Master's thesis

The impact of summertime food consumption by vendace on the abundance of zooplankton the following spring

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ABSTRACT

The main objective was to study the delayed density dependent effect by the vendace population on the zooplankton the following spring. Thus, the strong predation in the previous summer and autumn on the zooplankton population by an abundant vendace year-class may have a negative impact on the zooplankton abundance in the following spring, which leads to a decreased spring or summer survival of the new offspring. The early spring abundance of zooplankton in four successive years (2003-2006) in Lake Southern Konnevesi, central Finland, was analysed and determined from samples collected randomly at five zooplankton sampling stations around the lake. The lake was previously included in a national cooperative monitoring- and assessment programme including vendace (*Coregonus albula* (L.)) and whitefish (*Coregonus lavaretus* (L.)), two fish species of major commercial importance in the Finnish inland fisheries. The annual monitoring of this lake included sampling of vendace and whitefish larvae, which were sampled simultaneously with zooplankton. In this study, the annual zooplankton abundance in spring was related to the annual densities of vendace larvae and several other indices of vendace abundance in the previous summer. The mean density and biomass of zooplankton were correlated to the previous year vendace larval and 0+ fish abundance, the total and spawning vendace biomass and to the following summer survival of 0+ fish. The findings suggested strong top-down regulation of vendace on its main prey *Bosmina coregoni*. A decrease was observed in the density among all zooplankton groups following a year with extreme larval densities, which indicates strong zooplanktivorous regulation during the summer by an abundant 0+ juvenile age-group. Due to the absence of significant correlations between relevant vendace indices and main prey groups in the following spring, it was concluded that the role of density dependent regulation of larval survival is probably of minor importance in the regulation of vendace year-class strength. The effects of intraspecific interactions in relation to external factors (weather conditions, temperature and predation) should be further investigated, by intensifying the sampling effort, extending it over several seasons. Furthermore, applying a population specific bioenergetics model and increasing sampling frequency and effort in counting and identification, would be better for elucidating of vendace food consumption patterns in relation to zooplankton productivity.

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TIIVISTELMÄ

On esitetty hypoteesi, että muikun voimakas kaksivuotisvaihtelu voisi selittyä viiveisellä tiheysriippuvalla säätelyllä siten, että runsaan muikkuvuosiluokan voimakkaan planktivorian vaikutuksestaa seuraavan kevään eläinplanktontiheys on alhainen, mikä vuoristaan johtaa poikasten suureen kuolevuuteen. Tämän työn tarkoituksena oli tutkia muikkutiheyden ja seuraavan kevään eläinplanktontiheyden välistä yhteyttä sekä eläinplanktontiheyden ja muikunpoikasten säilyvyyden välistä yhteyttä Etelä-Konnevedellä. Eläinplanktontiheys määritettiin jäänlähdön jälkeisellä viikolla viideltä satunnaisesti valitulta näytepisteeltä vuosina 2003-2006. Planktontiheyden yhteyttä muikkukannan edellisen kesän tiheysindekseihin sekä saman kevään muikunpoikastiheyteen ja kesänaikaiseen säilyvyyteen tutkittiin korrelaatioanalyysillä. Muikku näytti säätelevän voimakkaasti pääsaalislajinsa *Bosmina coregoni* -vesikirpun seuraavan kevään tiheyttä. Myös muiden eläinplanktonryhmien tiheys oli alhainen runsasta 0+ -ikäryhmää seuraavana keväänä. Planktontiheyden ja muikkujen säilyvyyden välillä ei kuitenkaan ollut selvää assosiaatiota, mikä viittaa siihen, että ravintovarat eivät kuitenkaan säätele voimakkaasti muikun populaatiodynamiikkaa. Tulokset eivät siis tue yllä esitettyä hypoteesia.

Contents

1. INTRODUCTION

Recruitment variability in both freshwater- and marine fish populations have been immensely studied due to its implications for fish population dynamics and ecology (e.g. Myers 2001). Moreover, knowledge on the population dynamics and behaviour of harvestable fish stocks is of importance to the sustainability of fisheries and in management of fish resources (May 1974, Viljanen 1988, Cushing 1988, Mertz & Myers 1994, Myers *et al.* 1998, Marjomäki 2003). Many mechanisms underlying recruitment variations in both marine and freshwater environments have been proposed, although controversy still exists as to the relative importance of different factors involved (Rose *et al.* 2001). The ecological simplicity of freshwater ecosystems compared to those in oceans makes them especially suitable for uncovering regulatory factors and mechanisms responsible for variations in fish recruitment (Helminen *et al.* 1997, Karjalainen *et al.* 2000). Several studies have focused on the year-class strength (defined as the number of individuals in a cohort recruited to a fishery (Myers 1998)) and its variations in the vendace (*Coregonus albula* (L.)) (e.g. Marjomäki 2003). Studying the underlying causes of recruitment variability of this species has important implications in the sustainable inland fisheries and management in Scandinavia, as the vendace is of major commercial importance in Finland and neighbouring countries (Sipponen 1999, Nyberg *et al.* 2001, Sipponen & Valkeajärvi 2002, Rova 2004).

Vendace populations are highly size-structured and characterised by fast and density dependent growth (Hamrin & Persson 1986, Karjalainen 1992, Helminen *et al.* 1997). For vendace, the youngest age of recruitment to the fishery may in some populations be as young-of-the-year fish (age 0+) in their first winter (Helminen 1994), although in general, it is at the end of their second growing season (at age 1+). This is also the age of maturation and first reproduction (Viljanen 1986). Semelparity (i.e. reproduction occurring once during a lifetime) may occur and result in one spawner generation being responsible for most of the annual reproduction. The scarcity of older (>1+) individuals in many populations is then explained as partly resulting from high harvesting (fishing) rates and/or interspecific predation (Auvinen 1994, Huusko & Hyvärinen 2005, Valkeajärvi & Marjomäki 2004). High and variable mortality in the vendace has been suggested to occur at several life stages (Marjomäki 2003), but have shown to be most pronounced and concentrated to the initial larval stage, between the age of 1-3 weeks (Viljanen 1988). Survival and growth in the larval stage has been shown to be negatively dependent on the density of larvae (Karjalainen 1992) but a high larval density is generally required for a strong year-class to arise (Karjalainen *et al.* 2000). These characteristics make density dependent processes potentially important in the regulation of annual abundance.

The regulatory effect of intraspecific competition (between age-groups) in maintaining or inducing variations in year-class strength has been shown for a number of fish populations (Hamrin & Persson 1986, Townsend *et al.* 1990, Helminen *et al.* 2002). The two main responsible mechanisms for the 2-year abundance fluctuations in vendace populations are asymmetrical food competition; the competitive advantage of 0+ juvenile vendace over older age-groups (cohorts) affecting the fecundity and egg quality (Hamrin & Persson 1986) and, secondly, the delayed effect of zooplanktivory by older year-classes on the food abundance and its availability to vendace larvae the following spring. The top-down effects of planktivorous fish influencing zooplankton community structure and population size distribution is well known from earlier studies (Hrbacek *et al.* 1961, Brooks & Dodson 1965, Carpenter *et al.* 1985). During the summer months, the high densities of 0+ juveniles in many fish populations are potentially capable of depressing populations of large cladocerans and copepods (Mehner & Thiel 1999). The vendace feeds on zooplankton throughout its life with considerable diet overlap of different cohorts. This has been shown to impact the size- and community structure and thus the dynamics of their main prey (Helminen *et al.* 1990, Bøhn & Amundsen 1998, Northcote & Hammar 2006). The seasonal succession of zooplankton populations is similar in many Finnish lakes. The termination of diapause and subsequent reproduction of cyclopoid copepodites (*Mesocyclops/Thermocyclops*) occurs in connection with lake ice-off and the first offspring of overwintering cyclopoids usually hatches during May. Cladoceran populations become more abundant as temperature increases (Karjalainen 1992). According to Viljanen (1983), the seasonal dietary shifts of vendace are a result of prey availability and the activity and behavior of both prey and predator. The initial larval stage diet consists mainly of small-sized zooplankters such as rotifers and young (naupliar stage) copepods (Viljanen 1986, Auvinen 1988a). To some extent also small-sized daphnids and adult copepods are included in the larval diet (Karjalainen 1992). Later in summer, larger cladocerans and copepods become important in the diet of vendace juveniles and in July-August the strong feeding impact of these fish may even alter the zooplankton community from a dominance of large-sized crustaceans to one largely dominated by rotifers (Helminen & Sarvala 1997). Helminen *et al.* (1990) concluded that age 0+ vendace in Lake Pyhäjärvi (southwest Finland) had the potential to affect the population dynamics of *Bosmina coregoni*. According to Helminen & Sarvala (1994), the zooplanktivory of vendace in this lake was shown to reflect their interannual recruitment variations, implying a strong regulatory effect of 0+ vendace zooplanktivory in maintaining the vendace population fluctuations.

Auvinen (1988b) proposed that an abundant year-class of adult vendace feeding on zooplankton in autumn may influence the larval food availability in spring and thus lead to larval starvation or difficulties of larvae to find food. In support of this, a negative association was found between a high autumn abundance of vendace and zooplankton density in spring. Moreover, there was a strong positive association between the feeding conditions of larvae (i.e. the number of cladocerans and copepods in the guts of 11-15 mm long vendace larvae) and the density of cladocerans and copepods in samples taken in spring (when the mean length of vendace larvae was 10-14 mm). A negative association was found between larval feeding conditions and the density of the recruited (previous year) vendace stock. The findings of Auvinen (1988b) suggest that in years following an abundant year-class of adult vendace, larval survival may be regulated through delayed density dependence and produce a 2-year cycle in abundance, maintained by self-regulating intraspecific competition. Helminen *et al.* (2002) proposed that delayed density dependence through intraspecific asymmetrical competition was important for the 2-year fluctuations observed in the vendace population of Lake Pyhäjärvi.

The main objective of this study was to determine the interannual spring abundance of zooplankton in Lake Southern Konnevesi (central Finland) during a period of strong interannual fluctuations in the abundance of vendace. Based on the idea of delayed density dependence, the relationship between springtime zooplankton abundance and the vendace year-class strength was investigated in 4 successive years. I hypothesized that the zooplanktivory of a strong vendace year-class in the previous growing season has a negative effect on the abundance of edible zooplankters in the following spring. This study is probably the first that is concerned primarily with the effects of delayed density dependence in vendace populations. The findings provide further important insight to the role of delayed density dependent regulation in the vendace population of L. S. Konnevesi. The study was part of the long-term research programme 'Finnish Coregonid Stock

Research and Monitoring Network' (CORNET), a collaborative stock monitoring- and assessment project which included the annual collection of recruitment data on vendace and whitefish (*Coregonus lavaretus* (L.)) in 14 of the most important vendace lakes in Finland.

2. BACKGROUND

The vendace is an obligate planktivorous fish species in the coregonid family (*Coregonidae*) inhabiting the pelagic areas of lakes and brackish waters throughout much of the Northern Hemisphere (Hamrin 1979). Typical features linked to its life-history are the high fecundity and variable but typically fast growth, occasionally resulting in large interannual variation in mortality and fluctuating year-class strength (Hamrin 1979, Viljanen 1988). In Sweden, the commercial vendace fisheries are regionally important in some of the larger inland lakes, especially Lake Vänern and L. Mälaren (Nyberg *et al.* 2001). An active commercial coastal fishery targeting vendace is also found in the northern, mainly Swedish, parts of the Bothnian Bay area. The vendace is the most important fish species in the Finnish commercial inland fisheries (Viljanen 1988). In Sweden, the roe of vendace is primarily harvested (known as bleak roe or *löjrom* in Swedish); the fishery is highly seasonal and practiced mainly during the vendace spawning season during October-November (Rova 2004). In Lake Mälaren, the commercial vendace catches decreased by 90 % during the period 1990-2004. The recruitment in L. Vänern has remained low since the 1990's. Commercial catches peaked with 576 tonnes being caught in 1996, thereafter catches have decreased radically. In 2007, the catch amounted to 208 tonnes. The current (2008) 1+ age-group in this lake is estimated to be weak (Ask & Westerberg 2008). The main reason for the recruitment failure of vendace in Swedish lakes is suggested to be increased early spring temperature, resulting in a mismatch in the timing of hatching with optimal larval feeding conditions, thereby affecting larval survival and thus later recruitment success. Moreover, a negative effect of warm winters, i.e. the timing of ice break or even a lack of lake ice-cover is suggested to influence the vendace recruitment success in Lakes Vänern, Vättern and Mälaren (Nyberg *et al.* 2001).

Two different types of year-class fluctuations in vendace populations may be distinguished. The short-term fluctuations, known as high-stock periods, typically oscillate with a period of 2-4 years (Viljanen *et al.* 2004). Annual growth rates vary markedly between successive years, sometimes by 50-100 % in length and the recruitment strength may vary 10-fold between strong and weak year-classes (Viljanen 1988). Contrastingly, low-stock periods are characterised by longer periods of recession with low recruitment levels. These are probably maintained by the presence of predatory fish such as perch (*Perca fluviatilis* (L.)) (Valkeajärvi & Marjomäki 2004). The unpredictable abundance fluctuations in many vendace stocks presents a challenge to both the management of vendace and its fisheries, especially in light of climate change, as recruitment variability has been found to be strongly influenced by synchrony in environmental factors and variable temperature- and weather conditions (Nyberg *et al.* 2001, Marjomäki *et al.* 2004). The effects on recruitment variability of environmental factors, mainly meteorological, are also likely to be enhanced through environmental induced synchronization of vendace predator populations, e.g. perch (Marjomäki *et al.* 2004). However, the short-term 2-year fluctuations in some vendace populations have been suggested to occur mainly as a response of biotic factors, such as predation and competition (Hamrin & Persson 1986, Auvinen 1994, Marjomäki 2003). The relative importance of these factors in population regulation at different life-stages, and their underlying mechanisms, generally depend on lake-specific conditions (Viljanen 1986, Auvinen 1988b, Helminen *et al.* 1997).

The regulatory impact of density dependent factors on the characteristic cyclic alternation of strong and weak year-classes has been shown for several vendace populations (Hamrin & Persson 1986, Auvinen 1988b, Helminen *et al.* 1997). The central hypotheses behind these regular year-class fluctuations are based on intraspecific competition; the density dependent competition for food between age-groups. Sandlund *et al.* (1991) noted that, based on either juvenile or adult dominance, the principal difference between the two hypotheses is the relative competitive advantage of different cohorts in competition for food resources.

The effect of these two hypotheses may manifest itself through several mechanisms based on delayed density dependence, i.e. the negative effect of previous year-classes on prerecruit survival (Townsend 1989, Levy & Wood 1992). Intraspecific food competition during the growing season will (1) affect the spawning part of the population by decreasing fecundity (lowering reproductive output; the quality or quantity of eggs) or (2) affect the food availability for larvae through food depletion and thereby influence larval survival. Intraspecific "asymmetrical" food competition was suggested by Hamrin & Persson (1986) to explain the observed 2-year fluctuations in the south Swedish Lake Bolmen. This mechanism favours smaller sized vendace (0+ juveniles in their first growing season) over older age-groups in the same population, due to the lower metabolic demands of younger fish, their faster growth rates and overall higher density. A strong year-class of young-of-the-year (0+) vendace depletes the food resources during summer and is consequently small-sized in autumn. The strong competition from 0+ fish will further lead to a low reproductive output (quantity and quality of eggs) of co-occurring slow growing adults (mainly 1+ vendace). In the following year the former 0+ size-class (now 1+ fish in their second year) will start to grow fast due to (1) the lack of competition from the current year's 0+ fish and (2) their own relatively small size. Fast growth leading to a high reproductive output of mainly 1+ fish, will produce a strong following year-class.

A second regulatory mechanism was initially proposed by Auvinen (1988b) to be important in maintaining the 2-year cycles of the vendace population in Lake Karelian (S.E.) Pyhäjärvi. This type of mechanism is similar to the adult dominance hypothesis, in which adult fish depletes the food resources or in some other way suppress the activity of young fish (Sandlund *et al.* 1991). Delayed density dependence is based on the delayed effect of zooplanktivory by a strong previous vendace year-class on the emergence of a weak following year-class, affected by low larval food availability in spring (Auvinen 1988b). Accordingly, an abundant previous year-class of vendace heavily predating on crustacean egg-bearing females or zooplankters about to enter diapause in autumn might influence the abundance and availability of edible zooplankters for newly hatched vendace larvae in the following spring. The decrease in abundance of zooplankters might lead to a reduced capability of vendace larvae to find food or even lead to direct starvation of the larval population, resulting in the development of a weak following vendace year-class. Auvinen (1988b) found a supportive positive association between the strength of the previous vendace year-class and the spring density of zooplankton and between the larval feeding conditions and the following year-class strength. In addition, Viljanen (1988) observed that the future year-class strength is fairly predictable from the abundance of 3 weeks old larvae. A high larval abundance is generally needed to produce a strong year-class (Karjalainen *et al.* 2000). Salojärvi (1987) suggested that starvation induced mortality in the larval stage is the most important factor in generating year-class fluctuations. Delayed density dependence was suggested by Auvinen (1988b) to be important in the 2-year fluctuations in the vendace population of L. S.E. Pyhäjärvi. Helminen *et al.* (2002) showed that delayed density dependence was important for the 2-year fluctuations in the vendace population of *Säkylän* (S.W.) Pyhäjärvi. In this highly productive Finnish lake, Helminen & Sarvala (1997) demonstrated a significant top-down effect of vendace on crustacean zooplankton, by showing that the zooplanktivory in vendace varied according to the size of the year-class. Further, their study showed a clear effect of especially 0+ vendace on the seasonal succession of zooplankton biomass and in the mean size of crustacean zooplankton in summer. In years with a dominating year-class of 0+ vendace the zooplankton community shifted from large-bodied cladocerans to one largely dominated by rotifers. In addition, long term analyses of successive vendace year-classes in Lake S.W Pyhäjärvi imply a decisive role of late summer zooplanktivory of 0+ vendace on mean zooplankton biomasses in August.

Seasonal changes in the occurrence and distribution of zooplankton populations are largely determined by physical factors such as temperature, photoperiod and water quality (Gyllström & Hansson 2004). On the other hand, the impact of feeding by planktivorous fish on lake zooplankton community dynamics was recognised early in small-pond experimental studies (Hrbacek *et al.* 1961, Brooks & Dodson 1965). Considerable effects of planktivorous fish on the zooplankton population size structure and species composition has been found from a large number of research studies, both field- and mesocosm experiments, although a majority of these often lack a direct quantification of fish consumption and sufficient estimations of zooplankton dynamics and production (Mehner & Thiel 1999). The seasonality of zooplankton abundance and its spatial distribution in the littoral parts of Lake Pääjärvi, an oligotrophic brown-water lake in southern Finland, was studied by Lehtovaara & Sarvala (1984). They concluded that zooplankton abundance was clearly higher in the littoral zone of the lake than in the pelagial, and that the relative occurrence of different zooplankton species showed a clear seasonal pattern in abundances. The greatest impact on the littoral zooplankton community in summer was attributed to the presence planktivorous fish in that zone. Viljanen & Karjalainen (1993) found the total cladoceran and copepod densities in L. S.E. Pyhäselkä to be higher in the pelagic zone. The authors suggested these density differences to be a consequence of higher planktivore presence in the littoral.

The vendace population of L. S. Konnevesi is characterized by slow growth and high fecundity. Seine catch samples suggests that several cohorts are present in the population and so spawning older age-groups (>1+) may potentially contribute significantly to the annual reproduction in the lake. The only potential competitor for food resources in the pelagic area is the semi-planktivorous smelt (*Osmerus eperlanus* (L.)) (T.J. Marjomäki 2008, pers. comm.). In Lake Konnevesi, the level of recruitment may be forecasted by the numbers of vendace larvae in spring during periods of low larval densities. On the other hand, high larval densities may give rise to strong or weak recruitments, depending on initial environmental conditions, such as water temperature and larval predation affecting initial growth and survival (Karjalainen *et al.* 2000). High initial larval densities are thus not necessarily the only precondition for successful recruitment (Valkeajärvi & Marjomäki 2004), as is also the case in many other Finnish lakes (Karjalainen *et al.* 2000).

Standardised zooplankton sampling has been conducted in L. S. Konnevesi since the late 1990’s. Despite a large amount of sample material, few investigative studies on the interannual zooplankton dynamics exist. Hakkari (1978) studied the zooplankton population dynamics in relation to water quality and vendace planktivory in three central Finnish lakes. The study reveals some features from the Lake Konnevesi zooplankton community, but it is not dealt with as comprehensive as for the other two lakes (e.g. samples included in the data analysis were collected from only two lake locations).

During the last decades, the vendace stock in L. S. Konnevesi has experienced both long- and short term fluctuations. The stock recession period of the vendace population in 1982-1992 was proposed to be due to the perch predation, which in combination with low larval densities and a low spawning stock yielded successive recruitment failure in the vendace population during those years. In their analysis, Valkeajärvi & Marjomäki (2004) found that the density of large perch was highest during the high-stock period of vendace, implying a regulation of older vendace age-groups through predation, partly replacing the effects of fishing. The fishing effort has decreased significantly since the mid-1990's and presumably has little current influence on the population dynamics. The appearance of alternating strong and weak year-classes from 2000 and onwards and the recent dramatic fluctuations in prerecruit (larvae and 0+ fish) densities (O. Urpanen, T.J. Marjomäki & J. Karjalainen, University of Jyväskylä, unpubl.) suggest that strong regulation through intraspecific competition may be involved in the interannual variations in vendace abundance in this lake.

3. MATERIAL AND METHODS

3.1. Study area

The sampling was conducted in the moderately shallow Lake Southern Konnevesi (62º 40´N, 26º 30´E), covering an area of 119.5 km^2 and situated about 60 km north-west of the city of Jyväskylä in central Finland. The mean depth of the lake is 12.5 m and the maximum depth is estimated to 56 m. The lake is characterised as meso-oligotrophic with a mean phosphorous level of 7 µg/l (Herve 1995).

The commercial vendace fishing is practiced on a relatively small scale since the 1990's, due to a low-stock recession period in the vendace population affecting the profitability of fishing activities (Valkeajärvi & Marjomäki 2004). Currently two commercial trawlers operate in the pelagic area and there is some near-shore seining conducted on a small scale throughout the autumn and winter. Fishing effort in the lake is thus considered low and is presumed to have minimal influence on the population dynamics in the lake (T.J. Marjomäki 2008, pers. comm.).

3.2. Sampling procedures

Vendace larvae and zooplankton were sampled during daytime (8:00-16:00) at five sampling stations (sites) around the lake, in mid May and in the beginning of June, during the first and third week after lake ice-off. Coinciding with the hatching and start of exogenous feeding of vendace larvae, randomized sampling during this period gives a reliable estimate of larval abundance (Urpanen *et al.* 2005). Vendace larvae were collected using stratified random sampling in the littoral and pelagic area following standardised sampling methods described in Urpanen *et al.* (2008). These sampling methods are commonly used in Finnish lakes to assess larval spatial distributions (see also Karjalainen & Viljanen 1992 and Karjalainen *et al.* 1998). Data on age 0+ vendace abundance were obtained by combining fish density estimated from echosounding (individuals ha^{-1}) with CPUE (catch per unit of effort) from autumn gillnetting (3x30 m, knot-to-knot mesh size 14-18 mm). The CPUE of 1+ vendace (individuals in gillnets) were used as an index of 0+ recruitment the previous year (Valkeajärvi & Marjomäki 2004). As pre-analysed data on vendace larval and 0+ densities were only used in correlation, a comprehensive description on the fish sampling methodology is left out, but see the above given references for further details.

3.2.1. Zooplankton sampling

Zooplankton samples were collected using a large Limnos tube sampler (length 1 m, volume 7.1 l) from five randomised sampling stations, reached with a 5 m vessel. At the stations, samples were taken at two different depth zones. The Limnos was deployed by hand from the side of the standing vessel and water samples were collected in every 1 m of the water column. Each collected sample was obtained by composite sampling in three and two layers (strata) representing the littoral (0-0.5 m, 0-1 m and 1-2 m => 0-2 m) and the pelagic zone (0-5 m, 5-10 m) respectively. The shallow littoral layer (0-0.5 m) was sampled 3 times by lowering the Limnos horizontally, whereas the other depth layers were sampled with 3 (0-1 m) and 2 (1-2 m, 0-10 m) vertical hauls per meter. Samples from the deep pelagic layer (5-10 m) were left out from the identification and data analyses.

The total water volume collected with each haul was washed through a concentrating net with mesh size 50 µm (also allowing entrapment of rotifers) into a small plastic collecting tube at the net end. At each sampling depth, the content of this tube was after ten composite hauls emptied into one sample bottle (i.e. one littoral sample was obtained by combining the hauls from the three littoral strata). Three sample bottles representing the different depth zones were thus obtained from each sampling station. The samples were instantly preserved by adding about 250-300 ml solution mixture of ethanol (70%) and formalin (1%) to the sample bottle before labelling the bottles with lake- and station number, time, temperature, depth layer and zone.

Zooplankton identification and data analyses were undertaken in the Ambiotica building at the University of Jyväskylä. The initial laboratory work included sorting and preparation of subsamples, identification and counting of zooplankters. The information from the identification protocols were thereafter converted to abundance estimates; zooplankter density and biomass. The values obtained were tested for mean (arithmetic mean) differences between years using the statistical software SPSS 14.0 for Windows. Microsoft Excel was used for data preparation. Correlations were analysed in SPSS and later edited in Excel.

3.3. Laboratory analyses

3.3.1. Sample preparation

Previously collected zooplankton samples (in the years 2003 – 2006) were obtained from a storage facility and the sampling bottles were sorted by year, station number and depth. Each sample was partitioned with a volume range of 300 – 450 ml into a beaker and placed on a magnetic stirrer plate for 10 – 15 s, allowing complete mixing of the solution content. 10 or 20 ml of the sample solution from the beaker was pipetted into a vial tube overlying the counting chamber and diluted to a volume of 50 ml. This procedure was repeated 4 times in order to obtain a set of 5 subsamples. The subsampling ensured that site-specific replicates representing each depth zone were obtained. The subsamples were stored over night (ca. 10-14 hours) or for a minimum of five hours during the day, for complete particle settlement. Prior to initiating the identification, the vial tube was carefully removed and the counting chamber placed on the microscope.

3.3.2. Identification, counting and taxonomic division

Individual zooplankters were counted, identified and measured with an inverted microscope (wildM40) using 10x objective magnification. Altogether, a total number of 49 samples (or 245 subsamples) were counted. However, the number of samples used in the data analysis was reduced to 37 since, due to time limitations, only samples counted from the first sampling occasion (mid-May, first week after ice-off) were decided to be analysed further. The identification of individual zooplankters was made on the level of species or grouped to the closest identifiable taxon using standard identification procedures described by Särkkä (2004). Identified specimens were then assigned standardised taxon-specific codes. Not more than 100 individuals per taxon and subsample were counted.

Identified rotifer species were *Kellicottia longispina, Keratella cochlearis* and *K. hiemalis*. All other rotifers were grouped to their respective suborders (*spp.*); *Asplanchna, Polyarthra, Synchaeta* and *Trichocerca*. All identified cladocerans (Table 1) were determined down to species level, except daphnids (*Daphnia spp.*). Individuals of different copepodid developmental stages (C4-C6) were grouped as copepod adults+copepodites, on the basis of measured individual total length. Young copepods (naupliar stages) were assigned to either *Cyclopoida spp.* or *Calanoida spp.* based on their morphology (described in Särkka 2004). Small-sized cyclopoid copepods (<399µm), categorised as *Mesocyclops leukartii* and *Thermocyclops oithonoides,* were identified as one taxonomical unit (*Mes./The.*), due to difficulties in separating the two species by inverted microscope.

3.3.3. Length measurements

The total lengths of cladocerans and copepods were measured from the head to the end of the furca (abdomen) with an ocular micrometer, calibrated against a stage micrometer scale for the utilized magnification. All counted zooplankters were assigned into one of nine different size-classes corresponding to a particular body length. Individual cladocerans were measured from the cephalon to the base of the posterior spine (mucro). The total length of individual copepods was measured from the cephalon to the end of the anal segment. The length of some specimens was not determined because of body deformation during the process of sample preservation or at the subsample preparation stage.

3.4. Data analysis

A total of 37 samples from two depth zones were included in the analysis, of which some were incorporated from previous identification work for statistical analyses. Pre-analysed vendace data were obtained and used in the correlation analyses (section 3.4.3).

3.4.1. Estimation of zooplankton density and biomass

The number of counted individuals in each subsample was sorted by sampling date, sample volume and sample depth and thereafter calculated to individuals per 10 litres (ind/10 l), by dividing the multiplied number of zooplankters to the quotient of total- and subsample volumes with one tenth of the total Limnos volume. This upscaling of density was done in order to avoid using unnecessarily low estimates of density. The density estimates were transformed to biomasses (µg C/10 l) based on species-specific carbon values (Rahkola *et al.* 1998) using the biomass conversion software ENO (J. Karjalainen, unpubl.). The arithmetic mean value of all counted samples per year was used as a measure of annual average abundance. The standard error, based on the mean standard deviation and squared number of samples per year, was calculated to provide a measure of precision of the data.

3.4.2. Data normalisation and ANOVA

The arithmetic mean values were normalised initially, using natural logarithms of original values (ln(value+0.1)), in order to fullfil the statistical assumptions in further analysis, i.e. to make the data more normally distributed and in order to decrease the variance. Repeated measures ANOVA was preformed in order to assess the importance of different depth zones as components of the total variance between samples. Correlations between the density at the littoral and pelagial depth zones were constructed to further clarify the effect of differences in average densities at different depth zones. Statistically significant differences in the average density and biomass between years of all zooplankton taxa were tested using univariate (one-way) ANOVA.

3.4.3. Correlation analyses

Pearson correlation coefficients and p-values were obtained by SPSS, the y-axis variables were the average abundance estimates (normalised values) of *Bosmina spp.*, *Daphnia spp.* and small-sized copepods (Table 2). On the basis of their importance as food for 1-3 weeks old vendace, the abundance of these taxa were plotted against several indices of vendace abundance. The previous total and spawner biomass (kg/ha) and autumn abundance of 0+ vendace was chosen to represent the strength of the previous vendace year-class, reflecting the potential feeding impact of 0+ and adult (≥ 1+) fish on the zooplankton population in autumn. In addition, the larval spring density (individuals/ha) and summer survival (S) were correlated with the zooplankton abundances to detect the possible delayed effect of predation by 0+ vendace on the following spring zooplankton abundance and the impact on the survival of the new vendace year-class.

4. RESULTS

4.1. Zooplankton density and biomass

In general, there was a high average abundance of rotifers in the first two years, decreasing in 2005 followed by a slight increase in 2006 (Figure 1). The total rotifer biomass differed significantly between years ($F_{3,33}=2.929$, $p=0.048$), but there was no significant difference in densities ($F_{3,33}=2.521$, $p=0.075$). *Keratella cochlearis* and *Kellicottia longispina* dominated in most of the samples analysed, however *Asplanchna* and *Synchaeta* occurred occasionally in high numbers. *Trichocerca* was least abundant and occurred only sparsely in some years (Table 1).

The total cladoceran density differed significantly between years ($F_{3,33}=3.186$, $p=0.036$) and within this group the average density of *Bosmina spp.* was highest in all samples. *Bosmina coregoni* dominated the average biomass in all years, whereas *Daphnia spp.* and larger cladocerans was less frequently encountered in samples (Table 1).

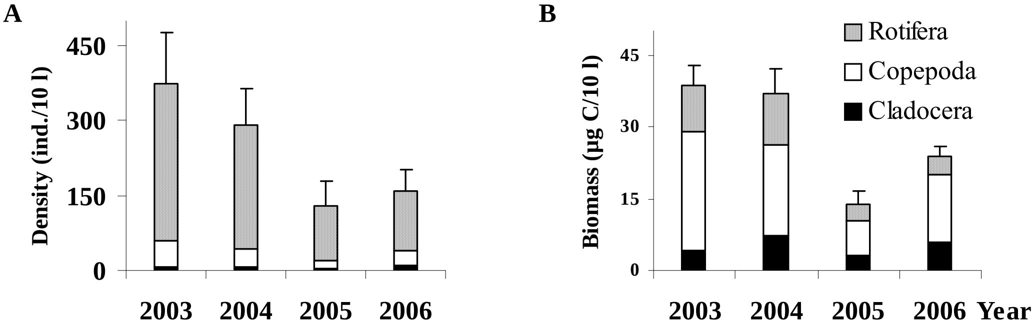

Figure 1. Annual average densities (ind. /10 l) (A) and biomasses (µg C /10 l) (B) of the main groups of zooplankton; rotifers, copepods and cladocerans. The standard error (S.E.) is given for the total density of all three groups.

Table 1. Interannual average densities (individuals/10 l) and standard errors (±S.E) by depth zone (1=littoral, 2=pelagic) of all identified zooplankton taxa.

Taxon	**Year**	**2003**	**2004**	**2005**	**2006**
	n	**10**	**10**	**7**	**10**
Rotifera (total)	1	155.8±53.6	164.4±61.0	136.7±57.6	115.3±48.1
	2	468.6±80.4	328.8±65.1	74.9±11.5	116.9±26.9
Asplanchna	1	5.4±1.5	1.8±1.2	2.1±0.8	5.3±1.7
	2	14.6±4.0	12.7±3.8	0.6±0.4	4.7±1.5
Kellicottia longispina	1	31.5±12.0	4.6±1.3	27.2±12.8	44.8±18.9
	2	77.4±15.5	27.0±5.0	27.6±8.4	34.9±10.6
Keratella cochlearis	1	42.1±15.2	9.2±3.4	31.2±13.0	23.2±11.3
	2	168.2±32.2	40.6±7.7	17.6±1.8	16.8±4.4
Synchaeta	1	53.6±26.8	11.3±4.2	38.9±9.8	27.5±11.1
	2	138.4±31.7	66.2±12.7	20.0±1.1	39.1±11.2
Trichocerca	1	0.8±0.2	0.1±0.1	0.1±0.1	0.5±0.3
	2	2.3±1.4	0.6±0.2	0.4±0.3	0.7±0.3
Cladocera (total)	1	5.7±2.0	7.0±1.4	5.8±2.2	12.3±1.5
	2	4.5±0.6	9.2±1.3	1.8±0.4	8.4±1.8
Bosmina spp.	1	3.1±1.3	5.3±1.7	5.2±2.1	11.0±1.5
	2	3.0±0.4	6.9±1.2	1.6±0.4	6.7±1.4
B. coregoni	1	2.5±1.1	5.3±1.7	5.2±2.1	10.9±1.5
	2	2.8±0.4	6.9±1.2	1.6±0.4	6.7±1.4
B. longispina	1	0.3±0.2	0	0	0
	2	0.2±0.1	0	0	0
B. longirostris	1	0.3±0.2	0	0	0.1±0.1
	2	0	0	0	0
Daphnia spp.	1	0.4±0.3	0.3±0.2	0	0.8±0.2
	2	0.4±0.2	0.3±0.1	0.1±0.1	0.7±0.2
Chydorus sphaericus	1	0.1±0.1	0	0.2±0.1	0.3±0.2
	2	0	0	0	0
Diaphanosoma brachyrum	1	0	0.1±0.1	0.3±0.2	0
	2	0.3±0.2	1.1±0.4	0	0.6±0.2

Table 1. Continued from previous page

Holopedium gibberum	1	1.5±0.9	0	0	0
	2	0.2±0.1	0	0	0
Polyphemus pediculus	1	0.4±0.2	0.7±0.5	0	0.1±0.1
	2	0.2±0.1	0.2±0.2	0	0.3±0.1
Limnosida frontosa	1	0	0.2±0.1	0	0
	2	0.3±0.2	0.7±0.2	0	0.1±0.1
Bythotrephes longispina	1	0	0.1±0.1	0.1±0.1	0.1±0.1
	2	0.2±0.1	0	0	0
Leptodora spp.	1	0.1±0.1	0	0	0
	2	0	0	0	0
Copepoda (total)	1	59.3±14.6	28.1±6.2	18.1±2.2	36.3±5.3
	2	51.5±7.6	43.4±1.7	11.6±1.3	25.5±3.6
Cyclopoida nauplii	1	16.4±3.1	15.5±5.3	10.5±1.6	12.6±2.9
	2	28.9±4.8	22.6±3.0	8.5±1.3	12.1±2.3
Calanoida nauplii	1	11.5±3.1	1.6±0.4	1.6±1.2	4.4±1.8
	2	4.1±1.4	5.2±1.3	0	3.0±1.0
Cyclopoida copepodites+adults	1	29.2±11.4	9.7±1.5	5.6±1.5	17.5±3.9
	2	14.5±2.3	11.0±1.3	2.9±0.03	9.2±1.4
Calanoida copepodites+adults	1	2.3±0.9	1.3±0.5	0.5±0.2	1.8±0.6
	2	4.1±1.4	4.6±0.6	0.3±0.1	1.2±0.3
Mesocyclops/Thermo-cyclops	1	22.6±5.9	15.5±4.0	11.8±2.1	20.2±4.1
	2	34.9±5.8	20.7±4.0	7.8±1.2	17.4±3.6

The total copepod density differed significantly between years ($F_{3,33}$=5.175, p=0.005). Cyclopoids were most numerous in the samples compared to other copepods, reflected by the overall higher mean densities (Table 1). Their densities also differed between years ($F_{3,33}$=6.072, p=0.002). The density of calanoid adults (including copepodites) differed significantly between years ($F_{3,33}$=3.280, p=0.033), as did also the density of calanoid nauplii ($F_{3,33}$=3.467, p=0.027). The calanoid nauplii were however less abundant than cyclopoid nauplii, the latter group typically occurring more frequently in all samples analysed (Table 1). The biomass of copepod adults and copepodites differed significantly between years ($F_{3,33}$=4.784, p=0.007 and $F_{3,33}$=3.495, p=0.026). The biomass of three groups representing the potential preferred food for vendace larvae; small (<399 µm) cyclopoids (*Mes./The.*), *Daphnia spp.* and *Bosmina spp.* exhibited a fluctuating pattern between years, with alternating low and high average biomasses in both groups (Figure 2).

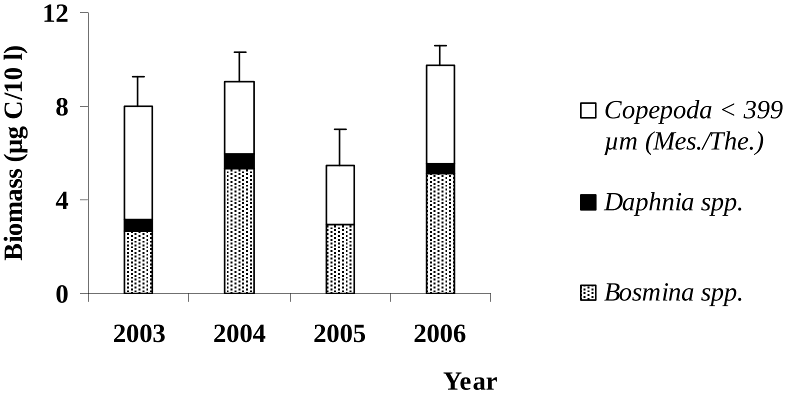

Figure 2. Annual average biomasses (µg C /10 l) of three potentially important groups in the diet of vendace larvae; small cyclopoids (*Mes./The.*), *Daphnia spp.* and *Bosmina spp.*. The standard error (S.E.) is given for the total biomass of all three groups.

4.2. Differences in zooplankton abundance between littoral and pelagic zones

The Repeated Measures ANOVA revealed no statistically significant differences in normalised (ln(x+0.1)) values of average zooplankton abundances between the littoral and pelagic depth zones. This justified the use of ANOVA in comparing differences between years, without taking into account the effect of different depth zones as components of the total variance between samples. Differences in the average abundance between depth zones are however apparent for some groups examined graphically (Figure 3). The average biomass of *Bosmina spp.* was higher in the littoral zone than in the pelagic, except in 2004, when the density in the pelagial was slightly higher (Figure 3 A). On the other hand, while there was no or minor differences in the average densities of *Daphnia spp.* between years, their average biomass in every year seemed somewhat higher in the pelagic zone. Furthermore, this group was completely absent in the littoral zone in 2005 (Figure 3). No clear pattern of the occurrence of copepods was observed and this group seemed to differ randomly in their distribution between the littoral and pelagic zone in all years (Figure 3).

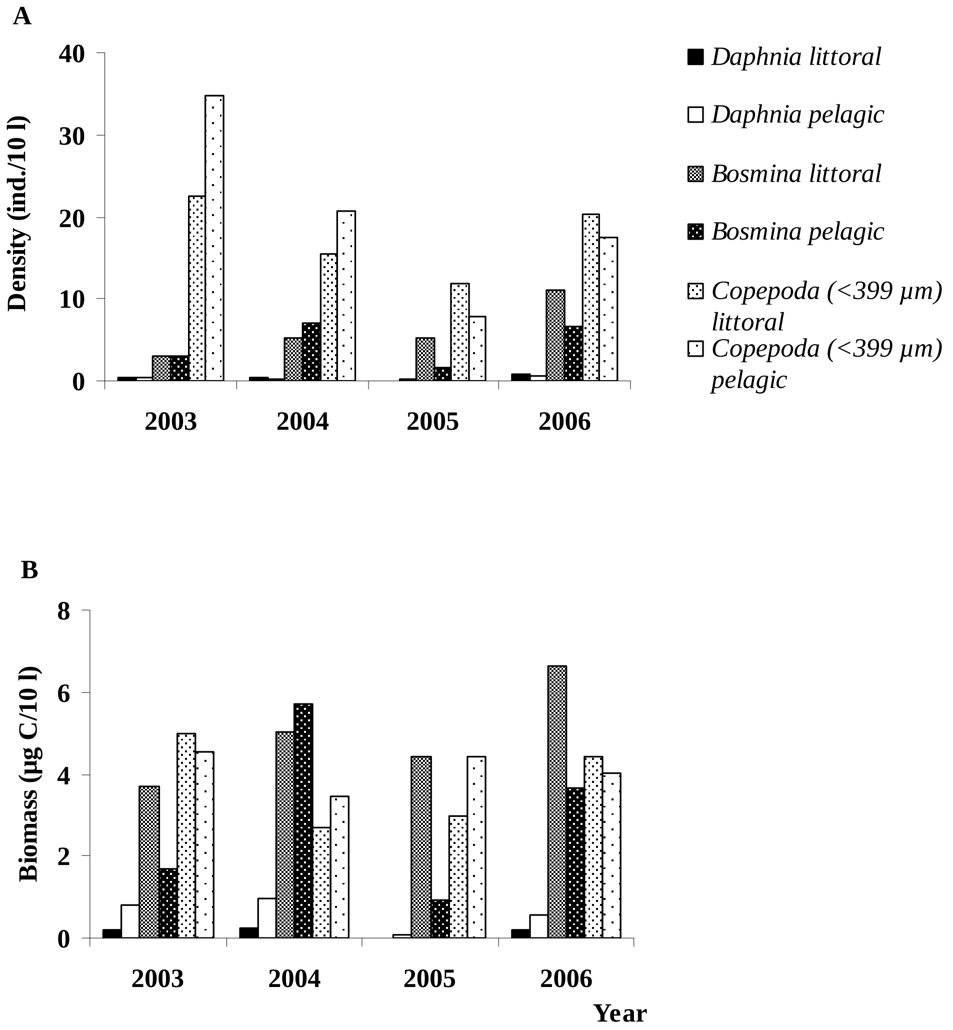

Figure 3. Annual average densities (ind. /10 l) (A) and biomasses (µg C /10 l) (B) in the littoral and pelagic zone for *Bosmina spp.*, *Daphnia spp.* and small-sized *Copepoda* (>399 µm). The copepod density in the size-class <399 µm represents *M. oithonoides/T. leukartii* (*Mes./The.*).

4.3. Variation in vendace abundance in relation to zooplankton biomass

During the study period, the abundance of 0+ vendace in the previous autumn fluctuated with alternating strong and weak year-classes every second year (Figure 4). The summer survival also fluctuated between years, showing the highest value in 2003 (0.17). Considering the larval densities, an exceptionally high density occurred in 2004. This is the highest density of larvae observed in Lake Konnevesi since the start of monitoring. After a sharp decrease in 2005, the larval density increased slightly in 2006. A decrease was apparent from 2003 in the total spawner biomass (Figure 4). The average biomass of *Daphnia spp.* and *Bosmina spp.* fluctuated with the 0+ vendace abundance in autumn (Table 1, Figure 4), whereas the average biomass of small copepods (*Mes./The.*) decreased from 2003 to 2005 followed by an increase in 2006 (Table 1, Figure 4).

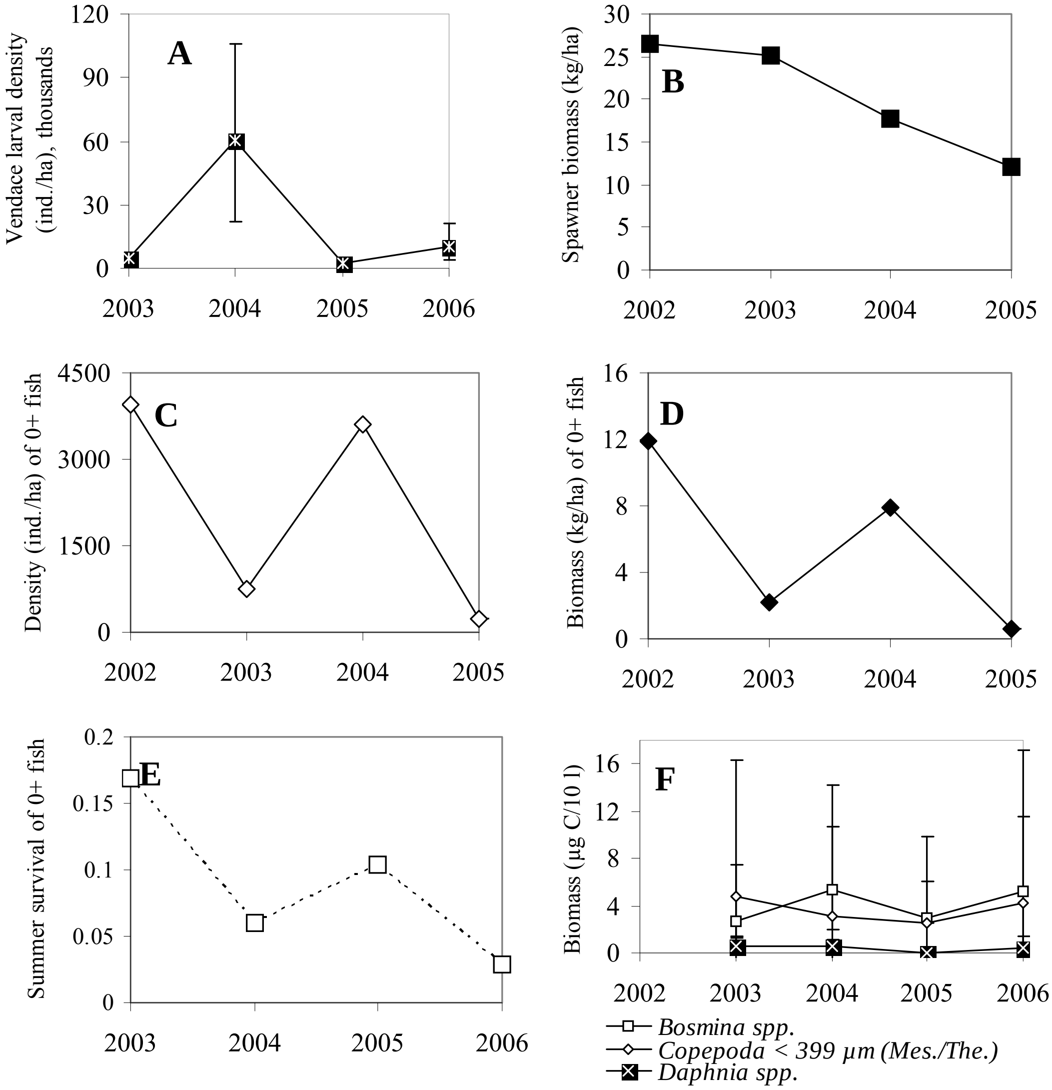

Figure 4. Annual changes in different variables describing the vendace stock; The density of larvae (A), previous autumn (2002) spawner biomass (B), density (C) and biomass (D) of 0+ fish in the previous autumn and the following summer survival of 0+ fish (E). In the bottom right-hand corner are the total average biomasses (µg C/10 l) of the three most important prey groups (F) for larval and 0+ vendace. 95 % confidence intervals are given for the density of vendace larvae and the zooplankton biomasses.

4.3. Correlation analysis

A strong negative association between the biomass of *Bosmina spp.* and the previous autumn density of 0+ vendace and the total biomass of vendace in the previous year was found (Table 2, Figure 5). The biomass of *Bosmina spp.* was also correlated negatively with the previous autumn biomass of 0+ vendace (Table 2). The biomass of *Bosmina spp.* correlated negatively also with vendace summer survival (Table 2).

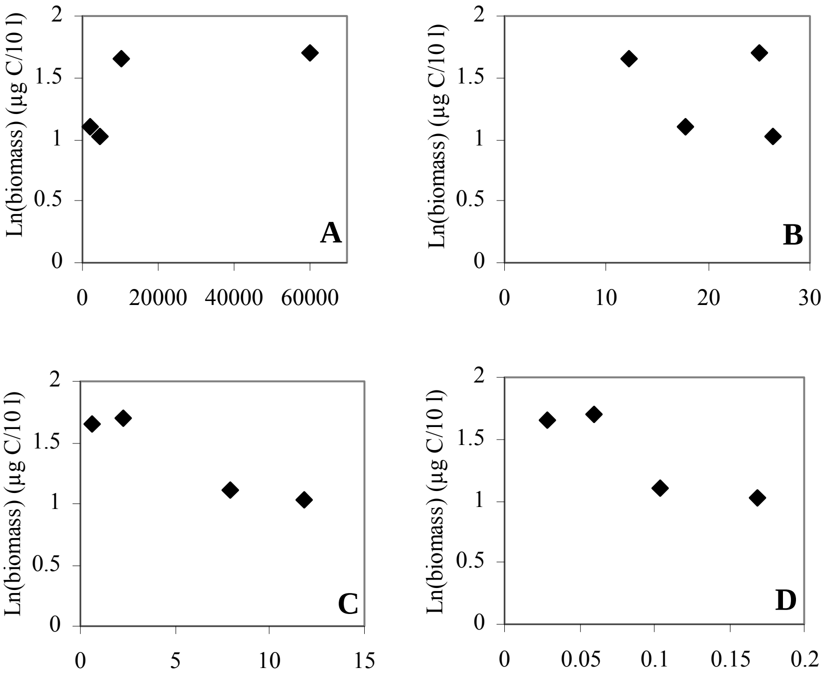

Figure 5. Scatterplots showing the association between the normalised (ln(x+0.1)) average biomass (µg C/10 l) of *Bosmina spp.* and different variables describing the vendace stock. The units of each variable depicted on the x-axis represent; the previous spring larval density (ind./ha) (A), previous autumn spawner biomass (kg/ha) (B), previous autumn biomass of 0+ fish (C) and summer survival (D).

Generally, no significant correlations were found between the abundance of all three groups (*Bosmina spp.*, *Daphnia spp.* and *Mes./The.*) and total vendace biomass the previous year. No significant correlations were found between the biomass of *Daphnia spp.* and vendace abundance variables (Table 2, Figure 6). Furthermore, no significant associations were found when correlating the biomass of small copepods (*Mes./The.*) to the vendace abundance variables (Table 2, Figure 7).

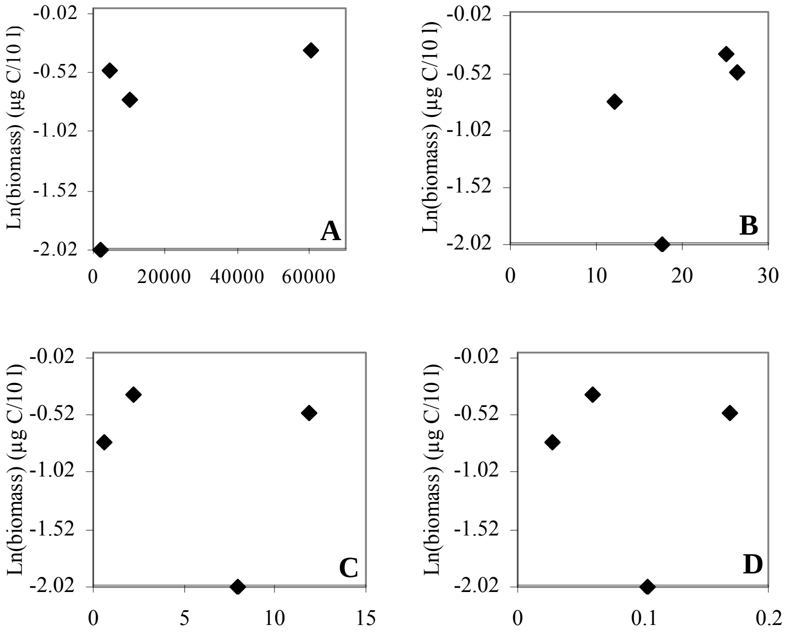

Figure 6. Scatterplots showing the association between the normalised (ln(x+0.1)) average biomass (µg C/10 l) of *Daphnia spp.* and different variables describing the vendace stock. The units of each variable depicted on the x-axis represent; the previous spring density of larvae (A), previous autumn spawner biomass (SB) (B), previous autumn biomass of 0+ fish (C) and summer survival (D).

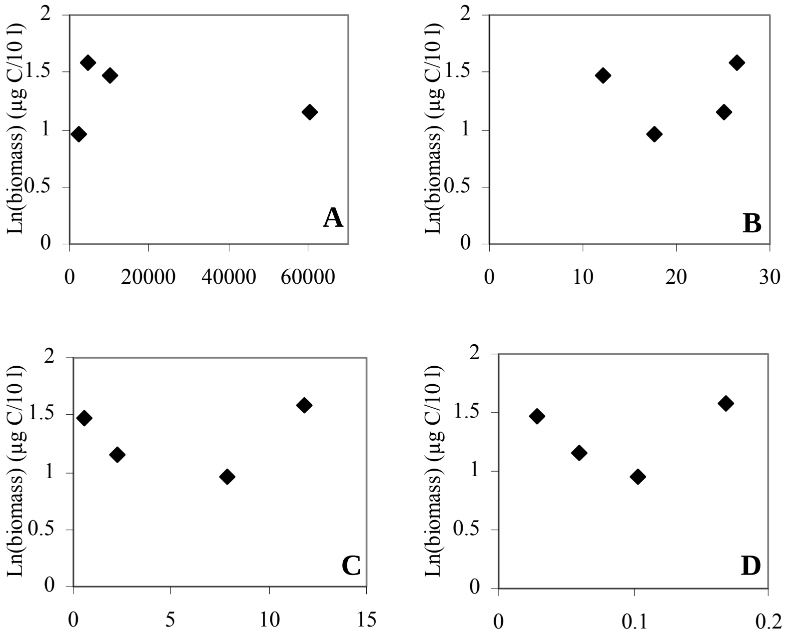

Figure 7. Scatterplots showing the association between the normalised (ln(x+0.1)) average biomass (µg C/10 l) of small (<399 µm) copepods (*Mes./The.*) and different variables describing the vendace stock. The units of each variable depicted on the x-axis represent; the previous spring density of larvae (A), previous autumn spawner biomass (SB) (B), previous autumn biomass of 0+ fish (C) and summer survival (D).

Table 2. Correlation coefficients and probability values in the analysis of different variables of zooplankton abundance and their associations to vendace abundance variables. Bold values indicate statistically significant ($p<0.05$) correlations.

Zooplankton abundance		larval spring density	Previous year spawning biomass (SB)	Previous autumn biomass of 0+ fish	Previous autumn density of 0+ fish	summer survival (S)
Bosmina density	Pearson Correlation	0.392	-0.614	**-0.973**	**-0.974**	**-0.956**
	Sig. (2-tailed)	0.608	0.386	**0.027**	**0.026**	**0.044**
Bosmina biomass	Pearson Correlation	0.700	-0.311	**-0.960**	**-0.987**	-0.901
	Sig. (2-tailed)	0.300	0.689	**0.040**	**0.013**	0.099
Daphnia density	Pearson Correlation	0.125	-0.159	-0.430	-0.607	-0.336
	Sig. (2-tailed)	0.875	0.841	0.570	0.393	0.664
small Copepoda (MesThe) density	Pearson Correlation	0.078	0.470	0.200	-0.037	0.332
	Sig. (2-tailed)	0.922	0.530	0.800	0.963	0.668
small Copepoda (MesThe) biomass	Pearson Correlation	-0.239	0.109	0.142	-0.062	0.228
	Sig. (2-tailed)	0.761	0.891	0.858	0.938	0.772
Rotifera density	Pearson Correlation	0.403	**0.990**	0.513	0.359	0.639
	Sig. (2-tailed)	0.597	**0.010**	0.487	0.641	0.361

5. DISCUSSION

The abundance of potentially important larval prey groups, especially the bosmids (*Bosmina spp.*), fluctuated inversely with the strength of the 0+ vendace year-class the previous autumn. The correlation analysis showed a significant negative association between the abundance of Bosmina in spring and the density of 0+ vendace in the previous autumn. This is interpreted here as the effect of predation by the previous year-class of 0+ vendace on their most favoured prey species. The negative association found between *Bosmina spp.* and the previous autumn biomass of 0+ vendace is in accordance with Helminen *et al.* (1990), who found that in L. Pyhäjärvi (SW Finland), a strong year-class of 0+ vendace has the potential to affect the population dynamics of *Bosmina coregoni*. Hamrin (1983) showed that the abundance of *Bosmina coregoni* in the southern Swedish Lake Bolmen varied inversely with the abundance of 0+ vendace in the population. Both of these lakes are classified as oligotrophic waterbodies (Hamrin 1983, Helminen 1994). The observed correlations suggest that populations of Bosmina are sensitive to changes in planktivory following the year-class variations of vendace, when 0+ occurs as the dominant age-group in the population. The results from this study indicate a delayed effect of summertime predation by vendace, contrary to the studies by Hamrin (1983) and Helminen *et al.* (1990), in which a direct predation impact by vendace biomass of crustaceans (mainly bosmids) was detected. Here, I show that the previous year predation by vendace probably dictates the level of zooplankton abundance also in the beginning of the next growing season.

The importance of rotifers in the larval diet generally increases with increasing latitude (Sutela *et al.* 2002) and has been linked to poor feeding conditions (Auvinen 1988a). In this study, the densities of rotifers were rather high and constant between years, indicating that this group was less affected by vendace predation. Cladocerans and copepods, when abundant, are probably preferred over rotifers in the diet of larvae (Auvinen 1988a). The absence of significant associations between daphnids and *Mesocyclops/Thermocyclops* and the previous year vendace abundance was not expected, as the parental population and offspring of these taxa, respectively, have been shown to constitute a major part of late autumn diet of 0+ vendace and the first food of vendace larvae (Auvinen 1988a, Helminen *et al.* 1990, Karjalainen & Viljanen 1992, Karjalainen *et al.* 1996). Measurement errors in the zooplankton identification and counting process together with the low number of years (or number of samples) studied, yielding low statistical power, might decrease the capability of observing any effect of delayed density dependence.

Previous studies on variations in vendace year-class strength in relation to zooplankton abundances suggest an important regulatory role of intraspecific food competition, either by juvenile or adult dominance (Sandlund *et al.* 1991), causing or maintaining the regular 2-year fluctuations observed in many vendace stocks (Hamrin & Persson 1986, Auvinen 1994, Helminen & Sarvala 1993, Helminen *et al.* 2002). However, regular cyclic fluctuations may arise also in absence of these mechanisms if the positive relationship between population fecundity and recruitment is strong enough (Marjomäki 2003). Although at a high vendace abundance level, such as the conditions in Lake Konnevesi, the effects on the observed fluctuations of intraspecific competition might be stronger than other (density independent) mechanisms. Generation cycling may appear in populations where a single year-class is responsible for the annual reproduction, the cycle length being equal to the time interval from egg fertilization to the first spawning of an individual developing form this egg, i.e. from spawning to the onset of maturity in the population (Townsend 1989). In this case, necessary preconditions for fluctuations to appear are high adult mortality and semelparity in the population. Semelparity arises when a single year-class at first spawning is responsible for majority of the annual reproduction (Townsend 1989). Townsend *et al.* (1990) showed by modelling a roach (*Rutilus rutilus* (L.)) population with high adult mortality, that a 2-year generation cycle could occur in the absence of delayed density dependence. A strong year-class arose every second year due to the roach maturing at the age of 1+. The high mortality and scarcity of older individuals in the population was attributed to lake eutrophication (Townsend & Perrow 1989). According to seine catch samples, a large part of the total vendace population in Lake S. Konnevesi seems to comprise of adult vendace (>1+) (Valkeajärvi 2008, unpubl.). Older vendace may contribute to the annual recruitment of young fish, making semelparity in the population less likely. If the population is semelparic, the 2-year cycle might thus appear without delayed density dependence. However, in Lake Konnevesi, the absence of delayed density dependence is unlikely, since the spawning biomasses during 2003-2006 was high every year and the vendace of L. S. Konnevesi clearly is iteroparic (i.e. spawning more than once during its lifetime) (T. Marjomäki 2008, pers. comm.).

Nissinen (1972) suggested that an abundant vendace year-class produced a following abundant year-class where the adult (post-spawning) mortality was high enough to create a situation where one year-class was responsible for the majority of the reproduction. The mediating effect of compensation (i.e. the negative feedback on population size by density dependent processes) at several life-stages may counteract the dependence of large a spawning population on recruitment success (Rose *et al.* 2001). If the S-R relationship is linear, it implies no delayed density dependence. However, most of the analyses performed by Marjomäki (2003) on the vendace S-R relationship for several vendace populations in a large number of Finnish lake basins, showed a non-linear and thus clear density dependent S-R relationship. Theoretically, compensation is most likely to occur at high population densities (Marjomäki 2003), but so far it is uncertain which population model (the compensatory Cushing and Beverton-Holt or the over-compensatory Ricker-model) sufficiently describes the density dependence in the S-R relationship for vendace (provides the “best fit” to the S-R data) (Marjomäki 2004). Marjomäki (2004) found strong evidence of compensatory density dependence in the central Finnish Lake Puulavesi.

According to Helminen *et al.* (1990), the 0+ vendace are the main consumers of zooplankton during most of the summer and changes in zooplanktivory reflect variations in recruitment (Helminen & Sarvala 1993). The appearance of 2-year fluctuations in the vendace population of Lake S.W. Pyhäjärvi was hypothesized by Helminen *et al.* (2002) to result from delayed density dependent regulation via population fecundity, supporting the hypothesis of intraspecific asymmetrical competition (Hamrin & Persson 1986). Auvinen (1988b) found a negative association between the abundance of vendace in autumn and the spring zooplankton density and discussed the possible effects of a previous abundant year-class on the larval survival the following spring. This mechanism would favour older age-groups by their influence through zooplanktivory on the availability of food for newly hatched vendace larvae, thus affecting their survival in the following spring. By heavily “grazing” down the population of mature (egg-bearing) female zooplankters (cladocerans and copepods) or zooplankters about to induce overwintering dormant stages, exceptionally strong year-classes of older vendace might influence the occurrence or production of zooplankton in spring. The food availability for vendace larvae is of crucial importance to their survival in spring (Viljanen 1986) and starvation, occurring as a consequence of food shortage, was suggested by Salojärvi (1987) as an important factor in generating year-class fluctuations. On the other hand, Karjalainen (1991) noticed that vendace larvae are rather resistant to starvation, indicating that mortality through starvation plays a less important role in determining the total prerecruit mortality and thus the development of the new year-class. The presence of delayed density dependence and its regulatory role on the observed 2-year fluctuations is strengthened by a positive correlation between the abundance of zooplankton in spring and that year’s summer survival of the 0+ vendace. Accordingly, abundant food resources (a high abundance of edible zooplankters) in spring would increase the vendace survival in summer. An important finding of this study is that the zooplankton abundance was, in contrast, negatively associated with the following summer survival of vendace, which is clearly contradictory to the above mentioned studies. This indicates that the spring abundance of zooplankton in Lake S. Konnevesi is not a desicive factor in determining the following summer survival of vendace.

The absence of significant correlations between the abundance of zooplankters (copepod nauplii, *Mesocyclops/Thermocyclops* and daphnids) important in the diet of vendace larvae and the previous year total biomass (representing the previous year zooplanktivory) implies that delayed density dependence is not alone responsible for the observed fluctuations. The alteration of high and low average density of *Bosmina spp.* might be attributed to direct predation by larvae in combination with heavy zooplanktivory in autumn, by the previous year’s abundant 0+ vendace population. The exceptional high larval density and the following strong 0+ year-class in 2004 was followed by a decrease in all zooplankton groups in 2005. This indicates that the zooplanktivory by an abundant vendace year-class in the previous year can potentially cause a decline in spring zooplankton abundance. However, it does not necessarily translates into a weak vendace year-class the following year, due to the presence of other decisive factors, such as seasonal temperatures, wind forcing and predation in regulating the interannual recruitment (e.g. Marjomäki 2003).

The relative strength of interrelating factors and mechanisms may be different in different years and this is difficult, if not impossible to determine by simply using correlative analyses. The commonly used correlative approach in studying factors underlying recruitment variations in vendace and other species of fish is less useful when interpreting the effect of one variable on the other because correlations do not demonstrate “cause-and-effect” (Marjomäki 2003). The correlations presented in this study show merely the associations between the zooplankton spring abundance and vendace variables. However the relationships found do not provide any direct evidence of the feeding impact of vendace on zooplankton in autumn. Furthermore, any associative linkage between the zooplankton autumn abundance to their abundance in spring is difficult to make based on the data available. To improve the statistical power of the correlations longer time series would have been necessary. The random appearance or absence of significant correlations in several taxa may simply be an artefact of the low number of years analysed.

The spatial distribution of zooplankters between depth zones in different years was not statistically significant. However, the average density and biomass of *Bosmina spp.* were higher in the littoral zone, whereas the density of small-sized copepods appeared to be more random in all years, showing no obvious difference between the two depth zones. Sutela *et al.* (2002) found no difference in the feeding success of vendace larvae between the littoral and pelagic zones. Vendace larvae tend to aggregate in the littoral zone immediately after hatching (Auvinen 1994, Karjalainen 1992) and their feeding impact should thus be greater in this zone. The relative occurrence of vendace larvae in the littoral and pelagic zones has been suggested to result from differences in water colour or the location of spawning grounds. In lakes with clear water, spawning may occur at greater depths and most vendace larvae spend their first weeks in the pelagic zone. In more humic lakes, where spawning grounds are located in closer to the shore, the occurrence of newly hatched larvae is higher in the littoral zone (Karjalainen *et al.* 2000, 2002).

The interannual variations in zooplankton abundance observed in the spring may not be solely dependent on the predation pressure by vendace in autumn. Differences in the distribution and spatial aggregation of zooplankters are influenced by variations in local abiotic factors (e.g. water temperatures, cloudiness and wind conditions) and biotic factors (competition and predation) (Pinel-Alloul *et al.* 1988, Gyllström & Hansson 2004). In Finnish lakes, the older vendace usually starts feeding on zooplankton about two months before the break-up of ice from the lake. As suggested by Auvinen (1988b), it is likely that this direct predation by older vendace before larval hatching may affect the observed spring abundance of zooplankters. Direct changes in the distribution and occurrence of zooplankters also arise as a response to other factors, such as dispersion by wind or currents, water quality and temperature differences in their immediate environment and interspecific competition or invertebrate predation (Gyllström & Hansson 2004). Changes in photoperiod length and temperature have been suggested to cue the hatching of zooplankton resting eggs and emergence of overwintering adult stages (Gyllström & Hansson 2004). According to Hämäläinen & Karjalainen (1994) the density of benthic copepods can be expected to correspond to the number of cyclopoids in the overlying water column proceeding the diapausing period. The authors further proposed that the density of hatching resting eggs and zooplankters terminating diapause in spring might be determined by fish predation during the period prior to diapause induction. However, they found no indication of this, as they noticed higher densities of benthic cyclopoids and cladocerans in the sediments than in the overlying water layers. The proposed explanation was based on earlier observations that considerable parts of the Mesocyclops populations can live in the sediments throughout the entire growing season, possibly utilising detritus as a food resource (Papinska 1984). The benthic part of the population, residing within the sediments, could act as a buffer to the planktonic population in times of altering environmental conditions and function similar to the seed banks as seen in terrestrial plants.

The findings from this study highlight the potential importance of *Bosmina coregoni* as a major food source in vendace and imply that variations in annual densities of this species are sensitive to predation from abundant year-classes of 0+ fish. The absence of significant correlations in other important groups might result from measurement errors in identification. Perhaps more importantly; the capability to detect the impact of delayed density dependence was probably reduced due to the low statistical power of the correlations, arising from the low number of years from which samples were analysed. The true mechanism underlying the year-class fluctuations cannot possibly be revealed on the basis of correlations alone. Since no significant associations were found in this study between the zooplankton abundance and the previous year total biomass, the mechanism involved in the alteration of strong and weak year-classes is likely to be different from that expected. The following summer survival of 0+ vendace showed a negative association with zooplankton abundance in spring. This contradicted what was expected initially, namely a positive association between the zooplankton abundance and summer survival. The summer survival was negatively associated with the density of vendace larvae in spring. By judging from the observed larval densities observed in 2003, the low density of bosmids (about half of that in 2004) was apparently sufficient to support the low larval density in 2003, but not high enough to support the extremely dense larval population of 2004. Although fish density determines the density of *Bosmina*, the interannual variation is probably very low compared to some other (yet unknown) factor causing the dramatic variation in vendace survival between spawning and hatching. Delayed density dependence as proposed by Auvinen (1988b) is thus probably less important in the regulation of vendace year-class strength between years in L. S. Konnevesi. The role and consequences of intraspecific competition in determining the year-class variation still remains an open question. Moreover, the importance of external (density independent) factors, such as stage-specific temperature development (Koho 2002, Helminen & Sarvala 1994) and interspecific predation during the growing season (Nyberg et al. 2001, Valkeajärvi & Marjomäki 2004) is likely to be more important in ultimately determining the interannual recruitment dynamics in vendace populations in L. S. Konnevesi and other similar northern vendace lakes.

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