicates where the various individuals (genotypes) may be situated; A and B are two extreme genotypes. Dotted line indicates hypothetical range of exhibited traits. For comparison with trade-off conditions in a lake with surface food maxima see Fig. 3 in *Chapter I*.

ture and food may create strong conflicting pressures on zooplankton. Therefore, a trade-off between rapid development but low energy input in the warm surface waters, and slow development but higher food availability in deep waters is likely (Fig. 2). Although predation pressure by fish was evident in the Oberer Arosasee, the migration behaviour of *D. galeata* was not consistent with the predator-avoidance hypothesis; i.e. *D. galeata* did not respond in behaviour and life history to changes in fish biomass (*Chapters III* and *VI*). Field studies are often hampered by the fact that there may be cryptic factors one cannot control (Dini and Carpenter, 1992). Therefore, it was essential to conduct a laboratory experiment to investigate the impact of fish kairomones on vertical migration behaviour. Interestingly, in the plankton tower experiment *D. galeata* clones from the Oberer Arosasee responded to fish kairomones (*Chapter VI*) by migrating downward during the day.

The question remaining to be answered was why daphnids migrate upwards at night in the Oberer Arosasee? According to empirical population fitness estimations, the deep habitats had optimal fitness output (*Chapters V* and *VI*). The uncoupling of food and temperature maxima in the Oberer Arosasee may explain the migration of *D. galeata* to optimise their fitness. However, light-dependent mortality risk must be involved because the vertical migration was cued by predictable environmental factors, especially light level.

DVM of zooplankton is a highly variable and complex behaviour that apparently cannot be explained by any single factor. Regarding the wide spectrum of specific modes of DVM over many different taxa, populations and environments, it has been suggested that several physical, chemical and biological conditions of the water may modify this general behavioural response. Likewise, the physiological status of the zooplankters (i.e. their nutritional state), genetic differences of the populations and predation types are also important determinants of the specificity in DVM and other predator-mediated plastic traits (Tollrian and Dodson, 1999).

Moreover, DVM behaviour observed in the field is a population phenomenon and not much is known about the vertical migration behaviour of individual animals. *Daphnia galeata* from the Oberer Arosasee are known to perform vertical migration behaviour as shown in *Chapter VI*. However, the phototactic behaviour of the clones was not empirically determined. Different genotypes may exhibit different migration strategies, including no movement (Dawidowicz and Loose, 1992; De Meester and Weider, 1999).

The influence of mortality risk

A survey of eight Tatra lakes showed that *Cyclops abyssorum* migrates only in lakes with predatory fish and most strongly when the copepod has lived with the fish for centuries (Gliwicz, 1986). It would be interesting to compare behavioural adaptations of *Daphnia* in lakes with deep food maxima with and without fish. From our tower experiment (*Chapter VI*), we can only speculate that they might not migrate in lakes without fish, but remain both day and night at a depth with the highest expected fitness or migrate to optimise the energetic input and egg development. In high-elevation lakes, ultraviolet radiation also might induce downward migration (*Chapter VII*). Thus, in high-mountain lakes DVM is an essential adaptive behaviour to avoid high mortality risk and increase fitness. Yet, there is no study that investigated how phototactic responses to ultraviolet radiation interact with predation and other factors known to be important in DVM.

The influence of food

There is some controversy concerning the role of food in shaping DVM. By investigating the vertical distribution of food quality for *D. galeata* in a lowland and a high-mountain lake (*Chapter V*), we found that food is not necessarily poorer in deep layers of the high-mountain lake. In fact, the occurrence of higher food concentration in deeper water is in opposition to the central assumption of DVM theory that the surface waters of lakes and oceans are more food-rich than deeper strata. Deep-water food maxima are not only found in high-mountain lakes but also have been documented in the ocean and other lake types (Williamson et al., 1996). The migration pattern of daphnids in the high-mountain lake studied in this thesis supports the idea that upward migrations at night are not always driven by the benefits of food-rich surface strata. Moreover, our study suggests that high food levels may not compensate for low temperature in deep layers. Further studies will benefit from an increased emphasis documenting the vertical distribution of food resources.

Resource level may indirectly be involved in migration patterns via the nutritional state of zooplankton. Studies of inducible defences showed that behaviour or morphological responses are most pronounced at higher food levels. For example, Johnsen and Jakobsen (1987) showed that *Daphnia* sp. stopped migration when food was limited. In our study, carbon analyses and fecundity indicated that daphnids were food limited during a large part of the year; however, their low nutritional value was obviously not poor enough to affect migration amplitude (*Chapters III*, *IV* and *VI*).

Influence of temperature

Our results support temperature as an important factor in modifying vertical migration. Originally, lower temperatures were invoked as an advantage rather than a disadvantage for migrating zooplankton, because at lower temperatures metabolic processes are slower, and hence animals are more frugal with their available energy (McLaren, 1974; Enright, 1977). However, costs in terms of a decrease in the intrinsic rate of population increase as a result of slower developmental rates are much more important (Loose and Dawidowicz, 1994). In fact, Kerfoot (1985) and later Loose and Dawidowicz (1994) argued that the temperature effect was much more important than the effect of differences in food availability. The retardation of zooplankton growth rates under low temperatures in migrating animals is a well-known phenomenon. Thus, it is surprising that the importance of temperature differences between day and night depths has been overlooked in a number of

DVM studies. Our study strongly suggests the importance of temperature as a modifying factor of DVM. Temperature may play a more important role than food in determining a demographic advantage in stratified surface waters.

The effect of temperature on DVM, however, is more complicated because predation pressure depends not only on migratory animals themselves but also on the predators whose feeding and other actions are also influenced by temperature. At low temperature, predation activity greatly decreases and similarly the amount of chemically mediated cues. At this time, the predation pressure defined by fish abundance may be overestimated.

In order to predict DVM behaviour under natural conditions there is a large demand for further experimental field and modelling investigations. Further studies will benefit from an increased emphasis documenting the vertical distribution of food resources and temperature and on investigating vertical migration behaviour around the year, not just in summer. Detailed information about environmental conditions may help to explain why the observed patterns of vertical migration are so variable. The question at present is whether we will be able to find a unifying theory that explains the different patterns in the diverse taxa. The only unifying concept we have at the moment is that vertical migration may not evolve without light-dependent mortality in the surface waters.

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Curriculum Vitae

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