

**Pro gradu – tutkielma**

**Littoral - pelagic zone food web interactions in fishless,  
highly humic Lake Mekkojärvi**

**Piia Aarniosalo**



**Jyväskylän yliopisto**

Bio- ja ympäristötieteiden laitos

Limnologia ja hydrobiologia

6.10.2007

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos  
Limnologia ja hydrobiologia

AARNIOSALO PIIA, P.: Ranta- ulapparavintoverkkojen vuorovaikutukset kalattomassa, runsashumuksisessa Mekkojärvässä.

Pro gradu: 30 s.

Työn ohjaajat: Prof. Roger I. Jones

Tarkastajat: Prof. Roger I. Jones, FT Heikki Hämäläinen

Lokakuu 2007

---

Hakusanat: ravintoverkko, vakaat isotoopit, petoselkärangattomat

## TIIVISTELMÄ

Pieni, runsashumuksinen Mekkojärvi Etelä-Suomessa rikastettiin kolme kertaa  $\text{NaH}^{13}\text{CO}_3$  bikarbonaatilla keväällä, kesällä ja syksyllä 2005. Rikastuksen tarkoituksena oli tutkia petoselkärangattomien asemaa ravintoketjussa ja  $^{13}\text{C}$  hiilen kiertoa litoraalivyöhykkeessä käyttäen apuna vakaita isotooppeja ja arvioida onko *Daphnia longispina* ravinnonlähde petoselkärangattomille. Tarkoituksena oli myös tutkia mitä *Daphnia* tuotannolle tapahtuu kun normaalisti eläinplanktonia kuluttavat kalat puuttuvat ekosysteemistä. Kolmen koekerran aikana lisätty  $\text{NaH}^{13}\text{CO}_3$  kasvatti nopeasti pintaveden DIC  $\delta^{13}\text{C}$  pitoisuutta. Liunneen epäorgaanisen hiilen  $^{13}\text{C}$ -rikastus siirtyi aikuisiin ja nuoriin *Daphnia* -vesikirppuihin, joiden  $\delta^{13}\text{C}$  arvo rikastui noin 10‰ alkutilanteeseen verrattuna. Sudenkorennon toukat eivät kuluttaneet *Daphnia* -vesikirppuja, mutta *Notonecta* spp. voi olla yksi vesikirppuja saalistava petoselkärangaton Mekkojärvässä. Ainoatakaan *Chaoborus*-toukkaa ei saatu pyydystettyä, joten yksi ravintoverkon tärkeä osa jäi puuttumaan.

UNIVERSITY OF JYVÄSKYLÄ, Faculty of Science

Department of Biological and Environmental Science

Limnology and hydrobiology

AARNIOSALO PIIA, P.: Littoral-pelagic food web interactions in fishless, highly humic Lake Mekkojärvi

Master of Science Thesis: 30 pp.

Supervisors: Prof. Roger I. Jones

Inspectors: Prof. Roger I. Jones, Dr. Heikki Hämäläinen

October 2007

---

Key Words: Food web, stable isotopes, macroinvertebrate predators

## ABSTRACT

Small, polyhumic lake Mekkojärvi in southern Finland was enriched three times with  $\text{NaH}^{13}\text{CO}_3$  in spring, summer and autumn in 2005 to examine the trophic positions of invertebrate predators and the carbon pathways in the littoral food web using stable isotope methods and specifically to evaluate if *Daphnia longispina* is a food resource for invertebrate predators. This would provide an answer to the puzzle of what happens to all the *Daphnia* production in this lake when there are no planktivorous fish that would normally consume *Daphnia*. During the three experimental periods, the added  $\text{NaH}^{13}\text{CO}_3$  quickly increased the epilimnetic DIC  $\delta^{13}\text{C}$ . The  $^{13}\text{C}$ -enrichment of DIC was transmitted to adult and juvenile *Daphnia*, which became about 10‰ more enriched than their initial  $\delta^{13}\text{C}$  values. Odonates did not consume *Daphnia*, but *Notonecta* spp. might have been feeding on *Daphnia*. No *Chaoborus* individuals were caught, so one important part of the food web was missing. The results indicate that littoral predators do not account for a significant part of the large secondary production by *Daphnia* in the lake. Therefore, the question remains open regarding the fate of the *Daphnia* production in this fishless lake.

## Contents

<b>1. INTRODUCTION</b> .....	5
1.1. Limnology of humic lakes and the importance of allochthonous carbon.....	5
1.2. Basic food web concepts.....	6
1.3. <i>Daphnia</i> and invertebrate predators.....	7
1.4. Stable isotope analysis .....	11
1.5. Objectives of this study.....	13
<b>2. MATERIALS AND METHODS</b> .....	13
2.1. Lake Mekkojärvi.....	13
2.2. <sup>13</sup> C enrichment and data collection.....	14
2.3. Data analysis.....	14
<b>3. RESULTS</b> .....	14
<b>4. DISCUSSION</b> .....	20
<b>ACKNOWLEDGEMENTS</b> .....	22
<b>LITERATURE</b> .....	23

## 1. INTRODUCTION

### 1.1. Limnology of humic lakes and the importance of allochthonous carbon

Lake ecosystems are supported by organic carbon from two distinct sources. Autochthonous carbon is produced by photosynthesis within an ecosystem by autotrophic organisms. Allochthonous carbon is produced elsewhere and transported in to the lake. Consumers may use allochthonous carbon with consequent influences on population dynamics, predator-prey relationships and ecosystem processes (Polis et al. 1997). Humic matter in dark stained waters of boreal forest lakes of Scandinavia originates from catchment areas that contain much humic matter (Meili 1992). Allochthonous input can provide resources that may enhance consumer abundance beyond levels supported by within-system primary production (Nakano and Murakami 2001). The organic matter imported across ecosystem boundaries can affect the metabolic balance of the receiving system by providing a substrate for microbial respiration in excess of local primary production (Webster and Mayer 1999).

The humic compounds of DOC are the major factor controlling water colour in lakes (Pace and Cole 2002). Elevated levels of DOC ( $> 5 \text{ mg/L}^{-1}$ ) are typical for many northern temperate lakes. More than 80% of Finnish lakes have DOC concentration  $>5 \text{ mg/L}^{-1}$  (Kortelainen, 1993). Light penetration down the water column is also severely restricted creating an adverse environment for photosynthesis (Jones 1992). However, DOC absorbs infrared light, which can lead to a shallower and warmer epilimnion and a colder hypolimnion (Fee et al. 1996). Moreover, the hypolimnia of high-DOC lakes tend to have lower oxygen levels than clear lakes, making them less accessible to fish. Oxygen levels are reduced in coloured lakes partly because oxygen-consuming bacterial metabolism is enhanced by DOC (Hessen and Andersen 1990, Arvola et al. 1996) and also because rapid warming in the spring causes these lakes to stratify early, before water mixing can replenish the oxygen levels in the hypolimnion. Usually small forest lakes are also surrounded by trees, which reduce wind-induced turbulence to the water and promotes rapid and steep stratification. Hypoxia is restrictive to fish but not so much for many zooplankton. The hypolimnia of high-DOC lakes can provide refugia for zooplankton against fish predation because the water is too dark for visually predating fish and too low in oxygen for fish survival. The same conditions that make high-DOC lakes favourable for avoiding fish predation also make them better environments for large invertebrate predators. Planktonic macroinvertebrates, such as larvae of *Chaoborus*, are voracious predators of zooplankton. Macroinvertebrates in high-DOC lakes would have the same refuge from predators as their zooplankton prey in low-oxygen hypolimnia (Wissel et al. 2003), but macroinvertebrates like Odonata, Ephemeroptera etc. do not tolerate severe hypoxia.

While these connections and subsidies have had a long history of study in stream ecosystems there has been far less work in lakes. Lakes are examples of ecosystems that receive large inputs of allochthonous organic matter with inputs often equal to or exceeding internal primary production (Caraco and Cole 2004). Even though only a small fraction of this allochthonous material is respired, a consequence for many lakes nevertheless is that total respiration (R) exceeds gross primary production (GPP), so that net ecosystem production is negative (Cole et al. 2000), implying the metabolism of exogenous carbon (Cole et al. 2000). Autochthonous production is low, but humic materials support bacterial metabolism (Hessen 1992) and associated heterotrophic

organisms in the microbial loop (Tranvik 1992). Allochthonous fluxes of DOC are usually large but difficult to assimilate, in contrast to autochthonous DOC, which is used more easily (Cyr and Pace 1993, Wetzel 1995). Ecosystem metabolism in lakes suggests that allochthonous support of food webs could be significant if degradation of terrestrial carbon is also coupled to consumer production (Cole et al. 2002). Studies of zooplankton using natural abundances of stable isotopes support this view and indicate that zooplankton acquire some of their carbon from terrestrial sources. Aquatic bacteria use allochthonous DOC and consumption of bacteria by predators provides a pathway for transfer into food webs (Jones et al. 1999, Grey et al. 2001). It is also possible, that some consumers use allochthonous carbon directly (Kerner et al. 2003, Roditi et al. 2000), but this possible path is poorly understood.

Terrestrial organic matter may be incorporated into aquatic food webs by several mechanisms (Cole et al. (2006). Terrestrial dissolved organic carbon (t-DOC) enters lakes in flowing water and is degraded by bacteria that are consumed by grazers (Hessen 1998, Tranvik 1998). Terrestrially derived particulate organic carbon (t-POC) enters lakes by both fluvial and aeolian transport. T-POC may be available to bacteria through decomposition and to other consumers through direct ingestion (Hessen and Nygaard 1992). Terrestrial-prey items (t-prey) include insects, amphibians, small reptiles and mammals, which both intentionally or accidentally enter lakes and, at least in small lakes, can be a variable but significant resource for predators (Hodgson and Hansen 2005). A large fraction, about half, of the DOC acquired by bacteria is of autochthonous rather than allochthonous origin (Kritzbeg et al. 2004, 2005). Terrestrial POC heavily subsidized (22-75%) zooplankton unless primary production was stimulated by nutrient addition (Cole et al. 2002, Carpenter et al. 2005). Through consumption of zooplankton their predators, such as *Chaoborus*, also derived a significant subsidy from t-POC. T-POC was also the largest source of organic carbon to benthic invertebrates, but terrestrial prey was a very minor C input in the study of Cole et al. (2006).

## 1.2. Basic food web concepts

The structure of a food web critically affects the functions of the ecosystem to which it belongs. The resilience of an ecosystem to perturbation and how tightly an ecosystem retains its inorganic nutrients are examples of ecosystem functions dependent on food web design (Pimm 1982). The movement of food energy from primary producers to herbivores and ultimately to carnivores is referred to as a food chain. Early workers realized that many species belong to several food chains and that these chains form food webs (Hardy 1924, Elton 1927). Since their conception a large amount of theoretical work has been developed around food webs. However, theoretical, as well as empirical, aspects of food chain theory are largely based on consumption; that is, most studies presuppose that the only important interaction between predator and prey is that they actually meet and that the prey is consumed.

Pimm (1982) recognized the following general characteristics of food webs: Food chains tend to be short and connectance decreases hyperbolically with the number of species in the web. Omnivory (feeding on more than one trophic level) is rare and is more common in food webs dominated by insect-predator-parasitoid interactions. Donor (prey) – controlled dynamics are expected in some systems such as detritivore webs, and these webs have complex patterns of omnivory. Loops and oddities, such as predators without prey and two top predators feeding on same prey, are rare.

There are certain problems among data collection in the field (Paine 1988). Because all organisms are not easily observed, most food webs tend to be deficient in the inclusion

of “ecologically subtle” species. Species that are observable are often highly mobile, and as such they may be underrepresented in food web models. These species may affect trophic relationships significantly. The influence of species that are transient and not normally part of any local assemblage, and ontogenetic changes in the diets of species that are common, are often overlooked. General lack of examination of the role of microorganisms and the microbial loop in affecting the cycling of nutrients at primary levels in food webs brings new problems to model food webs.

Conceptualization of niche as an  $n$ -dimensional hypervolume (Hutchinson, 1957) was a crucial foundation and since then ecologists have tried to understand the development of community structure. Occupied niche space implies resource use. Niche parameters can respond very rapidly to changes in intraspecific and interspecific competition as well as prey abundance. Trophic niche width, often assessed using dietary diversity, is the most tractable and frequently studied component of niche space. Before temporal integration of dietary information trophic niche width was often difficult to quantify, because many dietary studies were snapshots of diet at a point of time. If population appears to show a large dietary niche, it is important to know whether it is composed of generalist individuals all taking a wide range of food types or individuals each specializing on a different but narrow range of food types (Van Valen, 1965; Grant et al. 1976).

### 1.3. *Daphnia* and invertebrates predators

In fishless lakes and ponds, where invertebrate predators are more important, large zooplankton species dominate (Mazumder 1994). The scarcity of small zooplankton species has been explained by size-selective predation on small zooplankton species by invertebrate predators (Vanni 1988, Arnott and Vanni 1993). Another possibility, according to the size-efficiency hypothesis, is competitive suppression of small zooplankton by large, more efficient, filter feeding species, particularly daphnids (Carpenter 1988, Arnott and Vanni 1993). Some large invertebrate species can consume the same sizes of zooplankton that fish eat, but these prey are not preferred (Pastorok 1981). Invertebrate predators mostly consume small- to medium-sized prey and zooplankton communities subjected to heavy invertebrate predation are commonly dominated by large-bodied species (Riessen et al. 1988). Increased water colour can shift the balance between fish and *Chaoborus* as a planktivorous predator, leading to the dominance of large zooplankton species in brown-water lakes (Wissel et al. 2003). Most invertebrate predators are tactile, not visual, hunters and so do not rely on light to detect prey (Giguere 1980). Fishless ponds have usually more diverse insect fauna than ponds containing fish.

In this study of Mekkojärvi the main invertebrate predators of interest were *Notonecta* (Hemiptera), *Chaoborus* (Diptera) and Odonata, which all have different strategies and occupy different habitats. *Chaoborus*, or phantom midge larvae, occupy the pelagic zone and show strong vertical migrations, feeding on zooplankton in the epilimnion by night, but moving to the anoxic hypolimnion in the day. Odonata, dragonfly, larvae live among water plants and sphagnum mats in the littoral zone, and are sit-and-wait predators. *Notonecta*, water-boatman, is a large active organism susceptible to fish predation and hence generally restricted to the littoral zone; however, in fishless Mekkojärvi notonectids are able to forage widely in the open water. *Daphnia longispina* is the most abundant crustacean zooplankton in the lake, where planktivorous fish are absent, and the main invertebrate predators are thought to be *Chaoborus* larvae and *Notonecta* spp.

Dragonfly nymphs are a very conspicuous component of the fauna of many freshwater habitats, especially permanent lakes, ponds and marshes. In permanent waterbodies at high latitude, life cycles may take as long as five years or even more, depending on the species and habitat. Emergence from the last nymphal stages to the adult usually takes place after the nymph has climbed above the water surface on an emergent plant or rock. Odonata larvae have become specialized so that different species occupy a wide range of habitats, and a diversity of microhabitats, within a single body of water. Their unvarying possession of an extensible, prehensile labium indicates that all Odonata larvae are predatory, being appropriately classified as swallows (Cummins 1973). The free-living dragonfly larva requires animal food for maintenance and growth. Normally prey is detected by its movement and caught alive, but larvae of Zygoptera and Anisoptera sometimes eat dead or immobile prey that they recognize visually by its shape or by chemical cues. A larva captures living prey by remaining cryptic and almost immobile until the prey comes within range of the extended labium (the ambush or sit and wait mode), or by walking, often at night, to search for prey (the hunting or active mode) (Janetos 1982). Most species use both modes at different times. Choice and frequency are characteristic of a species and being influenced by exogenous factors such as the kind and density of prey and the presence of predators, usually fish.

Odonate larvae diets (e.g. Thompson 1978a) in nature consist mainly of other macroinvertebrates, larvae of Diptera and planktonic animals. Larval odonates can catch animals above the water surface, for example water striders (*Gerris* spp.) (Spence 1986) or terrestrial and ovipositing insects (Johnson 1968, Godfrey and Thompson 1987). Mature gastropods and larval amphibians are eaten by *Aeshna* (Belyshev and Belyshev 1976, Crump 1984). It can be assumed that, depending on their availability, all taxa of freshwater invertebrates, as well as fishes and amphibians, serve as prey for odonate larvae, as do other odonates. Previous studies of odonate larvae diets are based on analysis of the contents of faecal pellets. This method needs no dissection and larvae can be returned alive to nature, but it is rather ineffective, because prey has been usually crushed by the mandibles. These problems might nowadays be overcome using stable isotope analysis.

According to Ward (1992) Hemipterans are members of truly aquatic families and leave the water only during migratory dispersal flights. All aquatic Hemiptera bugs, except a few species with plastron respiration, must periodically surface to renew their air supply. The general Hemipteran life cycle in the temperate zone involves egg laying in the spring, nymphal development during summer, adults appearing in July/August/September, and over-wintering as an adult (Damgaard 1997; Kurzatowska 1993). The Notonectidae, or backswimmers/water-boatman are distributed worldwide (Schuh and Slater 1995). They are frequent components of the fauna of fishless ponds, where they are located at the top of pelagic food webs (Brönmark and Hansson 1998). All Notonectidae are aquatic predators as nymphs (all the five instars) and adults, which detect their prey both visually and through mechanoreceptors (Cooper et al. 1985). They feed upon zooplanktonic organisms and other prey from the water column, such as insect pupae, which swim towards the water surface and to a lesser extent on dead aerial insects floating at the water surface (Gilbert and Burns 1999). Large individuals can also kill smaller individuals of same species. Hemipterans do not ingest their prey but kill them by poison injected through their piercing mouthparts after which they suck out the prey juices. Svensson et al. (2000) found that *N. glauca* was present in 63 out of the 72 *Notonecta* inhabited waters and in all habitat types, strongly indicating a generalistic mode of life, as suggested also by Damgaard (1997) and Kurzatowska (1993). Since nymphs do not have wings, they have to feed in the ecosystem



where they hatched. They may therefore integrate all the possible changes occurring at lower levels of the food web.

*Chaoborus* larvae (Chaoboridae, Diptera) are normally regarded as the only planktonic insects. Because they are relatively large and motile, chaoborids could be categorized as nekto plankton. *Chaoborus* occur in the deepest parts of lakes and they migrate vertically to the upper water column at night to feed. In larval *Chaoborus* the tracheal system is reduced to two kidney-shaped air sacs, functioning solely as hydrostatic organs (Saether 1972). *Chaoborus* are predators on zooplankton and can be as important predators as fishes for zooplankton population dynamics (Ramcharan et al. 2001a, b). Phantom midges generally consume young *Daphnia*, preferring individuals of certain sizes and shapes (Dodson 1989).

Usually Chaoboridae uses the dark parts of water column as a refuge from fish predation. Light plays a major role in the diel vertical migration. Pope et al. (1973) found out in fishless ponds phantom midges may have reduced vertical migration and remain within the epilimnion during day. Some investigations have also reported additional migration from pelagic to the littoral zone during spring (Wood 1956, Roth 1968). Such movements may be adaptations enabling mature larvae to be exposed to warmer water prior to pupation and emergence as an adult (Borutsky 1939). Using a sonar system, a horizontal component in the diel migration has also been documented (Franke 1987). The first larval instars are nonmigratory and remain near the surface. As larvae mature, they tend to move progressively deeper during the day (Swift and Forward 1980).

In recent years it has become apparent that planktonic *Daphnia*, a typical and important member of the pelagic food web (Scheffer 1998), exhibits diel horizontal migration behavior (DHM) between the pelagic and the littoral (Kvam and Kleiven 1995, Lauridsen and Buenk 1996). DHM seems primarily an anti-predation strategy, driven by the presence of pelagic predators (Burks et al. 2002). Migrating to the littoral, however, may impose a new threat: mortality due to littoral predators. The possible influence of littoral predators on *Daphnia* and their DHM has repeatedly been stressed, but relevant empirical data are scarce. There are at least two studies that strongly suggested a negative effect of littoral odonates on *Daphnia* densities in the field (Blois 1985, Burks et al. 2001b), indicative of a direct pelagic - littoral link. As such, it is not known whether *Daphnia* recognizes the presence of littoral predators and responds with adaptive anti-predation strategies. Induced anti-predation behavior may influence the impact of littoral predators and may impact the DHM itself. No studies have yet focused on this behavioral link between pelagic prey and littoral predators.

Ecologists commonly characterize *Daphnia* as pelagic zooplankters, but recent studies suggest that daphnids also occur in littoral habitats (Lauridsen and Buenk 1996). Littoral–pelagic links may be important structural forces in aquatic food webs in smaller shallow lakes. Daphnids are keystone grazers (sensu Power et al. 1996) in lakes because they control algal populations (Scheffer 1998). However, because of their size, daphnids are also the preferred food of planktivorous fish in the pelagic zone. Recent research suggests that daphnids adaptively seek refuge in macrophytes when they perceive a predation threat from pelagic planktivorous fishes (Lauridsen and Lodge 1996, Burks et al. 2001a), although the degree of migration depends on plant density and distribution and abundance of the fish (Jeppesen et al. 1998). Horizontal migration to escape pelagic fish or pelagic predatory invertebrates (Kvam and Kleiven 1995), however, forces daphnids into the domain of other predators associated with littoral vegetation and sediment. Only one previous field study strongly linked pelagic zooplankton as prey to predatory odonates

(Blois 1985). Three different species of dragonflies (*Anax imperator*, *Aeshna cyanea*, and *Libellula depressa*) all readily consumed *Daphnia* (based on availability) in a small, vegetated pond in France (Blois 1985). Burks et al (2001b) suggested that, in some situations, daphnids occupying the littoral zone can suffer high mortality from odonate predation. Body size of prey in their field experiment may explain why odonate predation significantly reduced daphnids, but not ceriodaphnids, at low macrophyte densities. Size-selective foraging theory suggests that predators will preferentially consume the largest prey (Brooks and Dodson 1965). Odonates easily consume large (>2 mm) daphnids in laboratory studies (Thompson and Pickup 1984, Wissinger 1988). In addition, jerky swimming movements of large *Daphnia* probably attracted the attention of sit-and-wait odonate nymphs.

Although invertebrates generally are considered to be less efficient predators than fish, they may also cause substantial reductions of zooplankton prey species. This has been shown for backswimmers (*Notonecta*), phantom midge larvae (*Chaoborus*) and calanoid and cyclopoid copepods (Murdoch et al. 1984, Brett 1992, Arnott and Vanni 1993). Many invertebrate predators (e.g. *Chaoborus*) prefer small size classes of prey that are easier to handle and ingest (Swift and Federenko 1975, Black and Hairston 1988). In contrast, early instar backswimmers selectively prey on the largest size classes of zooplankton. Members of the genus *Notonecta* are capable of co-existing with, as well as eliminating, daphnids under natural condition (Scott and Murdoch 1983, Murdoch et al 1984). In the absence of fish, macroinvertebrate predators may significantly reduce densities and change the size distribution of zooplankton, which may have repercussions on lower and/or higher trophic levels (Murdoch et al. 1984, Black and Hairston 1988, Brett 1992). *Notonecta* selectively preyed on *Daphnia* and the intense predation reduced the *Daphnia* populations to extinction within 4 weeks in a rock-pools-like experiment, only one adult *Notonecta* were presented to *Daphnia* and all daphnids were gone in the laboratory after few days (Arnér et al 1998).

Spatial avoidance behaviour has been particularly well documented in cladocerans of the genus *Daphnia* and can include both vertical migration (Boersma et al. 1998, De Meester et al. 1999) and horizontal migration (Lauridsen and Buenk 1996, Burks et al. 2002). Several invertebrate predators with contrasting habitat use have been shown to induce vertical migration in *Daphnia*. In the presence of only larval *Chaoborus* predators and only adult *Notonecta* predators and their chemical cues, upward and downward movements of *Daphnia* have generally been reported, respectively (reviewed by De Meester et al. 1999) So far, only Nesbitt et al. (1996) confronted *Daphnia* with both types of predators. In the presence of both *Chaoborus* and *Notonecta*, the upward migration response to the presence of *Chaoborus* was modified in the daytime (but not at night) to a simultaneous avoidance of areas occupied by each predator.

Several invertebrate predators have striking horizontal patterns of distributions in ponds (Marklund et al. 2001; Hampton 2004) and may have a large predation impact on cladoceran communities, especially in fish-free habitats (Wissel et al. 2000, Blumenshine and Hambright 2003). Van de Meutter et al. (2005) showed that the horizontal distribution of *Daphnia* in an environment consisting of an open water zone and a vegetated zone was affected by the presence of damselfly larvae and *Chaoborus*, by quantifying the predation impact of these invertebrate predators on *Daphnia* in open water and a vegetated environment. It is expected that these results apply mainly to small and shallow lakes, where open water and vegetated areas are closely connected, and where *Daphnia*, *Chaoborus* and *Ischnura* are especially likely to interact with each other.

#### 1.4. Stable isotope analysis

Natural abundance stable isotopes have become an important tool for determining element fluxes and cycling in a variety of systems. Carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) are the most frequently used isotopes in food web and ecosystem studies. Stable Isotope Analysis (SIA) is based on predictable changes in isotopic ratios, known as fractionation, as elements move in food chains (Peterson and Fry 1987). The isotope ratios from samples are referred to international standards and the differences are given parts per thousand (‰) delta values ( $\delta^{13}\text{C}$ ). Isotope fractionation is defined by O'Leary (1988) as:

$$\Delta\delta = \frac{[\delta * X(A) - \delta * X(B)]}{1 + \delta * X(A) / 1000}$$

where  $\Delta$  is the change in the isotope ratio that occurs in the reaction from substrate A to product B, and  $*X(A)$  and  $X(B)$  are the corresponding stable isotope ratios.

The utility of isotopes lies in the fact that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in predictable manner (Hobson, 1999a). The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  exhibits a stepwise enrichment (increase in the value  $\delta^{13}\text{C}$ ) at each trophic level and consequently the  $\delta^{13}\text{C}$  values in the tissues of consumers tend to be in the order of 1‰ higher than those of their food (DeNiro and Epstein 1978, Fry and Sherr 1984). The carbon isotopic composition of consumer tissues are thus a function of increases in the enrichment value ( $\delta^{13}\text{C}$ ), the relative proportions of each prey species assimilated, the isotopic fractionation associated with converting prey tissues into consumers tissues and in certain instances foraging location. The stable isotope signatures of tissues generally reflect the diets over the period during which the tissue was synthesized (Bearhop et al. 2002).

Before SIA, food web studies were based on snapshot samples of organism diets, and studied gut samples have included particles that are unidentified or do not really belong to the diet. SIA also incorporates omnivory and therefore traditional discrete trophic levels can be viewed more accurately as a continuous scale. Stable isotope ratios in animal tissues can be used to reconstruct diets, to trace movements, to assess physiological condition and to determine the fate of assimilated nutrients within an animal. Using the isotopic signal in an animal's tissues to determine the relative contribution of different food items to its diet relies on a very important assumption, that the isotopic composition of an animal's tissues equals the weighted average of the isotopic composition of the constituents of its diet. However, in practice this assumption is rarely valid, because 1) animals assimilate dietary components with varying efficiencies, 2) animal tissues fractionate the isotopes in their diet and 3) animals allocate nutrients in their diet differentially to specific tissues (Gannes et al. 1997).

Traditionally, food web studies using stable isotopes have provided qualitative depictions of trophic structure of single systems. Yet major advances in the use of stable isotopes have involved quantitative estimates of food web parameters, allowing examination of food web patterns and treatment of applied problems. Such quantitative applications require assumptions about the behaviour of the isotopic tracer, and in particular the change in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from prey to predator. Provided  $\Delta\delta^{15}\text{N}$  and  $\Delta\delta^{13}\text{C}$  are known, variables such as omnivory, trophic position, food chain length, and energy flows and sources can be calculated (Vander Zanden 2001).

Bearhop et al. (2004) made assumptions for use of stable isotope techniques as a measure of food niche width. First, prey species must differ isotopically. This can be assessed by isotopic characterization of potential prey items. If variation doesn't exist, then this assumption would be invalid. Second, the isotope signatures at the base of the food-web and the diets of prey species remain relatively invariant over time. Baseline isotope signatures can change over time as a consequence of primary production shifts or nutrient inputs, and dietary preferences of prey may also change. Third, the tissue analysed reflects the period over which the niche width is expressed. In a population of generalists, variability in diet among individuals will tend to exist at only shorter temporal scales, and this variation is likely to become lost through averaging of the stable isotope signature over longer periods.

Stable isotopes of carbon can help to distinguish organic matter sources (Peterson et al. 1985), but often isotopic differences between autochthonous and allochthonous materials are not distinct. If there is a sufficient contrast between the  $\delta^{13}\text{C}$  of terrestrial and aquatic primary production, it is possible to relate components of the food web to these two extremes (Meili et al. 1996, France et al. 1997, Jones et al. 1999). However, in many cases this contrast is small and one cannot easily resolve alternative sources to the food web (Schiff et al. 1990, Cole et al. 2002). One approach is to construct a model of the lake food web and follow the paths of autochthonous and allochthonous carbon, but calibration and validation of such a model is difficult.

Cole et al. (2002) worked in softwater, humic lakes where the DOC and POC have isotopic  $\delta^{13}\text{C}$  signatures of (-26‰ to -29‰), which overlap values of terrestrial inputs. They reasoned that by manipulating the  $\delta^{13}\text{C}$  of dissolved inorganic carbon (DIC) in the lake, the autochthonous primary production would acquire a distinctive isotopic signature. Coupled with measurements of total C pools and most of the relevant C transformations, the  $^{13}\text{C}$  manipulation should create an ideal condition under which to test how  $^{13}\text{C}$  is fractionated during initial fixation under field conditions, subsequently moves through the food web and is diluted by the utilization of allochthonous C.

Pace et al. (2004) added  $\text{NaH}^{13}\text{CO}_3$  to enrich the  $^{13}\text{C}$  content of dissolved inorganic carbon, and subsequently of particulate organic carbon, zooplankton and fish. Carbon assimilated by *Daphnia* was transferred up the food web because *Daphnia* is a key prey for macroinvertebrate predators and fish. *Daphnia* fed primarily in the surface layer and not on sources from deeper layers including methanotrophic bacteria (Jones et al. 1999, Pace et al. 2004). POC turns over within 1-10 d through respiration, conversion to DOC, consumption or sinking (Cole et al. 2002) and new inputs must replace the continuous losses of POC. The  $^{13}\text{C}$  additions indicated that about half of this carbon came from sources other than autochthonous primary production, had a  $\delta^{13}\text{C}$  value consistent with that of terrestrial plants, was assimilated by animals and was passed up the food web (Pace et al. 2004). In a later study by Cole et al. (2006), the addition of  $^{13}\text{C}$  resulted in a large increase in the  $^{13}\text{C}$  content of the DIC in the lakes, primary producers and consumers. In all cases primary producers became highly labelled but the degree of labelling in the consumers, relative to the primary producers, was quite different among the lakes and type of consumer. Cole et al. (2006) suggested that an alternative food source such as unlabelled terrestrial carbon was supporting some consumers.

## 1.5. Objectives of this study

The objective of this study was to examine the trophic positions of invertebrate predators and the carbon pathways in the littoral food web using stable isotope methods and to evaluate if *Daphnia longispina* is an important food resource for invertebrate predators in small forest lakes. One question to answer is what happens to all the *Daphnia* production when there are no planktivorous fish that would normally consume *Daphnia*. Mekkojärvi is a very humic lake lacking the planktivorous fish which are normally considered as top predators. There are only a few small pike that mainly consume invertebrate prey such as dragonfly larvae (Syväranta 2004). Thus it must be assumed that invertebrate predators are the highest predators in the lake.

My study was conducted at the same time as Taipale and others (2007) did whole-lake  $\delta^{13}\text{C}$  additions to reveal seasonal shifts between multiple food source contributions to zooplankton diet. Experimental manipulation of the  $\delta^{13}\text{C}$  of the autochthonous organic matter produced within the lake by addition of  $^{13}\text{C}$ -enriched inorganic carbon (bicarbonate), which will lead to increased  $\delta^{13}\text{C}$  of primary producers utilizing the enriched carbon in their photosynthesis. The relative importance of different carbon sources to lake food webs may actually be seasonally highly variable. If there is a change in *Daphnia*  $\delta^{13}\text{C}$  values, then there should also be a change in predator  $\delta^{13}\text{C}$  values, if invertebrate predators consume *Daphnia*. It was also expected that the isotope signatures in *Daphnia* and invertebrate predators would change during the year, based on the fact that chaoborids, notonectids and odonates can all use zooplankton as a food resource and that there are no vertebrate predators to limit invertebrate predation and foraging for prey.

## 2. MATERIALS AND METHODS

### 2.1. Lake Mekkojärvi

Mekkojärvi (61°13'N 25°3'E) is a small (0.0035 km<sup>2</sup>) headwater pond in southern Finland with a high concentration of allochthonous humic matter (water colour 300-800 mg Pt L<sup>-1</sup>) and a rather high acidity (pH 4.6–6.2). The maximum and mean depths of the pond are 4.3 m and 2.0 m, respectively. It exhibits steep thermal and chemical stratification; in summer its thermocline lies at depths of 0.5–1.0 m and total anoxia with waters rich in hydrogen sulphide prevails below about 1.0 m. During ice cover, from mid-November to the beginning of May, Mekkojärvi becomes completely anoxic, which prohibits maintenance of a planktivorous fish population. Because of the dark water and the sheltered location the surface water temperature may reach nearly 30°C during sunny summer days. The oxygenated epilimnion of Mekkojärvi is only 50 cm deep and under this is an anoxic hypolimnion. Methanotrophic bacteria are found at anoxic/oxic interfaces. Due to its small size and hence absence of wave action, there is no traditional littoral, but the pond is surrounded by a floating *Sphagnum* and *Warnstorfia* moss mat. In addition to the high load of terrestrial organic matter, one of the most characteristic features of the pond is its very dense population of a large cladoceran *Daphnia longispina* (O. F. Müller) that almost exclusively contributes to the biomass of the summer zooplankton (Salonen & Lehtovaara 1992). Its abundance is largely explained by the absence of planktivorous fish. The lake is ice-free usually from the beginning of May to mid-November, and the whole water column turns over in autumn but only partially in spring. During summer the uppermost 1-m layer is oxic. The concentration of dissolved inorganic carbon is 3-12 mg C L<sup>-1</sup>.

## 2.2. <sup>13</sup>C enrichment and data collection

Three separate whole-lake <sup>13</sup>C-addition experiments were made during spring (16 May-3 June), summer (11 July-1 August) and autumn (19 September – 3 October) in 2005. For each experiment, initially a stock solution containing 0.24 mmol of NaH<sup>13</sup>CO<sub>3</sub> (99 atom%, CK Gas Products Ltd.), and subsequently 0.18 mmol of NaH<sup>13</sup>CO<sub>3</sub> was first diluted in 80 L of lake water and then spread into the epilimnion from a watering can while rowing around the lake. Additions were made three times per week and represented an increase in absolute epilimnetic DIC concentration of just 0.003% per day during each addition period. After enrichment, *Daphnia* and macroinvertebrates were collected from the lake with nets (total number of invertebrates in spring 16, summer 77, autumn 41). Collection was approximately standardised by using the same time in the same place when collecting samples. Samples were sorted taxonomically and the largest were placed individually in tap water tubes for 24 hours to evacuate their guts. All odonates and notonectids were analysed separately, but spiders, damselflies, corixids, caddisflies and ephemeropterans were dried and analysed as several individuals together. Samples were dried in the oven (~60 °C) and then weighed to get dry weight for division of size classes. All samples were ground to fine powder with a pestle in a glass vial and stored in a desiccator before stable isotope analyses. Several insects from the same taxa were used as replicates and same sized animals were treated as blocks to decrease treatment effects.

Samples were analysed in the Institute for Environmental Research, University of Jyväskylä. Samples were analysed in three parts during winter 2005-2006. For each sample a small amount of ground powder were weighed to tin cups, wrapped with tweezers to a small ball and analysed with continuous flow isotope mass spectrometry. Results are expressed with δ values. Carbon and nitrogen stable isotope ratios were expressed as parts per thousand (‰) delta values (δ<sup>13</sup>C and δ<sup>15</sup>N) referred to international standard. Standard reference materials are carbon in the PeeDee limestone and nitrogen gas in the atmosphere (Peterson and Fry 1987). These delta values were calculated using the following formula:

$$\delta^{13}\text{C} = [ ( X_{\text{sample}} / X_{\text{standard}} ) - 1 ] \times 1000$$

where X = <sup>13</sup>C/<sup>12</sup>C. The same equation is used with nitrogen values, expect X = <sup>15</sup>N/<sup>14</sup>N.

## 2.3. Data analysis

Trophic positions of organisms were assessed after stable isotope analysis from δ<sup>13</sup>C and δ<sup>15</sup>N scatter plots with Microsoft Excel. All *Libellula* sp. dryweights were plotted against δ<sup>13</sup>C and δ<sup>15</sup>N values to test for size-related changes. Sizeclasses were divided to three groups (Small = < 0.0009; Medium = 0.001-0.009; Large = >0.01 g dry weight) and tested with ANOVA and 2-ANOVA with SPSS 14.0 to test for differences between sizeclasses in carbon/nitrogen values during summer.

## 3. RESULTS

During spring 2005 (Figure 1) all observed odonata values were clearly separated from *Daphnia* values. Odonates were not sorted further to families. Only one individual *Asellus* was caught in spring, but this taxon is one possible food resource for odonates. Tadpoles and water striders could be easy targets for predators and have been suggested in the literature to be a food resource for odonates, but stable isotope analysis shows clearly that odonates had not been feeding on tadpoles in Mekkojärvi. Similarly, odonates had not

been feeding on *Gerris* sp. in spring in Mekkojärvi. All individuals were sampled at the same time but odonate values reflect their diet during the preceding weeks.

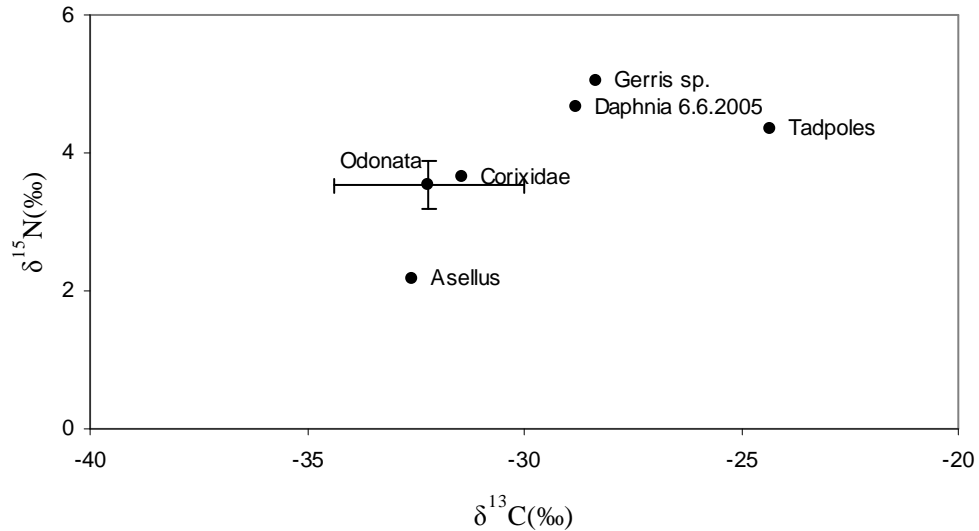


Figure 1. Stable isotope  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot representing part of the littoral food web in Mekkojärvi in June. All observations are mean values, bars for Odonata show standard deviations.

In July (Figure 2) *Daphnia*  $\delta^{13}\text{C}$  values were lower than in spring. The results suggest that Notonectidae might have been feeding extensively on *Daphnia* because carbon fractionates about 0.5 ‰ between food and consumers. The data also indicate that *Daphnia* may have been an important component of the diet of Aeshnidae at this time, but this does not appear to have been the case for Libellulidae.

In September (Figure 3), daphnids were even more highly depleted in  $\delta^{13}\text{C}$  and separation between them and odonata in carbon values was about 16 ‰, and also clearly shows that odonata did not consume *Daphnia*. Instead Ephemeroptera, Trichoptera and *Asellus* are possible food resources for odonates. Unfortunately no *Chaoborus* were caught during summer and so a potentially critical part of the food web is missing.

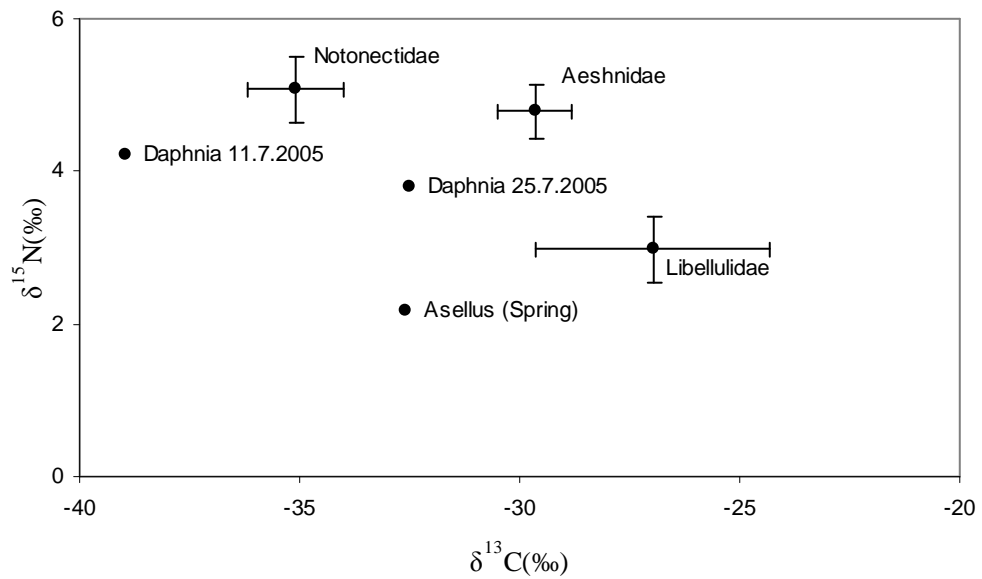


Figure 2. Stable isotope  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot representing part of the littoral food web in Mekkojärvi in July 2005. All observations except daphnids are mean values with standard deviations indicated by bars. Odonates are also divided to two different families. *Daphnia* is represented with two dates to show how the isotopic value changes within two weeks.

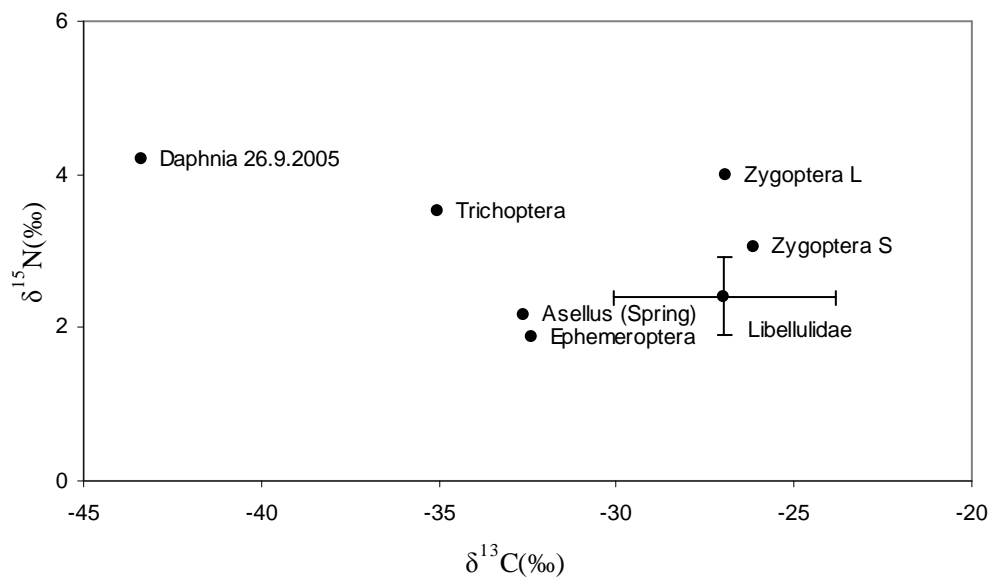


Figure 3. Stable isotope  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot representing part of the littoral food web in Mekkojärvi in September.



All *Libellula* sp. (Odonata) individual  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were plotted against dry weights (Fig 4.), and it can be clearly seen that larger individuals were feeding on more  $^{13}\text{C}$ - depleted food resources in autumn ( $r^2=0.525$ ), but in summer the relationship is less strong ( $r^2=0.145$ ).

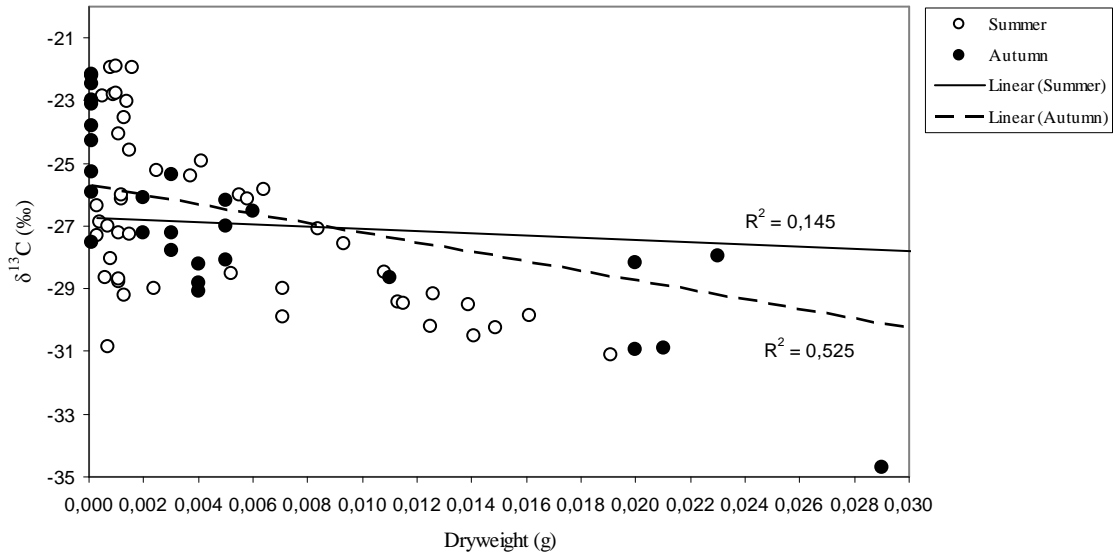


Figure 4. Dependence of individual *Libellula* sp.  $\delta^{13}\text{C}$  on dry weight in July and September 2005. Summer linear regression analysis  $r^2 = 0.145$ ;  $y = -26.73 - 35.66x$ ;  $p = 0.006$ . Autumn linear regression analysis  $r^2 = 0.525$ ;  $y = -25.67 - 152.01x$ ;  $p < 0.001$ . The four largest individuals (dry weights 0.059-0.143 g) are excluded from the figure but were included in the analysis.

There was also a quite strong relationship between  $\delta^{15}\text{N}$  and dryweight (Fig.5). The relationship was stronger in July than in September.

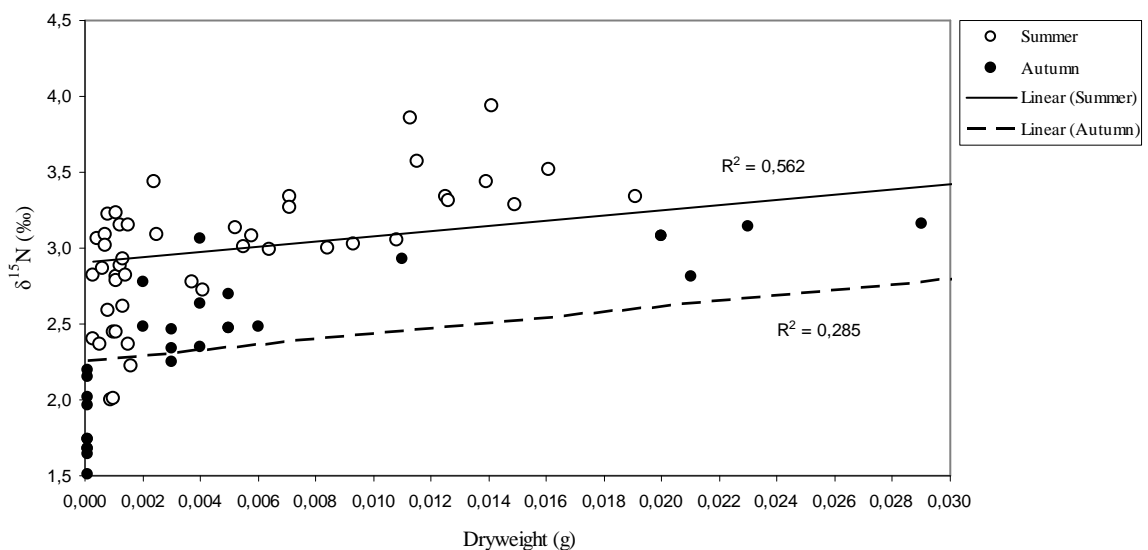


Figure 5. Dependence of individual *Libellula* sp.  $\delta^{15}\text{N}$  on dry weight in July and September 2005. Summer linear regression analysis  $r^2 = 0.562$ ;  $y = 2.9 + 17.2x$ ;  $p < 0.001$ . Autumn linear regression

analysis  $r^2 = 0.284$ ,  $y = 2.25 + 180.07x$ ,  $p < 0.001$ . The four largest individuals (dry weights 0.059-0.143 g) are excluded from the figure but were included in the analysis

Table 1. SPSS 14.0 for Windows 2-Anova results of  $\delta^{13}\text{C}$  carbon and  $\delta^{15}\text{N}$  nitrogen values and post hoc tests between the three size classes of *Libellula* sp.

ANOVA						
		Sum of Squares	df	Mean Square	F	p
$\delta^{13}\text{C}$	Between Groups	250.339	2	125.170	16.523	<0.001
	Within Groups	643.923	85	7.576		
	Total	894.262	87			
$\delta^{15}\text{N}$	Between Groups	16.632	2	8.316	29.470	<0.001
	Within Groups	23.985	85	0.282		
	Total	40.616	87			

Multiple Comparisons							
Tukey HSD							
Dependent Variable	(I) Sizeclass	(J) Sizeclass	Mean Difference (I-J)	Std. Error	p	95% Confidence Interval	
						Lower Bound	Upper Bound
$\delta^{13}\text{C}$	small	medium	2.54835(*)	0.73482	=0.002	0.7955	4.3012
		large	4.94341(*)	0.85995	<0.001	2.8920	6.9948
	medium	small	-2.54835(*)	0.73482	=0.002	-4.3012	-0.7955
		large	2.39506(*)	0.72244	=0.004	0.6717	4.1184
	large	small	-4.94341(*)	0.85995	<0.001	-6.9948	-2.8920
		medium	-2.39506(*)	0.72244	=0.004	-4.1184	-0.6717
$\delta^{15}\text{N}$	small	medium	-0.61226(*)	0.14182	<0.001	-0.9506	-0.2740
		large	-1.27286(*)	0.16597	<0.001	-1.6688	-0.8770
	medium	small	0.61226(*)	0.14182	<0.001	0.2740	0.9506
		large	-0.66061(*)	0.13943	<0.001	-0.9932	-0.3280
	large	small	1.27286(*)	0.16597	<0.001	0.8770	1.6688
		medium	0.66061(*)	0.13943	<0.001	0.3280	0.9932

All odonate individuals were divided to three size classes based on their dry weights and tested with ANOVA and 2-ANOVA for difference between size classes and time of year in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Most individuals belonged to sizeclass M (n=47) while sizeclasses S (n=20) and L (n= 21) contained fewer but about equal numbers individuals.

The difference between size classes was highly significant (Table 1) with both  $\delta^{13}\text{C}$  values (Fig. 6) (ANOVA,  $F = 16.523$ ,  $p < 0.001$ ) and  $\delta^{15}\text{N}$  values (Fig. 7) (ANOVA,  $F = 29.470$ ,  $p < 0.001$ ). There is an interaction between date and size class: both time of year and size class influence  $\delta^{13}\text{C}$  value (2-ANOVA,  $F = 5.007$ ,  $p = 0.009$ ), and  $\delta^{15}\text{N}$  value (2-ANOVA,  $F = 4.401$ ,  $p = 0.015$ ).

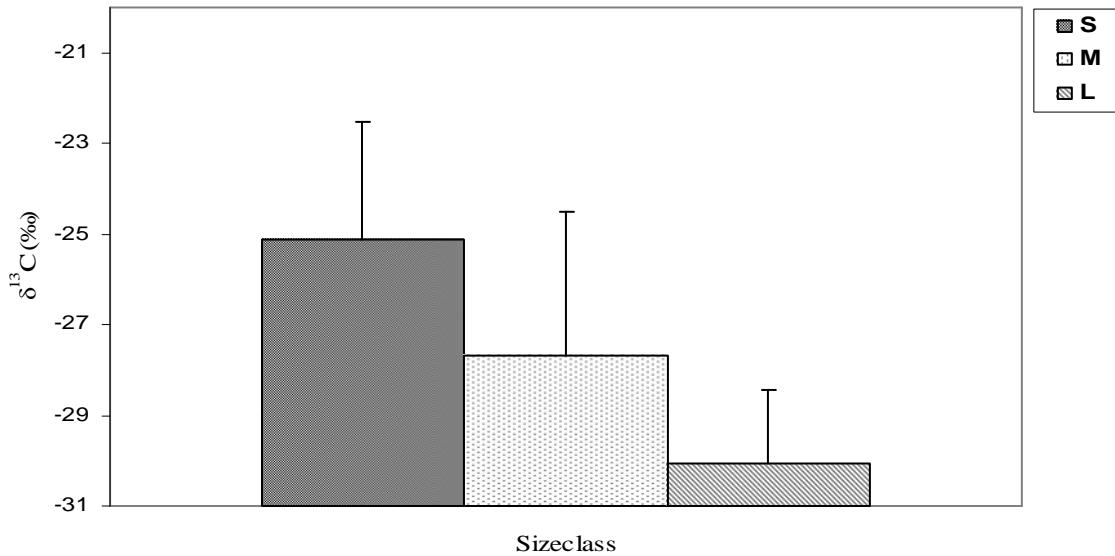


Figure 6. Differences in  $\delta^{13}\text{C}$  values between odonate size classes based on dry weight. Vertical lines present the standard error. All differences between size classes are statistically significant ( $p < 0.005$ ). Small individuals have more enriched values than medium sized and large individuals. The largest are feeding on more depleted food resources. In size class S  $n=20$ , in M  $n=47$ , and in L  $n=21$ .

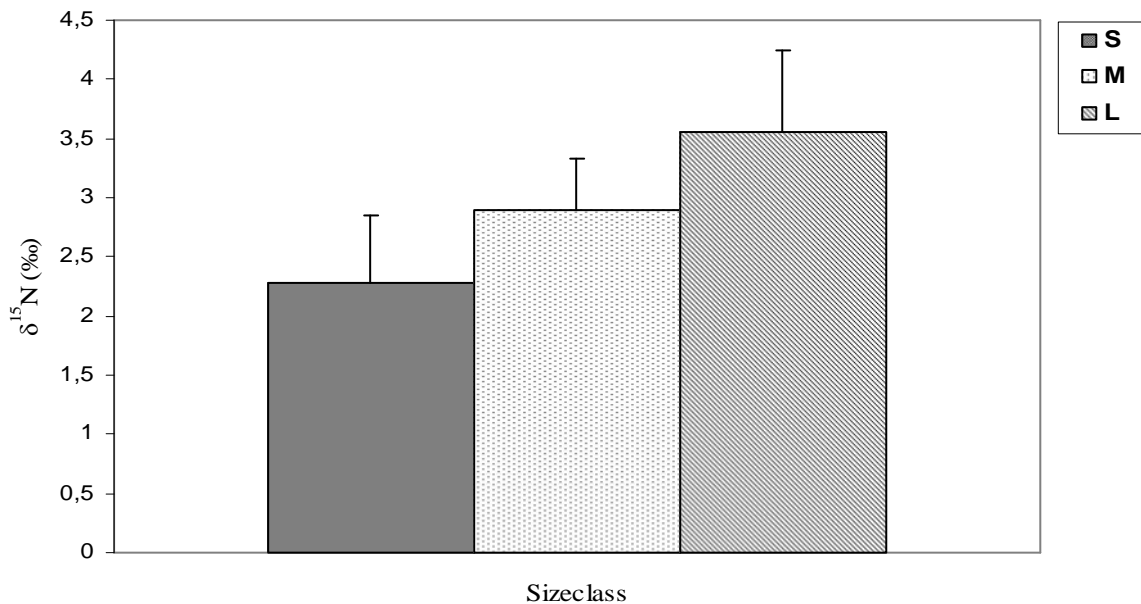


Figure 7. Differences in  $\delta^{15}\text{N}$  values between odonate size classes based on dry weight. Vertical lines present the standard error. All differences size class  $\delta^{15}\text{N}$  values are statistically significant ( $p < 0.001$ ). In size class S  $n=20$ , in M  $n=47$ , and in L  $n=21$ .

Values for each size class are means of multiple replicates, with associated standard errors. However, it should be noted that in some cases an individual analysis comprised several pooled individual odonates to provide sufficient material for stable isotope analysis.

#### 4. DISCUSSION

During the spring, summer and autumn periods, the added  $\text{NaH}^{13}\text{CO}_3$  quickly increased the epilimnetic DIC  $\delta^{13}\text{C}$ , but had negligible influence on DIC in the meta- and hypolimnion. The  $^{13}\text{C}$ -enrichment of DIC was quickly transmitted onwards to POM and to adult and juvenile *Daphnia*, which became about 10‰ more enriched than initial  $\delta^{13}\text{C}$  values (Taipale et al. 2007, in press). Odonate stable isotope values changed during summer, as hypothesized, but all observed odonate values were clearly separated from *Daphnia* values. In July the difference in  $\delta^{13}\text{C}$  values between odonates and *Daphnia* began to grow, as *Daphnia* evidently changed its food resource to include more  $^{13}\text{C}$ -depleted methanotrophic bacteria (Taipale et al. 2007a, 2007b). In September, daphnids were highly  $^{13}\text{C}$ -depleted and the distinction between them and odonata was over 16‰. At the same time, odonate  $\delta^{13}\text{C}$  values actually increased from spring to summer. This shows quite clearly that odonates in Mekkojärvi did not consume *Daphnia*, to any significant extent. In contrast, Ephemeroptera, Trichoptera and *Asellus* are all possible food resources for odonates in Mekkojärvi. With the samples collected it can be concluded that, contrary to initial expectation, *Daphnia* is not a significant food resource for odonate predators in Mekkojärvi.

In some scatterplot stable isotope biplots, *Daphnia* would even appear to be at a higher trophic level than odonates according to  $\delta^{15}\text{N}$  values, if the commonly accepted 3.4‰ increase in  $\delta^{15}\text{N}$  per trophic level is applied (Minagawa and Wada 1984, Vander Zanden 2001). However, this is clearly impossible and is due to two different food chains. The reason why odonates do not consume *Daphnia* and why they are in different food chains might be that large bodied daphnids and odonates do not meet because of *Daphnia* different diel migrations between pelagic/littoral zones and if odonates move only during night. One possible explanation, that *Daphnia* in Mekkojärvi are too big for the odonate larvae labium, is not consistent with the theory based on stable isotope analysis, that odonates are feeding on much more larger ephemeropterans, *Asellus* etc. Spence (1986) suggested that odonates feed on *Gerris* sp., but in my data there were no signs of this kind of interaction. Also the literature includes many references to amphibian-odonata relationship (e.g. Thompson 1978a), but in spring when tadpoles were found in Mekkojärvi, there was no evidence that they were a food resource exploited by odonates.

Other zooplankton species were not sampled, but littoral zooplankton species such as *Polyphemus pediculus* (L.) might be a possible food resource for odonata. In July there is good evidence that *Notonecta* sp. might be feeding on *Daphnia*. As Brönmark and Hanson (1998) argued, notonectids are a good alternative to be the top predators of zooplankton in lakes and ponds. This is likely also in Mekkojärvi. Since no *Chaoborus* were caught during summer this potentially critical part of the food web is missing.

In regression analyses the significance of the relation between dry weight and  $\delta^{13}\text{C}$  was higher in autumn after the growing season. When comparing size classes with carbon isotope values the mean values become more depleted as the size of animal increases. With nitrogen the mean value increases as the animals grow. This shows that bigger individuals feed on different food resources than smaller individuals. Also bigger odonates apparently lie at a higher trophic level than small individuals. In July the interaction between notonectids and *Daphnia* shows that at least part of the *Daphnia* population is consumed

by notonectids. However, it is hard to draw any specific conclusions about notonectids, which might be feeding on *Daphnia* in the lake, although the low abundance of notonectids probably means they cannot account for much loss from the dense *Daphnia* population. Thus the problem of what happens to all the *Daphnia* production in this lake still remains.

As Paine (1988) suggested, the data collection might be difficult because of highly mobile organisms. Especially water-boatmen and water striders are fast movers and hard to catch. In this study no Chaoborids were caught, even though *Chaoborus* larvae have previously appeared abundant in Mekkojärvi. It is clear that the provisional food web structure based on these observations constrains many assumptions and speculation. It is hard to draw any conclusion about omnivory, and it is also unclear how odonates locate in their own food web between primary producers and the top predator, pike, which is known to consume many odonates in Mekkojärvi (Syväranta 2004).

Van de Meutter and others (2004) strongly suggested open water to be a safer place than macrophytes for *Daphnia* with regard to the odonate *Ischnura*. Nesbitt et al. (1996) showed that *Daphnia* responds with different diel vertical migration behaviour in the presence of *Notonecta* than in the presence of *Chaoborus*. This suggests that *Daphnia* can distinguish between different macroinvertebrate predators and exhibit differential and adaptive anti-predation behaviour, although studies towards the chemical nature and characteristics of these macroinvertebrate kairomones, predator chemical cues, are scarce (Parejko and Dodson 1990). Macrophytes themselves can also have a strong repellent effect on *Daphnia* (Pennak 1973, Dorgelo and Heykoop 1985, Van de Meutter et al 2004), based on both structural and chemical characteristics of macrophytes (Lauridsen and Lodge 1996, Burks et al. 2001a).

In laboratory experiments, Burks et al (2001a) confirmed that daphnids greatly increased their use of macrophyte habitat only in the presence of fish, regardless of fish species. The pelagic zooplankton *D. magna* in both experiments (Burks et al. 2001a, Lauridsen and Lodge 1996) confirmed earlier findings that macrophytes repel zooplankton (Pennak 1973). Furthermore, results also provide strong support for the suggestion by Pennak (1973) that the zooplankton response to macrophytes is in part chemically mediated. Chemical repellence might differ among macrophyte species (Pennak 1973), but the identity of active compounds and differences in activity among macrophyte species are unknown (Lauridsen and Lodge 1996).

Traditional limnology categorizes *Daphnia* as pelagic prey and odonates as benthic and littoral predators, implying that this predator is unlikely to encounter that prey. However, in shallow lakes, daphnids undergoing DHM create a link between pelagic and littoral zones (Lodge et al. 1988). Most field studies document the impact of odonates on zooplankton by analyzing gut content or fecal pellet composition. Multiple studies have shown that larval odonates feed extensively on littoral-associated cladocerans (Pritchard 1964, Mahato and Johnson 1991, Koperski 1998a), and in some cases odonate diets include a substantial portion of typically pelagic zooplankton (Blois 1985). Even with this corroborative evidence, however, few field studies have directly tested the impact of odonate predation on pelagic zooplankton. Dragonflies consumed nearly every available daphnid in the laboratory experiments of Burks et al (2001b), despite high densities of vegetation. Daphnids increased in enclosures without odonates in the field experiment with low macrophyte densities, but declined in enclosures where damselflies and dragonflies were added. Their studies, therefore, provide direct evidence that littoral predators may strongly impact pelagic prey. (Burks et al 2001b). According to those studies it is even

more perplexing that in Mekkojärvi the difference between odonate and *Daphnia* stable isotope values was so significant.

Most odonate species are generalist feeders (Koperski 1998b), and will eat large cladocerans given the chance, although some odonate groups and ages may be more effective than others at consuming cladocerans (Westfall and Tennessen 1996). Libellulidae and Corduliidae species may be better suited for catching cladocerans than other dragonfly families because of cage-like mouthparts (Pritchard 1964), but in my study there was apparently no interaction between Libellulidae and *Daphnia*. Family Corduliidae commonly occur among littoral sediment and vegetation. These odonates are described as 'burrowers' or 'climbers' (Westfall and Tennessen 1996) and thus represent a potential littoral-zone predator of pelagic zooplankton. Migrating into the littoral zone introduces daphnids to an entirely different predator assemblage. Daphnids may undergo DHM to lower predation from pelagic predators, but Burks et al (2001b) suggest that mortality from littoral predators can be substantial. Therefore, the net benefit of DHM may differ among lakes as a function of the relative threat of pelagic and littoral predators. (Burks et al 2001b).

Strongly depleted zooplankton carbon isotope values in autumn must reflect consumption on methanotrophic bacteria and other chemoautotrophic bacteria (Taipale et al. 2007, in press), and not phytoplankton that have utilized  $^{13}\text{C}$ -depleted respiratory carbon for their photosynthesis as proposed by Lennon and others (2006). DOC in Mekkojärvi is overwhelmingly dominated by allochthonous material (Taipale et al. 2007), because DOC  $\delta^{13}\text{C}$  remained all year around  $-27.5\%$ , which is typical of terrestrial  $\text{C}_3$  plant detritus (Peterson and Fry 1987). Allochthonous carbon was the principal carbon source for *Daphnia* in anoxic layers, while autochthonous carbon was more important in the oxic epilimnion where primary production was highest.

High biomass and production of *Daphnia* in Mekkojärvi in the absence of planktivorous fish is evidently not strongly reduced by macroinvertebrate predators, because the amount of predators was not high enough to support this theory. Macroinvertebrates consume part of *Daphnia* population, but daphnids may use vertical and horizontal migration and the anoxic hypolimnion to escape predators. I did not examine if *Daphnia* migrates to the littoral zone where odonates sit and wait in the *Sphagnum*. At least this theory was not supported by the stable isotope values. *Chaoborus* and *Notonecta* together might be the most effective predators of *Daphnia*, but something was apparently restricting the *Chaoborus* population in summer 2005, because no individuals were caught. There are various possibilities for where the *Daphnia* production might go in Mekkojärvi, but at least the abundant odonate population is not feeding on *Daphnia*. Maybe the reason is simply that odonate larvae just do not encounter enough *Daphnia*. It might even be that *Daphnia* actively avoid the floating *Sphagnum* and *Warntorfia* mosses because of chemical cues from odonates or that the mosses have some repellent effect on cladocerans. In the future it would be interesting to investigate the horizontal migration of *Daphnia* in Mekkojärvi.

## ACKNOWLEDGEMENTS

I would like to thank my supervisor Prof. Roger Jones for his irreplaceable help and work during this long project; without him this work would have been impossible to finish. I am also grateful to Roger for keeping me in touch to the Masters and to studying while I was

on maternity leave. Jari Syväranta earns special thanks for his big help with samples, analyses and help when I had problems with data. I would also like to thank Heikki Hämäläinen for helping with data analyses and Lydia King for samples and analyses.

## LITERATURE

- Arnér M., Koivisto S., Norberg J. & KAutsky N. 1998. Trophic interactions in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. *Freshwater biol.* 39:79-90.
- Arnott S.E. & Vanni M.J. 1993. Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. *Ecology* 74:2361-2380.
- Arvola L., Kankaala P., Tulonen T. & Ojala A. 1996. Effects of phosphorus and allochthonous humic matter enrichment in the metabolic processes and community structure of plankton in a boreal lake (Lake Pääjärvi). *Can. J. Fish. Aquat. Sci.* 53: 1646-1662.
- Bearhop S., Waldron S., Votier S.C. & Furness R.W. 2002. Factors that influence assimilation rates, and fractionation of nitrogen and carbon isotopes in avian blood and feathers. *Physiol. Biochem. zool.* 75:451-458.
- Bearhop S., Adams C.E., Waldron S., Fuller R.A. & Macleod H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J. Am. Ecol.* 73:1007-1012.
- Belyshev B.F & Belyshev N.B. 1976. Trophic relations of the dragonfly larvae of the genus *Aeschna* (Odonata) with the molluscs. IR. *Trudy Biol. Inst. Sib.Otdel. Akad. Nauk. SSSR* 21:177-179.
- Black I.I.R.W & Hairston N.G. Jr 1988. Predator driven changes in community structure. *Oecologia* 77:468-479.
- Blois C. 1985. The larval diet of three anisopteran (Odonata) species. *Freshwater Biol.* 15:505–514.
- Blumenshine S.C. & Hambright H.D. 2003. Top-down control in pelagic systems: a role for invertebrate predation. *Hydrobiologia* 491:347–356.
- Boersma M., Spaak P. & De Meester L. 1998. Predator-mediated plasticity in morphology, life history, and behaviour of *Daphnia*: the uncoupling of responses. *Am. Nat.* 152:237–248.
- Borutsky E.V. 1939. Dynamics of the total benthic biomass in the profundal of Lake Beloye. *Works Limnol. Sta. Kossino* 22:196-218.
- Brett M.T. 1992. Chaoborus and fish-mediated influences on *Daphnia longispina* population structure, dynamics and life-history strategies. *Oecologia* 89:69-77.
- Brooks J.L. & Dodson S.I. 1965. Predation, body size and composition of plankton. *Science* 150:28–35.
- Brönmark C. & Hansson L.-A.. 1998. *The Biology of Lakes and Ponds*. Oxford University Press.
- Burks R.L., Jeppesen E., Lodge M.D. 2001a. Littoral zone structures as *Daphnia* refugia against fish predators. *Limnol. Oceanogr.* 46: 230-237.

- Burks R.L., Jeppesen E., Lodge M.D. 2001b. Pelagic prey and benthic predators: impact of predators on *Daphnia*. *J. N. Am. Benthol. Soc.* 20:615-628.
- Burks R.L., Lodge D.M., Jeppesen E. & Lauridsen T.L. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biol.* 47:343–365.
- Caraco N.F. & Cole J.J. 2004. When terrestrial organic matter is sent down the river: importance of allochthonous C inputs to lakes and rivers. In: *Food webs at the landscape level* (eds. Polis G.A., Power M.E. and Huxel G.). University of Chicago Press, Chicago, IL, pp.301-316.
- Carpenter S.R. 1988. *Complex interactions in lake communities*. Springer-Verlag, New York.
- Carpenter S.R., Cole J.J., Pace M.C., Van de Bogert M., Bade D.L., Bastviken D. et al. 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from <sup>13</sup>C addition to contrasting lakes. *Ecology* 86:2737-2750.
- Cole J.J., Pace M.L., Carpenter S.R. & Kitchell J.F. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulation. *Limnol. Oceanogr.* 45:1718-1730.
- Cole J.J., Carpenter S.R., Kitchell J.F. & Pace M.L. 2002. Pathways of organic C utilization in small lakes: results from a whole-lake <sup>13</sup>C addition and coupled model. *Limnol. Oceanogr.* 47:1664-1675.
- Cole J.J., Carpenter S.R., Pace M.L., Van de Bogert M.C., Kitchell J.L. & Hodgson J.R. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. *Ecol. Lett.* 9:558-568.
- Cooper S.D., Smith D.W. & Bence J.R. 1985. Prey selection by freshwater predators with different foraging strategies. *Can. J. Fish. Aquat. Sci.* 42:1720-1732.
- Crump M.L. 1984. Ontogenetic changes in vulnerability to predation in tadpoles of *Hyla pseudopuma*. *Herpetologica* 40:265-271.
- Cummins K.W. 1973. Trophic relations of aquatic insects. *ARE* 18:183-206.
- Cyr H. & Pace M.L. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148-150.
- Damgaard J. 1997: De danske vandtoegers utbredelse og status (Heteroptera: Gerromorpha & Nepomorpha). Faunistics and status of the Danish water bugs. *Entomol. Meddr.* 65: 49–108.
- De Meester L., Dawidowicz P., Van Gool E. & Loose C.J. 1999. Ecology and evolution of predator-induced behaviour of zooplankton: depth selection behaviour and diel vertical migration. In: Tollrian R, Harvell CD (eds) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, N.J., pp. 160–176.
- DeNiro M.J. & Epstein R.L. 1978. Influence of the diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta.* 42:495-506.
- Dodson S. 1989. Predator-induced reaction norms. *Bioscience* 39:447-452.



- Dorgelo J. & Heykoop M. 1985. Avoidance of macrophytes by *Daphnia longispina*. *Verh. Int. Ver. Limnol.* 22: 3369–3372.
- Elton C. 1927. *Animal ecology*. Sidgwick & Jackson, London. 204 pp.
- Fee E.J., Hecky R.E., Kasian S.E.M. & Cruikshank D.R. 1996. Effects of lake size, water clarity, and climatic variability on mixing depth in Canadian Shield lakes. *Limnol. Oceanogr.* 41:912-920.
- France R.L., Del Giorgio P.A. & Westcott K. A. 1997. Productivity and heterotrophy influences on zooplankton del <sup>13</sup>C in northern temperate lakes. *Aquat. Microb. Ecol.* 12: 85-93.
- Franke C. 1987. Detection of transversal migration of larvae of *Chaoborus flavicans* (Diptera, Chaoboridae) by the use of a sonar system. *Arch. Hydrobiol.* 109:355-366.
- Fry B. & Sherr E.B. 1984. <sup>13</sup>C measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* 27:13-47.
- Gannes L.Z., O'Brien D.M. & Martínéz del Rio C. 1997. Stable isotopes in animal ecology: assumption, caveats, and a call for more laboratory experiments. *Ecology* 78:1271-1276.
- Giguere L.A. 1980. Metabolic expenditures in *Chaoborus* larvae. *Limnol. Oceanogr.* 25: 922-928.
- Gilbert J.J. & Burns C.W. 1999. Some observations on the diet of the backswimmer, *Anisops wakefieldi* (Hemiptera: Notonectidae). *Hydrobiologia* 412:111-118.
- Godfrey C. & Thompson D.J. 1987. Diets of three aeshnid species in an acid pond. *JBDS* 3:29-31.
- Grant P.R., Grant B.R., Smith J.N.M., Abbott I.J. & Abbott L.K. 1976. Darwins finches: Population variation and natural selection. *Proceedings of the National Academy of Sciences USA*, 73:257-261.
- Grey J., Jones R.I. & Sleep D. 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnol. Oceanogr.* 46:505-513.
- Hampton S.E. 2004. Habitat overlap of enemies: temporal patterns and the role of spatial complexity. *Oecologia* 138:475–484.
- Hardy A.C. 1924. The herring in relation to its animate environment. Part 1. The food and feeding habitats of the herring with special reference to the east coast of England. *Ministry of Agriculture and Fisheries, Fisheries Investigations, Series II*, 7:1-45.
- Hessen D.O. & Andersen T. 1990. Bacteria as a source of phosphorus for zooplankton. *Hydrobiology* 206:217-223.
- Hessen D.O. & Nygard K. 1992. Bacterial transfer of methane and detritus; implications for the pelagic carbon budget and gaseous state. *Arch. Hydrobiol. Beib.* 37:139-148.
- Hessen D.O. 1992. Dissolved organic carbon in humic lake: Effects on bacterial production and respiration. *Hydrobiologia* 229:115-123.
- Hessen D.O. 1998. Food webs and carbon cycling in humic lakes. In: *Aquatic humic substances* (eds. Hessen D.O. and Tranvik L.J.). Springer-Verlag, New York, NY, pp.285-315.

- Hobson K.A. 1999a. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314-326.
- Hodgson J.R. & Hansen E.M. 2005. Terrestrial prey in the diet of largemouth bass, *Micropterus salmoides*, in a small north temperate lake. *J. Freshw. Ecol.* 20:793:794
- Hutchinson G.E. 1957. Concluding remarks. *Cold Spring Harb. Symp.* 22:415-427.
- Janetos A.C. 1982. Active foragers vs. sit-and-wait predators: a simple model. *J. Theor. Biol.* 95:381-385.
- Jeppesen E., Lauridsen T.L., Kairesalo T., & Perrow M.R. 1998. Impact of submerged macrophytes on fish-zooplankton interactions in lakes, p 91-114. In E.Jeppesen, Ma. Søndergaard, Mo. Søndergaard, and K. Christoffersen (eds.) *The structuring role of submerged macrophytes in lakes*, v. 131. Springer Verlag.
- Johnson C. 1968. Seasonal ecology of the dragonfly *Oplomaeschna armata* Hagen (Odonata: Aeshnidae). *AMN* 80:449-457.
- Jones R.I. 1992. The influence of humic substances on lacustrine planctonic food chains. *Hydrobiology* 229:73-91.
- Jones R.I., Grey J. & Arvola L. 1999. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* 86: 97-104
- Kerner M. et al. 2003. Self-organization of dissolved organic matter to micelle-like microparticles in river water. *Nature* 422:150-154.
- Koperski P. 1998a. Feeding in epiphytic, carnivorous insects: resource partitioning and the avoidance of intraguild predation. *Arch Hydrobiol* 142:467-483.
- Kortelainen P. 1993. Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. *Can. J. Fish. Aquat. Sci.* 50: 1477-1483.
- Kritzberg E.S., Cole J.J., Pace M.L., Granéli W. & Bade D.L. 2004. Autochthonous versus allochthonous carbon sources to bacteria – results from whole lake <sup>13</sup>C addition experiments. *Limnol. Oceanogr.* 49:588-596.
- Kritzberg E.S., Cole J.J., Pace M.L., & Granéli W. 2005. Does autochthonous primary production drive variability in bacterial metabolism and growth efficiency in lakes dominated by terrestrial C inputs? *Aqual. Microb. Ecol.* 38:103-111.
- Kurzatowska A. 1993. Investigations on the developmental biology of *Notonecta reuteri* Hung. and *Notonecta glauca* L. (Heteroptera). *Acta Hydrobiol* 35: 41-48.
- Kvam O.V. & Kleiven O.T. 1995. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. *Hydrobiologia* 307:177-184.
- Lauridsen T.L. & Buenk I. 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Arch Hydrobiol* 137:161-176.
- Lauridsen T.L. & Lodge D.M. 1996 Avoidance by *Daphnia magna* of fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. *Limnol. Oceanogr.* 41: 794-798

- Lennon J.T., Faiia A.M., Feng X. & Cottingham K.L. 2006. Relative importance of CO<sub>2</sub> recycling and CH<sub>4</sub> pathways in lake food webs along a dissolved organic carbon gradient. *Limnol. Oceanogr.* 51:1602-1613.
- Lodge D.M., Barko J.W., Strayer D., Mmelack J., Mittlebach G.G., Howarth R.W., Menge B. & Titus J.E. 1988. Spatial heterogeneity and habitat interaction in lake communities. Pages 181–208 in S. R. Carpenter (editor). *Complex interactions in lake communities*. Springer-Verlag, New York.
- Mahato M. & Johnson D.M. 1991. Invasion of the Bays Mountain Lake dragonfly assemblage by *Dromogomphus spinosus* (Odonata: Gomphidae). *J. N. Am. Benthol. Soc.* 10:165–176.
- Marklund O., Hargeby A. & Blindow I. 2001. Distribution and diurnal migration of macro-invertebrates within dense submerged vegetation. *Freshwater Biol* 46:913–924.
- Mazumder A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology* 75:1141-1149.
- Meili M. 1992. Sources, concentrations and characteristics of organic-matter in softwater lakes and streams of the Swedish forest region. *Hydrobiologia* 229:23-41.
- Meili M., Kling G.V., Fry B., Bell R.T. & Ahlgren I. 1996. Sources and partitioning of organic matter in a pelagic microbial food web inferred from the isotopic composition (d<sup>13</sup>C and d<sup>15</sup>N) of zooplankton species, p. 53-61. In M. Simon, H. Gude, and T. Weisse [eds.], *Aquatic microbial ecology*. E. Schweizerbartshe Verlagsbuchhandlung.
- Minagawa M. & Wada E. 1984. Stepwise enrichment of 15N along food chains: Further evidence and the relation between d15N and animal age. *Geochim. Cosmochim. Acta* 48: 1135–1140.
- Murdoch W.W., Scott M.A. & Ebsworth P. 1984. Effects of the general predator Notonecta (Hemiptera) upon a freshwater community. *J. anim. ecol.* 53:791.808.
- Nakano S. & Murakami M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Nat. Acad. Sci.* 98:166-170.
- Nesbitt L.M., Riessen H.P. & Ramcharan C.W. 1996. Opposing predation pressures and induced vertical migration responses in *Daphnia*. *Limnol. Oceanogr.* 41:1306–1311.
- O’Leary M.H. 1988. Carbon isotopes in photosynthesis. *BioScience* 38: 328-336.
- Pace M. L. & Cole J.J. 2002. Synchronous variation of dissolved organic carbon and colour in lakes. *Limnol. Oceanogr.* 47: 333-342.
- Pace M.L., Cole J.J., Carpenter S.R., Kitchell J.F., Hodgson J.R., Van e Bogert M.C., Bade D.L., Kritzberg E.S. & Bastviken D. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427:240-243.
- Paine R.T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69: 1648-1654.
- Parejko K. & Dodson S. 1990. Progress towards characterization of a predator prey kairomone *Daphnia pulex* and *Chaoborus americanus*. *Hydrobiologia* 198: 51-59.
- Pastorok R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311-1324.

- Pennak R. W. 1973. Some evidence for aquatic macrophytes as repellents for a limnetic species of *Daphnia*. *Int. Rev. Gesamten. Hydrobiol.* 58: 569–576.
- Peterson B.J., Howarth R.W. & Garrit R.H. 1985. Multiple stable isotopes used to trace organic matter in estuarine food webs. *Science* 227:1361-1363.
- Peterson B.J. & Fry B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18: 293-320.
- Pimm S.L. 1982. *Food Webs*. Chapman and Hall Ltd., London. 219 pp.
- Polis G.A., Anderson W.B. & Holt R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28:289-316.
- Pope G.E., Carter J.C.H., Power G. 1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River system, Quebec. *Trans. Am. Fish. Soc.* 102:707-714.
- Power M. E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. & Paine R.T. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Pritchard G. 1964. The prey of dragonfly larvae (Odonata; Anisoptera) in ponds in northern Alberta. *Can. J. Zool.* 42:785–800.
- Ramcharan C.W., Yan N.D., McQueen D.J., Perez-Fuentetaja A., Demers E. & Rusak J.A. 2001a. Complex responses of *Chaoborus* to changes in fish populations. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* 56: 81-100.
- Ramcharan C.W., Yan N.D., McQueen D.J., Perez-Fuentetaja A., Demers E. & Rusak J.A. 2001b. Analysis of food webs using individual-based models to estimate *Chaoborus* production and consumption. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* 56: 101-126.
- Riessen H.P., Sommerville J.W., Chiappari C. & Gustafsson D. 1988. *Chaoborus* predation, prey vulnerability, and their effect in zooplankton communities. *Can. J. Fish. Aquat. Sci.* 45: 1912-1920.
- Roditi H.A., Fisher N.S. & Sanudo-Wilhelmy S.A. 2000. Uptake of dissolved organic carbon and trace elements by zebra mussels. *Nature* 407:78-80.
- Roth J.C. 1968. Benthic & limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera:Chaoboridae). *Limnol. Oceanogr.* 13:242-249.
- Saether O.A. 1972. Chaoboridae. Das Zooplankton der Binnengewässer. 1. Teil. *Binnengewässer* 26:257-280.
- Salonen K. & Lehtovaara L. 1992. Migrations of a haemoglobin-rich *Daphnia longispina* in a small, steeply stratified, humic lake with an anoxic hypolimnion. *Hydrobiologia* 229:271–288.
- Scheffer M. 1998. *Ecology of shallow lakes*. Chapman and Hall.
- Schiff S.L., Aravena S.E., Trumbore S.E. & Dillon, P.J. 1990. Dissolved organic carbon cycling in forested watersheds: a carbon isotope approach. *Water Resour. Res.* 26:2949-2957.

- Schuh R.T. & Slater J.A. 1995. *True bugs of the world (Hemiptera: Heteroptera)*. Cornell Publishing Associates, Ithaca, New York. (Ref.)
- Scott M.A. & Murdoch W.W. 1983. Selective predation by the backswimmer *Notonecta*. *Limnol. Oceanogr.* 28:352-366.
- Spence J.R. 1986. Relative impacts of mortality factors in field populations of the waterstrider *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae). *Oecologia* 70:68-76.
- Svensson B.G., Tallmark B. & Petersson E. 2000. Habitat heterogeneity, coexistence and habitat utilization in five backswimmer species (*Notonecta* spp.; Hemiptera, Notonectidae). *Aquat. Insect* 22:81-98.
- Swift M.C. & Federenko A.y. 1975. Some aspects of prey capture by *Chaoborus* larvae. *Limnol. Oceanogr.* 20:418-425.
- Swift M.C. & Forward Jr. R.B. 1980. Photoresponses of *Chaoborus* larvae. *J. Insect. Physiol.* 26:365-372.
- Syväranta J.A.T. 2004. *Testing the link between mercury accumulation and increasing trophic position in lake pike (Esox lucius L.)* Masters thesis. Department of Biological and Environmental sciences, University of Jyväskylä, 24 pp.
- Taipale S., Kankaala, P., Tirola M. and Jones R.I. 2007. Whole -lake  $\text{DI}^{13}\text{C}$  additions reveal seasonal shifts between multiple food source contributions to zooplankton diet. In press.
- Thompson D.J. 1978a. The natural prey of larvae of the damselfly, *Ischnura elegans* (Odonata: Zygoptera). *FbW* 8:377-384.
- Thompson D.J. & Pickup J. 1984. Feeding rates of zygoptera larvae within an instar. *Odonatologica* 13:309-315.
- Tranvik L.J. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. *Hydrobiologia* 229:1-21.
- Tranvik L.J. 1998. Degradation of dissolved organic matter in humic waters by bacteria. In: *Aquatic humic substances* (eds. Hessen D.O. and Tranvik L.J.) Springer-Verlag, New York, NY, pp. 259-283.
- Van de Meutter F., Stoks R. & De Meester L. 2005. Spatial avoidance of littoral and pelagic invertebrate predators by *Daphnia*. *Oecologia* 142: 489-499.
- Van de Meutter F., Stoks R. & De Meester L. 2004. Behavioral linkage of pelagic prey and littoral predators: microhabitat selection by *Daphnia* induced by damselfly larvae. *Oikos* 107: 265-272.
- Van Valen L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* 99:377-390.
- Vander Zanden M. J. & Rasmussen J. B. 2001. Variation in  $\delta^{15}\text{N}$  and in  $\delta^{13}\text{C}$  trophic fractionation: Implications for aquatic food web studies. *Limnol. Oceanogr.* 46:2061-2066.
- Vanni M.J. 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. *Can J. Fish Aquat. Sci.* 45:1758-1770.

- Ward J.V. 1992. *Aquatic insect ecology. 1. Biology and habitat*. John Wiley & Sons, Inc. USA. Pp. 10-12, 76-81.
- Webster J.R. & Mayer, J.L. 1999. Organic matter budgets for streams: a synthesis. *J. North Am. Benthol. Soc.*, 16:141-161.
- Westfall M.J. and Tennessen K.J. 1996. Odonata. Pages 164–211 in R. W. Merritt and K. W. Cummins (editors). *An introduction to the aquatic insects of North America*. 3rd edition. Kendall/ Hunt, Dubuque, Iowa.
- Wetzel R.G. 1995. Death, detritus and energy flow in aquatic ecosystems. *Freshw. Biol.* 33:83-89.
- Wissel B., Freier K., Muller B., Koop J., & Benndorf, J. 2000. Moderate planktivorous fish biomass stabilizes biomanipulation by suppressing large invertebrate predators of Daphnia. *Arch. Hydrobiol* 149:177–192
- Wissel B., Boeing, W.J. & Ramcharan C.W. 2003. Effects of water colour on predation regimes and zooplankton assemblages in freshwater lakes. *Limnol. Oceanogr.* 48:1965-1976.
- Wissinger S.A. 1988. Effects of food availability on larval development and inter-instar predation among larval of *Libellula lydia* and *Libellula luctuosa* (Odonata: Anisoptera). *Can. J. Zool.* 66:543–549.
- Wood K.G. 1956. Ecology of *Chaoborus* (Diptera: Culicidae) in an Ontario Lake. *Ecology* 37:639-643.







