

**The role of a tapeworm
Diphyllobothrium ditremum Creplin
in the regulation mechanisms of a subarctic
whitefish (*Coregonus lavaretus* (L.)) population**

Arto Tolonen

Department of Limnology and Environmental Protection
University of Helsinki

Academic dissertation in Fisheries Science.

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in auditorium 1041, Biocenter, Viikinkaari 5, Helsinki, on January 26, 2001, at 12 noon.

Helsinki 2000

© Arto Tolonen

ISBN 952- 91-3083-X (nid.)

ISBN 952-91-3084-8 (PDF)

Yliopistopaino

Helsinki 2001

Abstract

The role of *Diphyllbothrium ditremum* plerocercoid larvae on the, growth condition, reproduction and mortality of benthic whitefish *Coregonus lavaretus* (L.) was studied in subarctic Lake Kilpisjärvi in 1964-1997 in order to find out long term changes in the host-parasite interaction. The main food consumption of fish commenced in July and reached maximum values in early August at 10°C. The yearly weight maximum was observed immediately before spawning in November. During winter the food intake was strongly reduced. The most important items in the diet of whitefish during March-April under ice cover were copepods, mainly calanoids. At low temperatures, feeding on dense, hibernating copepod populations may be more energetically efficient instead of the less digestible zoobenthos.

Of the *Diphyllbothrium* species whitefish were infected by *D. ditremum* plerocercoids only. The mean abundance in Lake Kilpisjärvi whitefish was 103.5 ± 71.3 plerocercoid larvae per host in 1992-1993. The proportion of copepods as a source of parasite infection in the present study decreased gradually in the whitefish diet, thus no accumulation of plerocercoids was detected after age 2. The estimated yearly loss of plerocercoids in whitefish was 49.5% and the rate of establishment 77 new larvae per fish per year. A mean life expectancy of 1.2 years was calculated for the plerocercoids in its fish host. There were two main periods of yearly transmission: one in spring before ice-break-up and another in autumn. The copepods, mainly *Eudiaptomus graciloides* Lilljeborg and *Cyclops scutifer* Sars were the most important prey items of whitefish during the early spring under ice-cover and again in autumn. Generally, there was a delay of a month to the increase in the numbers of plerocercoids from the time the peak of copepod consumption was detected. In Lake Kilpisjärvi whitefish the abundance levelled at the age group 3, and thereafter there was a decline in the variance to mean ratio but no clear decline in the abundance of the plerocercoids within the oldest age groups. The evidence of *D. ditremum* induced mortality in subarctic whitefish populations was not clear.

The effect of plerocercoids was studied during the early development of ovaries in February-April at the time of the onset of yearly gonadal growth and during the maturation of the gonads in autumn. The parasite abundance was a significant predictor of the weight of ovaries and the effect was negative. The parasite abundance had no significant effect on gonadosomatic index in female whitefish during the period from August to December, whereas it was a significant predictor for the relative energy density of gonads. There was also a negative effect of plerocercoid abundance on the relative fecundity. However, the dry matter content of a single egg was positively correlated to the plerocercoid abundance. Large eggs have been shown to produce larger fish larvae than small eggs, which have better opportunities for survival. Effects of *D. ditremum* infection as a regulatory control on the population level were discussed. Intensive stockings in early 1960s may have promoted a perturbation in host-parasite interactions. Thereafter parasite as a factor in the compensatory process may have kept the whitefish population within limits of the carrying capacity of the lake, since the growth and condition of the fish was found to have improved. The results of this study support the assumption of earlier workers that whitefish seems to be well adapted to sustain high abundance and prevalence of *D. ditremum*, which was explained with a high degree of stability in host-parasite interactions.

List of the original papers

- I) Tolonen, A. 1997. Size-specific food selection and growth in benthic whitefish *Coregonus lavaretus* (L.) in a subarctic lake. *Boreal Env. Res.* 2(4): 387-399.
- II) Tolonen, A. 1999. Application of a bioenergetics model for analysis of growth and food consumption of subarctic whitefish *Coregonus lavaretus* (L.) in Lake Kilpisjärvi, Finnish Lapland. *Hydrobiologia* 390: 153-169.
- III) Tolonen, A., Rita, H. & Peltonen, H. 2000. Abundance and distribution of *Diphyllbothrium ditremum* Creplin (Cestoda: Pseudophyllidea) plerocercoids in benthic whitefish *Coregonus lavaretus* (L.) in northern Finnish Lapland. *J. Fish Biol.* 57: 15-28.
- IV) Tolonen, A. & Rita, H. 1998. Effect of *Diphyllbothrium ditremum* (Creplin) plerocercoid infection on gonadal weight in benthic whitefish *Coregonus lavaretus* (L.) in Lake Kilpisjärvi, Finnish Lapland. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 50: 249-256.
- V) Tolonen, A., Paalavuo, M., Muje, P. & Rita, H., Energy density and fecundity in subarctic whitefish (*Coregonus lavaretus* (L.)) infected by *Diphyllbothrium ditremum* plerocercoids *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* (In press).
- VI) Tolonen, A. & Kjellman, J., Post-stocking perturbations in a subarctic whitefish *Coregonus lavaretus* (L.) population: effects on growth, condition and cestode infection. *Hydrobiologia* (In press).

Author's contribution

- III) The idea and design of this study was author's. He also wrote the article. The statistical analyses and model applications were made by the co-authors.
- IV) The idea of this study was author's. The statistical analyses were made by the co-author, and he also participated in writing the article.
- V) The idea and design of this study was joint. The parasitological analyses were made by the author and he wrote the article. The energetics analyses and model applications were planned and carried out by the co-authors.
- VI) The idea of this study was author's. The statistical analyses were made by the co-author, and he also participated in writing the article.

Copyright

- Article I © Finnish Zoological and Botanical Publishing Board
 Article II and VI © Kluwer Academic Publishers
 Article III © The Fisheries Society of the British Isles
 Article IV and V © E. Schweitzerbart'sche Verlagsbuchhandlung

Contents

1. INTRODUCTION	7
1.1. The genus <i>Diphyllbothrium</i> ; occurrence, life cycle and pathogenicity	7
1.2. Energy reserves and reproduction success	8
1.3. Parasite induced mortality and host response	9
1.4. Population regulation in whitefish	10
1.5. Objectives and research strategies	11
2. MATERIAL AND METHODS	12
2.1. Study area	12
2.3. Assessment of food consumption, energetics and growth	16
2.4. Parasitological methods	17
2.5. Assessment of the effect of <i>D. ditremum</i> infection on whitefish	19
2.5.1. Condition	19
2.5.2. Gonadal development	19
2.5.3. Reproduction effort	20
3. RESULTS AND DISCUSSION	21
3.1. Transmission dynamics of <i>D. ditremum</i> in whitefish	21
3.1.1. Effect of seasonal diet shifts on the plerocercoid recruitment	21
3.1.2. Effect of ontogenetic diet shifts on infection with age	25
3.1.3. Effect of habitat use on the infection level in sympatric whitefish forms	28
3.1.4. Rate of the parasite establishment	29
3.2. Growth of the whitefish	31
3.2.1. Seasonal and lifetime growth patterns	31
3.2.2. Effect of <i>D. ditremum</i> infection on growth and condition	33
3.3. Gonadal growth and energetics of reproduction	35
3.3.1. Effects of <i>D. ditremum</i> infection on the ovaries	37
3.4. Regulation in the whitefish population	38
3.4.1. Role of <i>D. ditremum</i> induced mortality	42
4. CONCLUDING SUMMARY	44
Acknowledgements	48
Tiivistelmä	49
References	51

1. INTRODUCTION

1.1. The genus *Diphyllobothrium*; occurrence, life cycle and pathogenicity

Three species of the tapeworm genus *Diphyllobothrium* Cobbold 1858 (Cestoda: Pseudophyllidea) occur in European and North American freshwater fishes: *D. latum* (L. 1758), *D. dendriticum* (Nitzsch, 1824) (syn. *D. norwegicum* Vik 1957) and *D. ditremum* (Creplin, 1825) (Halvorsen 1970, Bylund 1975, Andersen *et al.* 1987). The species status of a fourth species *D. vogeli* (Kuhlow 1953) is not confirmed, but is still under review (Andersen & Gibson 1989, Bylund & Andersen 1994). Plerocercoids of the genus are common parasites of freshwater fish, especially salmonids, and have caused serious problems in freshwater fisheries (Henricson 1977, Halvorsen & Andersen, 1984, Berube & Curtis 1986, Frandsen *et al.*, 1989, Sharp *et al.*, 1989, Curtis & Bylund 1991, Rodger 1991, Hristowski 1992, Rahkonen *et al.* 1996). Different species of Cyclopidae and Diaptomidae serve as the first intermediate hosts for diphyllobothriids (Vik 1964). *Eudiaptomus graciloides* Lilljeborg and *Cyclops scutifer* Sars are the dominating planktonic copepod species found to be the most possible first intermediate hosts for *D. ditremum* in northern lakes (Henricson 1978, Kristoffersen 1993, Knudsen & Klemetsen 1994). When the infected copepods are ingested by a fish intermediate host, the plerocercoid larvae will develop into plerocercoids. When eaten by the final avian host the plerocercoids emerge from the fish and complete their life cycle by developing into mature egg-producing cestodes (Halvorsen 1970).

Larval cestodes are known to be less host specific than adult cestodes in fish (Andersen & Valtonen 1992). Whitefish *Coregonus lavaretus* (L.) is known to be infected by plerocercoids of both species *D. ditremum* (Amundsen & Kristoffersen 1990) and *D. dendriticum* (Bylund 1972, Valtonen & Valtonen 1979, Valtonen *et al.* 1988, Andersen & Valtonen 1992). However, in northern Lapland and in the high mountain lakes of Norway whitefish have been found to be infected by *D. ditremum* only (Halvorsen 1970, Amundsen 1988, Tolonen 1992, Gustafsson 1996). The obvious dominance of *D. ditremum* in whitefish seems to be a very northern phenomenon, but also to be connected to the altitude. Halvorsen (1970) observed that in lakes close to the sea level the whitefish harboured more *D. dendriticum* larvae, while in lakes on higher altitudes *D. ditremum* was more abundant. In Lake Kilpisjärvi both burbot *Lota lota* (L.) (Tolonen & Lappalainen 1999) and Arctic charr *Salvelinus alpinus* (L.)

(Gustafsson 1996) are infected by both of those species. Halvorsen (1970) in Norway observed the similar disparity between *D. dendriticum* and *D. ditremum* in burbot and whitefish.

1.2. Energy reserves and reproduction success

Fish usually prefer to feed in the most energetically rewarding habitat available (Werner & Mittelbach 1981), where benefits include calories and nutrients ingested, whereas costs involve energy used up, time lost in other activities, or exposure to predators or parasites (Helfman *et al.* 1997). Interactions such as intraspecific competition (Haraldstad & Jonsson 1983, Persson 1983) and interspecific competition (Werner & Hall 1977) may also influence the foraging behavior and food habitat selection of the fish. Food resources may be the most limiting factor in freshwaters and the niche segregation according to habitat may be the most essential way to avoid competition (Schoener 1974, Hansson & Leggett 1985).

Ultimately, benefits and costs have to be measured in terms of an animal's lifetime reproduction success or fitness, measured as genetically related individuals produced in later generations (Krebs & Davies 1991). Gamete production, particularly in females is energetically expensive (Helfman *et al.* 1997). In Arctic the winter season is energetically critical for whitefish. The weight-to-length relation increases rapidly during the summer feeding season and decreases considerably during winter as fish use their energy reserves (Fechhelm *et al.* 1995). When reproduction involves the diversion of resources away from growth, the future fecundity of the fish will be reduced because of the reduction in growth (Wootton 1985). In Scandinavian subarctic lakes, which are ice-bound for eight months or even more, the period for the accumulation of energy reserves is often too short to spawn every year. Idle years in spawning of whitefish females have been observed in North-American coregonids (Hagen 1970) and in Europe (Reshetnikov 1967, Valtonen 1972).

Are there other factors than energy supply controlling the periodicity in spawning? Current interest in the nature and extent of effects of parasite species on their hosts arises in part from ideas about the impact of parasites on the ecology of host populations (Price 1990, Tierney *et al.* 1996). Parasites may play a role in regulating the size of the host population (Anderson & May 1978, Adjei *et al.* 1986). Population regulation occurs due to several different

mechanisms, more than one of which may be acting at the same time. The basis of the regulatory effect on the host population is that parasite-induced host mortality or reduction in fecundity is density-dependent (Spratt 1990).

Diminished fertility caused by the adverse effect of helminth toxins on the physiology of reproduction have been previously demonstrated in mammals (McCallum 1989, Spratt 1990) and in birds (Dobson & Hudson 1992, Hario *et al.* 1992). Few observations (Arme & Owen 1967, McPhail & Peacock 1983, Oliva *et al.* 1992, Tierney *et al.* 1996) have been reported on the host-parasite interactions of fish parasites. Oliva *et al.* (1992) found that even dead nematodes in gonads initiate a strong host response, reducing the gonadal volume and leading to lower fecundity in the host, although no histological damage to the infected fish's gonads was observed.

1.3. Parasite induced mortality and host response

Parasite induced mortality rates of the host have been assumed to increase by number parasites per host (Anderson & May 1979). As found in the case of *D. dendriticum* in northern salmonids the mortality does not only correlate with the total number of parasites but also with their seasonally varying proportions in different organs of the fish (Henricson 1978). The fish host is able to survive with hundreds of plerocercoid larvae on the body cavity organs (Rahkonen & Koski 1997) but even a single larva inside the heart atrium may be fatal (Rahkonen *et al.* 1996). The efficiency of the inflammatory response encapsulating *D. ditremum* and *D. dendriticum* worms varies according to the fish species (Bylund 1972, Sharp *et al.* 1989). Whitefish possess a more developed ability to encapsulate the penetrating plerocercoid larvae than other salmonids (Bylund 1972). *D. dendriticum* is able to penetrate to the heart and other vital organs of the fish host causing death (Rahkonen *et al.* 1996), while *D. ditremum* does not have the same power of migration in the host (Halvorsen 1970, Halvorsen & Wissler 1973). Also due to the higher intensity and overdispersion of infection in Arctic charr there is reason to believe that the pathogenicity of *D. ditremum* is lower and the lethal level thus higher when compared to *D. dendriticum* (Henricson 1977). Also the ability of plerocercoids to pass from prey fish to predatory fish is poorly developed in *D. ditremum* when compared to *D. latum* and *D. dendriticum* (Halvorsen 1970, Halvorsen &

Wissler 1973). *D. ditremum* has therefore been considered to have little effect on the fish host (Halvorsen, 1970).

Most helminth populations are aggregated within the host population, i.e. they are overdispersed (a few host individuals harbour the majority of the parasites). Overdispersion is an essential element in the regulation of host and parasite populations (Crofton 1971, Anderson & May 1978, Anderson & Gordon 1982, Gordon & Rau 1982), even though a very few hosts harbour a lethal load of parasites (Anderson 1995). Results of the models of Anderson & May show that the slightly pathogenic and randomly distributed macroparasites are even more effective than strongly pathogenic species in depressing the equilibrium of the host population. The increasing parasite aggregation has a stabilizing effect on the host-parasite interaction; when the host individuals with the greatest numbers of parasite will die, a lot of parasites will be eliminated from the host population as well (Anderson & May 1978). Therefore the regulatory effect of the macroparasites will decrease when the pathogenicity increases (Anderson 1979). Highly aggregated macroparasites may regulate host population growth more likely to a stable equilibrium than to stably sustained cycles.

1.4. Population regulation in whitefish

Many northern Scandinavian mountain lakes have dense and stunted populations of whitefish *Coregonus lavaretus* (L.) and other salmonid fishes (Amundsen 1988, Amundsen & Klemetsen 1988, Kristoffersen 1993). Whitefish has also been introduced or stocked at great densities to several lakes. During the short period of 1959-1964 also Lake Kilpisjärvi was stocked heavily with whitefish fry (Tolonen 1992). In the 1970s catches decreased drastically, and decline in growth and condition was observed. In 1982-1983, a clear increase in abundance of *D. ditremum* plerocercoids was noted, which was assumed to be an indication of perturbation in the host-parasite interaction caused by stockings (Tolonen 1992). Compensatory processes tend to increase mortality or decrease reproduction as population size increases. Those processes in fish populations operate, for example, through reproduction (fecundity, egg quality), growth, interspecific competition, cannibalism, predation, diseases and parasitism (Salojärvi 1992). Since the plerocercoids of helminth parasites such as *Diphyllbothrium* spp. and *Triaenophorus crassus* limit the feasibility of both recreational and commercial exploitation of fish populations (Amundsen 1988, Pulkkinen 1999), the

population density tends to grow due to the decreasing fishing mortality. Decreasing whitefish growth rate after stockings was observed also by Lehtonen & Niemelä (1998) and Sarjamo *et al.* (1989) in numerous mountain lakes of Northern Lapland, which refers to density-dependent growth. According to Salojärvi (1992) the long-term effects of stocking on fish yield and on the distribution and occurrence of parasites and pathogens are poorly known. The hybridization and introgression between stocks is also possible. Therefore the suitability of stockings as a fishery management method of whitefish has been questionable, especially in the lakes where natural reproduction is efficient.

1.5. Objectives and research strategies

The hypothesis that there is a positive correlation between fish densities and parasite infections has been earlier confirmed in subarctic whitefish populations (Kristoffersen 1993). Fish density reduction has been found to have a positive effect when preventing *D. ditremum* infection among benthic whitefish (Amundsen 1988), but very few field investigations have been undertaken to quantify the cost of parasites to fish host (Adlard & Lester 1994, Tierney *et al.* 1996, IV, V). By comparing the profit; energy gained from prey, against the cost of parasites on reproductive success, condition and survival, it may be possible to find the connections between different feeding strategies and the fitness of the fish (Knudsen 1997).

The whitefish population of Lake Kilpisjärvi was studied during three periods: 1982-83 (I, VI), 1992-93 (II, III, V, VI) and 1997-98 (IV, VI). In the following investigation I will deal with transmission dynamics of *D. ditremum* and its role as a regulatory factor on the reproduction, growth, condition and mortality of whitefish in order to reveal long-term changes in the host-parasite interaction between whitefish and its main food transmitted parasite.

The main objectives in detail of the present thesis are:

1. To investigate how the size-specific and seasonal dietary shifts contribute to the *D. ditremum* recruitment in a subarctic, benthic whitefish.
2. To find out whether the plerocercoid larvae of *D. ditremum* have effect on the growth, condition and mortality of the whitefish.
3. To find out whether the reproduction (gonadal development, maturity, fecundity, egg quality) of the host is affected by the parasite.

4. To explore long term transmission dynamics of *D. ditremum* in a subarctic, stocked whitefish population, and to reveal possible differences in the dispersion patterns when compared with other subarctic lakes where the whitefish populations are original.
5. To find out whether the parasite works as a regulatory factor in whitefish populations

2. MATERIAL AND METHODS

2.1. Study area

Lake Kilpisjärvi (33.7 km²), where most of the work in this study was done, is located in the northwestern corner of Finnish Lapland (69°00'N, 20°55'E), 463 m above sea level (Fig. 1). In article III, additional data from three other lakes (Lake Pöyrisjärvi, Lake Puolbmajavri and Lake Unkkajärvi) in northern Lapland were used. Lake Kilpisjärvi is a typical oligotrophic clear-water mountain lake in the Subarctic Birch Forest Zone. The thermic growth season of the study area lasts about 110 days.

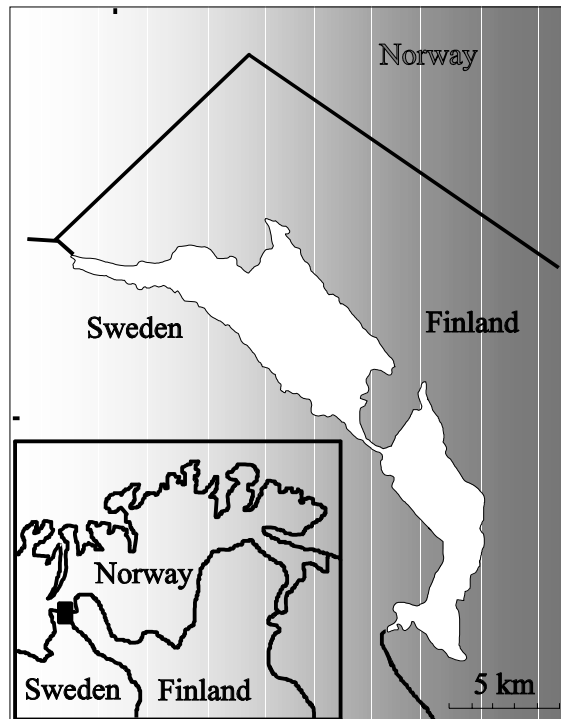


Figure 1. The location of Lake Kilpisjärvi

The annual primary production of phytoplankton in Lake Kilpisjärvi has been estimated to vary between 2 - 7 g C m⁻² year⁻¹. Average surface water temperature of 13.9 °C in maximum has been measured in August. The lake is dimictic and the median date for lake freeze-over is

November 25 and for ice break-up June 16 (Anon. 1983). The maximum depth in the upper basin is 48 m and in the lower basin 57 m, and the maximum water level amplitude is 0.6 m (Järnefelt 1956). The drainage basin of the lake covers an area of 290 km², and it drains via Tornionjoki river into the Bothnian Bay, Baltic Sea. Fish species in Lake Kilpisjärvi include the whitefish, Arctic charr, burbot, grayling *Thymallus thymallus* (L.), brown trout *Salmo trutta* L., alpine bullhead *Cottus poecilopus* Heckel and minnow *Phoxinus phoxinus* (L.). Also a few pike *Esox lucius* L. and perch *Perca fluviatilis* L. occur in the lake. During the relatively short period of years 1959-1964 more than 400 000 (25-85 ind. ha⁻¹ year⁻¹) whitefish fry originated from River Oulujoki (Montta hatchery), were stocked in the lake (Tolonen 1992).

2.2. Sampling and analyses

Whitefish samples from Lake Kilpisjärvi for food analyses and growth estimates were taken in 1982-1983 and in 1992-1993, using a series of 9 gill nets (1.8 * 30 m) with mesh sizes 12, 15, 20, 25, 30, 35, 45, 60, and 75 mm measured from knot to knot. The gill nets were kept in the lake 8-10 h during the summer and 16-24 h during cold-water season. Experimental fishing was performed weekly from the beginning of July to the end of September in 1982 and to mid-October in 1983 lasting nearly the whole ice-free season (Table 1, I). Another study period lasted from mid-February to mid-November 1993 including ice-covered and open water seasons. In winter, due to the low water temperature, the swimming speed and mobility of the whitefish is lowered. Therefore the sampling interval was prolonged even to 24 h to ensure sufficient sample size per fishing time.

Table 1. Study aims, periods and number of whitefish sampled from benthic gill net and seine catch of Lake Kilpisjärvi and other study lakes in 1982-1998.

Study aim/ original paper		Year	Month	Fishing gear	N
Feeding, size specific food selection	I	1982- 82	Jul-Oct	Gill net, experimental	696
Food consumption, growth, (bioenergetics)	II	1993	Feb-Oct	Gill net/seine catch	560
<i>D.ditremum</i> transmission dynamics, host mortal.	III	1992- 93	Sep-May	- " -	342
- effect on gonad weight of the host	IV	1993	Feb-Apr	Gill net, experimental	94
- transmission dynamics, host mortality	III	1997	Aug-Dec	Gill net, commercial catch	124
- effect on energy density and fecundity	IV	1997- 98	Mar-Dec	- " -	120
- effect on condition, population regulation	VI	1960- 90s	Feb-Dec	Gill net/seine	1594
- infection in other lakes, whitefish feeding	III	1993	Aug-Oct	Gill net/seine	220

For estimation of differences in the density of the whitefish population during the study period catch-per-unit-effort was recorded in 1983 and 1993 (VI). In 1983 the lake was fished 8 times with 4 - 9 nets. In 1993 the effort was 6 sets with 4 - 6 nets. Samples in 1997 were obtained from commercial catches fished with gill nets (3.0 * 30 m) with mesh sizes 25-35 mm respectively. CPUE was analysed as catch (kg net⁻¹ and ind. net⁻¹) with General Linear Model (GLM, Systat), with year as categorical, and number of day from the beginning of the year as independent variable.

Gillraker samples were taken from the upper basin in July, August and September 1982-1983 and from the upper and lower basin from February to December in 1992-1993 (VI). Gillrakers from the 1st outer gill arch including all rudimentary rakers in both limbs were enumerated under a binocular microscope in the samples 1982-1993. Distribution of the numbers of gillrakers in 1974-1977 was from Tuunainen *et al.* (1979). The gillraker counts from those three periods were analysed with pairwise *t-test* comparisons assuming separate variances.

Scales for age determination were taken from the ventral side of the fish as described by Einsele (1943). The age of the fish was determined with a micro fiche reader using pressed plastic slide copies of the scales. Traditionally, scales have been used for ageing coregonids besides other bony parts and otoliths. The otolith ages are considered to be more accurate than scale ages (Beamish & McFarlane 1995). Age determinations made from otoliths of slow growing whitefish have been found to show older ages than the determinations from scales (Raitaniemi 1999). Salojärvi (1989) concluded that ageing of whitefish from scales was sufficiently reliable except for the dwarfed populations.

Individual growth was estimated as length-at-age, where length was measured as total length. The samples from nearby years (1982-83, 1992-93, 1997) were pooled into three periods and length-at-age was analysed in GLM, with period as categorical, and age 2 - 10 as independent variable (VI).

Whitefish go through clear ontogenetic diet shifts during their life span (e.g. Bodaly 1979, Palomäki 1981, Miinalainen & Heikinheimo 1998). The size-specific diet and timing of the diet shift was studied during the ice-free seasons of 1982-1983 (I). Since some periodicity

was observed in the length-at-age curve, it appeared reasonable to classify the study material in phases with the curve. Stomach contents were analysed in 3 size categories of fish: < 150 mm, 150-220 mm and > 220 mm (I).

If not analysed immediately stomachs used for diet analyses were stored frozen (I, II). The fullness coefficient of the stomach was first estimated on a scale of 0 - 3. The fullness of the stomach can be considered not only as an indication of prey availability, but also as a function of the food digestibility, water temperature and length of the sampling interval. Strong and irregular fluctuation in the stomach fullness of whitefish have been observed in earlier studies (Jacobsen 1974, Heikinheimo-Schmid 1982). Undoubtedly, there is a possibility of under-estimation of digestible prey such as *Eudiaptomus* species. Therefore, empty stomachs and those containing trace material only were excluded from the analysis in order to minimize the error caused by the effect of digestion on the fragile prey items.

Frequency of occurrence and proportion in weight (ww) of each food taxon were used as the main criteria for characterization of the diets. The number of stomachs in which each food item occurred was recorded, and the frequency of occurrence was expressed as a percentage of the total number of stomachs examined (Windell 1971). Only the stomach contents from the oesophagus to the pylorus were analysed, and the stomach contents were then weighed to the nearest mg. Within zooplankton food the comparison among species was based on counting 200 zooplankton specimens from each stomach. Larger prey items such as molluscs and insects were picked out separately and identified under a dissecting microscope. Prey items were identified and counted at least to order. The method reveals the organisms fed upon, but gives no information on the proportions of various prey taxa; therefore, the diet was also described in terms of wet weight proportions of various prey. Differences in frequency occurrences between months and between size-groups of whitefish were analysed with χ^2 -test (I). Previously, the Kruskal-Wallis-test has been used more often in a similar context.

Since the transmission of *D. ditremum* from copepods to its intermediate fish host whitefish was an essential part of the present study, zooplankton availability was surveyed (II). Zooplankton samples were taken monthly from early February to early July and from mid-August to mid-November 1992 -1993 twice per month from the deepest point of the upper basin (depth 47 m) and from the littoral zone. Quantitative zooplankton samples were taken

with a 6.8 litre plastic tube-sampler, and filtered through a 50 µm filter. In the pelagic zone, 5 subsamples by 1 m intervals were taken from the depths of 0-5 m, 10-15 m, 20-25 m and 30-35 m and combined into one 34 litre sample of each. In the littoral zone at the depth of 3-5 m the subsamples were taken by 1 m intervals from the surface to near the bottom and combined into one sample. The zooplankton were preserved in 2% formalin, settled in cylinders and counted with a converting microscope.

2.3. Assessment of food consumption, energetics and growth

A bioenergetics model compiled by Hewett & Johnson (1992) was applied for the data collected during the year 1993 for exploring seasonal and life-time variations in the weight curve and food consumption of whitefish with a particular emphasis in the copepod consumption as an essential factor in the parasite transmission (II). The model is based on a balanced energetics equation (Elliott 1979):

$$\text{Growth} = \text{Consumption} - (\text{Respiration} + \text{Waste losses}) \quad (\text{Eq. 1})$$

Feeding data of Lake Kilpisjärvi whitefish from February to May and from July to October 1993 were available for the simulation. The treatment of the whitefish stomachs was the same as used during open water period 1982-1983. However, when analysing larger food items such as molluscs and insect larvae, calculations were based on reconstructed wet weights by counting partly digested food items as intact specimens (Hindar & Jonsson 1982).

Due to the diet shifts observed in whitefish (I) the feeding data was analysed according to 4 prey categories consisting of molluscs, insects, copepods, cladocerans and fish eggs. The separate diet files were specified for age groups 1-10. The model was used to estimate consumption at 15-day intervals of 5 prey items: molluscs, emerging insect pupae, cladocerans, copepods and fish prey, given the temperature patterns over each interval. The seasonal growth pattern covered a period of 1 year. Temperature values were measured at 5 m intervals; average temperatures were calculated at the depths of 5.0 - 30.0 m.

Data on the biochemical composition of subarctic whitefish in the literature are scarce. Coregonids have high energy density contents compared with those of other fish groups. Coregonid energy density increases with fish size, and it can be predicted from water content

(Rudstam *et al.* 1994). The relationship for whitefish between gross energy density and total fresh mass of fish was estimated by a bomb-calorimetric method (II) for variously sized whitefish (P. Muje, M. Paalavuo, J. Karjalainen & J. K. Karjalainen, unpublished manuscript). In spite of the different shape the total energy density curve ranged on the same level in paper V, as derived in the paper II. Thus the possible error caused by the estimated energy input data in the simulation was small.

The equation is:

$$ED = 4.029 W^{1.062} \quad (\text{Eq. 2})$$

ED = energy density (J g^{-1})

W = total fresh mass (g)

Seasonal changes in the ED of the whitefish were based on the results for Lake Pyhjärvi vendace *Coregonus albula* (L.) in southern Finland (Helminen *et al.* 1990). The energy contents of prey organisms were from Cummins & Wuycheck (1971). Egestion was assumed to be a constant proportion (25%) of ingested energy (Rudstam *et al.* 1994) and excretion a constant proportion (10%) of assimilated energy (Stewart & Binkowski 1986, Rudstam *et al.* 1994). In the present study females and males were not treated separately in the simulation, but a mean of 7.5% was used for male and female loss of body weight at spawning.

2.4. Parasitological methods

D. ditremum plerocercoid larvae were first identified from a random sample of freshly killed fish and fixed live in 70-80 % alcohol (see Andersen & Gibson 1989). In many earlier studies the larvae were removed from fish tissues using pepsin solution in physiological saline (Rahkonen 1998). Due to the high number of parasites per fish the whole sample was not studied immediately but the rest of the fish was stored frozen, and the larvae were studied from thawed material. The gastrointestinal tract, that is oesophagus, stomach, caeca and intestine were examined for plerocercoids, and opened from oesophagus to the pyloric curve. The plerocercoid cysts from the tissues were picked and counted. Other tissues in the abdominal cavity, liver, kidneys, heart, intestine, mesenteries and the musculature were also checked for the presence of other larval helminths. Cysts with dead plerocercoids were

rejected. Due to the negative binomial distributions in data, the differences in the numbers of plerocercoids were analysed with non-parametric methods.

The factors studied here (III) were the prevalence, and mean intensity (or abundance) of *D. ditremum* infection. The term prevalence refers to the percentage of fish individuals infected with *D. ditremum*, the term mean abundance refers to the mean number of individuals of *D. ditremum* per fish examined, while the term mean intensity indicates the mean number of *D. ditremum* individuals per infected fish in a sample (Bush *et al.* 1997).

Indirect methods of obtaining rates of parasite-induced host mortality were described by Anderson & Gordon (1982). Using their approach, mean abundance and variance to mean ratio (s^2/\bar{x}) of parasites by host age and sampling interval were calculated to give information on mortality of infected whitefish (III). Mortality of highly parasitized individuals will reduce dispersion and create stabilization or a decline in relative density and the variance to mean ratio (s^2/\bar{x}). Variance to mean ratio on the intensity was used to describe the degree of overdispersion (aggregation) of the parasite in its host population. Those statistics were calculated for every age group in Lake Kilpisjärvi.

The main factor for creating the increase in abundance of infection with age is the longevity of the plerocercoid in relation to the rate of infection (Halvorsen & Andersen 1984) Therefore the catalytic model developed by Muench (1959), and modified by Halvorsen & Andersen (1984) was used to estimate population dynamic rates of the plerocercoids in Lake Kilpisjärvi whitefish (III).

The model has the form:

$$M(t) = \lambda/u(1-e^{-ut}) \quad (\text{Eq. 3})$$

$M(t)$ = age-specific intensity

λ = rate of plerocercoid establishment,

u = death rate of plerocercoids

As $M(t) \rightarrow$ large, so $\lambda(u^{-1}) \rightarrow A$, and a regression of $-\ln[1-M(t) A^{-1}]$ against t forced through the origin will have a slope of u . A is the asymptotic value of abundance approached, when the death rate and rate of establishment are in balance.

2.5. Assessment of the effect of *D. ditremum* infection on whitefish

2.5.1. Condition

The effect of *D. ditremum* plerocercoid abundance on the length-mass relationship of the whitefish was analysed with age as an explaining, and plerocercoid abundance as an independent variable. The length-mass relationship was analysed with a non-linear regression, where mass was measured as total fresh mass (Eq. 4). The effect of other variables on the length-mass relationship was analysed using the residuals from the calculated relationship. The effect of year and month was analysed with ANOVA, where year was used as a factor and month as covariate. Differences between years were analysed with pairwise comparisons (Tukey). Due to the large sample sizes, differences were considered non-significant if $p < 0.01$. Effects of *D. ditremum* plerocercoid abundance was analysed with Spearman correlation analyses, where we expected fish with high plerocercoid abundance to have negative residuals (VI).

$$M = a * L^b \quad (\text{Eq. 4})$$

M = fresh mass (g)

L = length (mm)

a, b = parameters

2.5.2. Gonadal development

The effect of parasitic burden by *D. ditremum* plerocercoids on the gonadal development of adult, female whitefish (age groups 6+ - 8+) was investigated by describing the relationship between the number of plerocercoids and the fresh mass of paired ovaries during their early development in February-April (IV).

A power function model used was as follows:

$$W = \alpha * I^\beta \quad (\text{Eq. 5})$$

W = total weight of gonads

I = abundance of the parasites (larvae/fish)

α, β = parameters

2.5.3. Reproduction effort

The effect of plerocercoid abundance on the reproductive effort of whitefish during the gonad maturation in August-December was investigated by describing the relationship between the number of plerocercoids and the relative energy density (energy content of the paired ovaries/ fresh mass of the fish), respectively (V):

$$ED = \alpha * A^{\beta} \quad (\text{Eq. 6})$$

ED = relative energy density of the ovaries (kJ g^{-1})

A = abundance of the parasites (larvae/fish)

The parameters (α , β) were estimated using the unweighted least-squares criterion after logarithmic transformation.

3. RESULTS AND DISCUSSION

3.1. Transmission dynamics of *D. ditremum* in whitefish

3.1.1. Effect of seasonal diet shifts on the plerocercoid recruitment

The main infection periods by proceroids were not determined directly, but inferred indirectly from the course of intensity and variance to mean ratio curves for each sampling period. In August 1993 plankton samples of Lake Kilpisjärvi showed that *C. scutifer* and *E. graciloides* copepodids dominated the pelagic areas, where most of the *D. ditremum* infection is supposed to be acquired (see Knudsen & Klemetsen 1994). The reproduction period of *C. scutifer* is restricted during summer and its population density reached maximum in August. The species goes through diapause in the bottom mud as copepodids. According to Elgmork (1962) in some lakes, all individuals disappear from the mud in spring before ice break-up. In Lake Kilpisjärvi the preying of whitefish on the adults and copepodids was detected during February-April, while small nauplii avoided predation and seemed to be unaffected.

E. graciloides had two generations per year in the lake (Fig. 2). The 1st population peak of adults was detected in early May and another adult peak in September-October. In the pelagic zone the population density of the adult *E. graciloides* was considerably higher increasing to 3.8 ind. litre⁻¹ in September. During the most intensive feeding period from June to late September in 1993 the whitefish, however, fed more on benthic crustaceans such as *Euryercus lamellatus* (Fisher exact test, $p < 0.01$) and emerging insect pupae, mainly chironomids (Fisher exact test, $p < 0.05$, Tolonen *et al.* 1999). There was a descending trend in *D. ditremum* abundance from September to November. In contrast to the autumn of 1993, an intensive preying on copepods was observed in September 1997 (III) resulting in an increase in the plerocercoid recruitment in October (Fig. 2, III). Similar patterns of seasonal plerocercoid recruitment have been observed in Arctic charr by Henricson (1978) and by Knudsen & Klemetsen (1994).

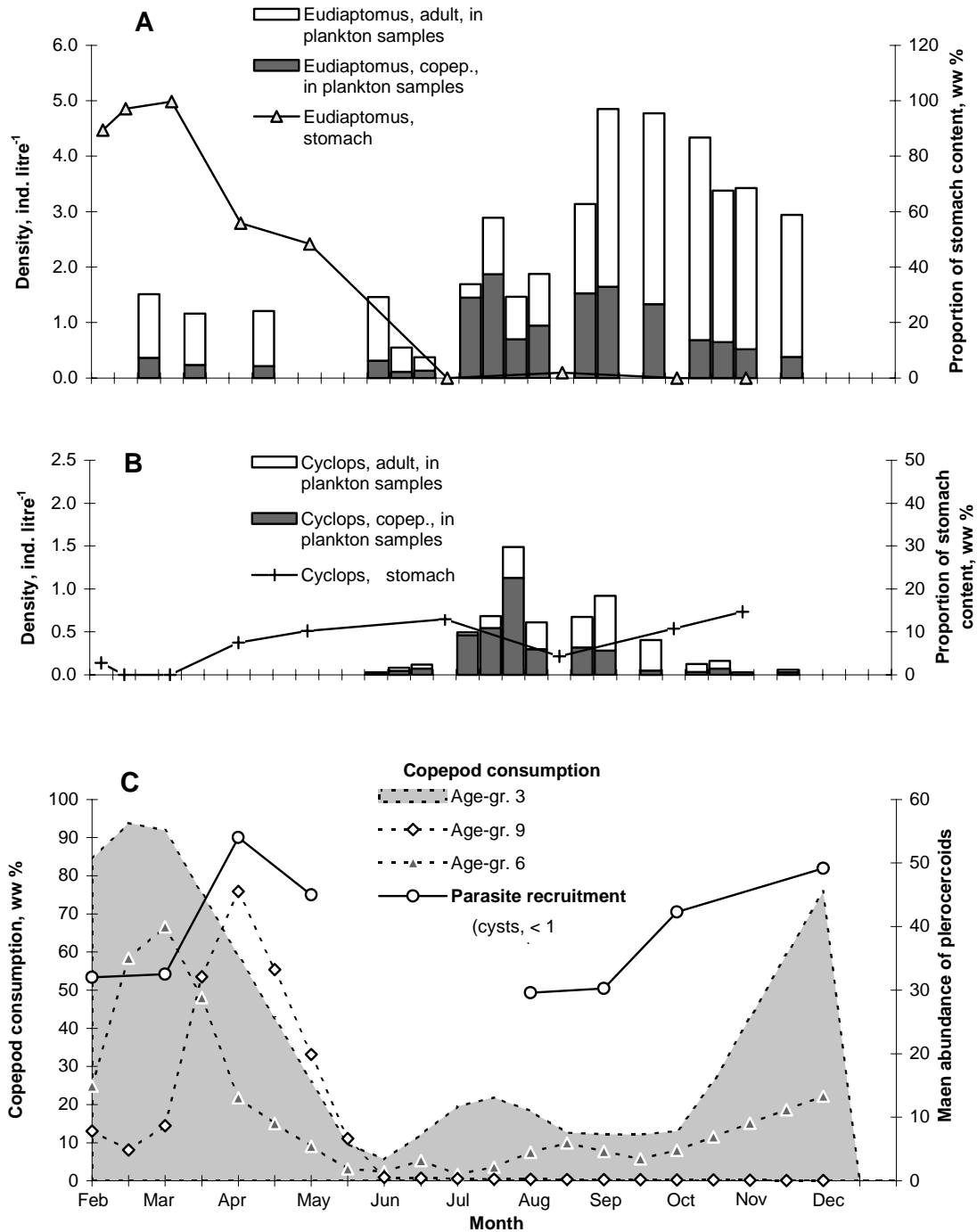


Figure 2. Proportion of *Eudiaptomus graciloides* (A) and *Cyclops scutifer* (B) in stomach contents of age 3 whitefish compared to the density of their different developmental stages in pelagial samples in Lake Kilpisjärvi during the year 1993. Mean abundance of newly acquired cysts (< 1mm) of *Diphyllbothrium ditremum* plerocercoids in whitefish compared to the proportion of copepod (*Eudiaptomus*, *Cyclops*) consumption (ww) in age groups 3 (shaded), 6 and 9 (C). The figure is based on the papers II and III.

The difference in observed abundance of the large cysts between September and October was significant (t -test, $p = 0.046$) in both sexes, while that of the small cysts indicating new

parasite recruitment, was significant in female whitefish only (t -test, $p < 0.001$). So, female whitefish preparing to spawn contributed the bulk of total transmission of *D. ditremum* into whitefish during that period. Such an abrupt increase in autumn can be explained by more intensive feeding of the females on copepods before the spawning season (III).

During winter the zooplankton community comprised various life stages of copepods (*E. graciloides*, *C. scutifer*) and the food intake of whitefish was reduced (II). There was no statistically significant change in the abundance of infection throughout the winter, November to March 1992-93. The $s^2:\bar{x}$ ratio was high and closely related to the abundance in the respective age groups (III). During the winter, mean abundance of the large cysts (> 1 mm) increased steadily, but the increase was not significant (regression, $p = 0.23$). A similar trend was observed in variance to mean ratio. The abundance of small, newly acquired cysts (< 1 mm) remained relatively low until March.

The frequency and proportion of copepod food (calanoids) eaten by whitefish reached a maximum in March, but during the whole ice-covered period more whitefish individuals ingested copepods and insect larvae (Fisher exact test, $p < 0.01$) (Tolonen *et al.* 1999). That was mainly due to the intensive feeding season under ice-covered conditions in March-April. Plankton samples revealed that the population densities of both *E. graciloides* adults and nauplii were generally low in February-March, but dominated the littoral samples later in April-May (II). In the pelagic samples the population density remained relatively high during the rest of the ice-covered season. Although the population densities of copepods in plankton were generally low, copepods (mainly *E. graciloides*) altogether constituted even 60-90% of the food consumption of the whitefish (Fig. 3, II). At that time of the year *C. scutifer* was less probable source of *D. ditremum* infection since the species occurred more abundant in littoral areas and were eaten by the whitefish mainly in May-June after the main transmission peak of the parasite. These observed differences in the diet between seasons were not due to differences in length, as no significant differences in length of the fish could be found between the open-water and ice-covered periods (Tolonen *et al.* 1999). So, also large whitefish preyed on copepods during the ice-covered season, and the copepod consumption reached maximum estimates in March-April (Fig. 3).

There was a certain delay between the maximum of copepod feeding and increase in *D. ditremum* abundance (III). The numbers of small cysts increased abruptly in April. On a

logarithmic scale the mean abundances in March and April differed (t -test, $p < 0.002$). Also an increase in variance to mean ratio was detected in May, indicating increased parasite transmission. Two seasons for the major plerocercoid recruitment was observed in Lake Kilpisjärvi whitefish depending on the proportion of the copepods in the diet (III). Similar patterns of seasonal population fluctuation have been observed in Arctic charr (Henricson 1978, Knudsen & Klemetsen 1994). Because the variation in the cestode plerocercoid population structure and intensity of infection demonstrate an annual infection cycle with two periods of recruitment, the autumn and spring, the potential first intermediate host should be among copepods which pass winter as copepodids or adults (Henricson 1978). *E. cracilis* a closely related to *E. graciloides* may also be infected with *D. ditremum*. *C. scutifer* usually, as observed here, has one year life cycle, but also two or three years cycles have been observed (Henricson 1978). So, not only plerocercoids in the fish (*E. graciloides*) but also the proceroids in the copepod populations may act as a reservoir of parasite infection in northern lakes (Henricson 1978).

In spite of the high energy density of planktonic copepods (see Cummins & Wuycheck (1971) they are regarded as having low profitability for predacious fish because they are energetically expensive to feed upon (Lazarro 1987). Why do benthic whitefish not feed on larger zoobenthos such as molluscs that may be available throughout the year? The theories of optimal diets by Werner & Mittelbach (1981) suggest that fish usually prefer to feed in the most energetically rewarding habitat and change it when the profitability of any habitat drops below that of another. At low prey densities predators feed intensively on the most numerous prey species and at high prey densities on the species having the highest energy value (I; Pulliam 1974, Palomäki *et al.* 1992). It is, however, probable that hibernating copepodids of *E. graciloides* are most vulnerable for predation (Henricson 1977, 1978) when they are aggregated on the bottom or escaping from the bottom. Another reason for the intensive copepod feeding observed at that time of the year may be the digestibility of small crustaceans. Temperature affects the maximum rate of gastric evacuation (Elliott 1972, Wootton 1991). The shells of molluscs undoubtedly cause relatively lower evacuation rates than that of copepods. At low temperatures, feeding on dense, hibernating copepod populations may be energetically more advantageous instead of the less digestible zoobenthos. The lipid level of blood in whitefish has been found to remain low with benthic food and to rise high during the period of planktonic feeding (Brown & Scott 1990, Pomeroy

1991). Also Knudsen *et al.* (1996) observed that Arctic charr had preference for a planktonic diet, although more profitable benthic prey items seemed to be available.

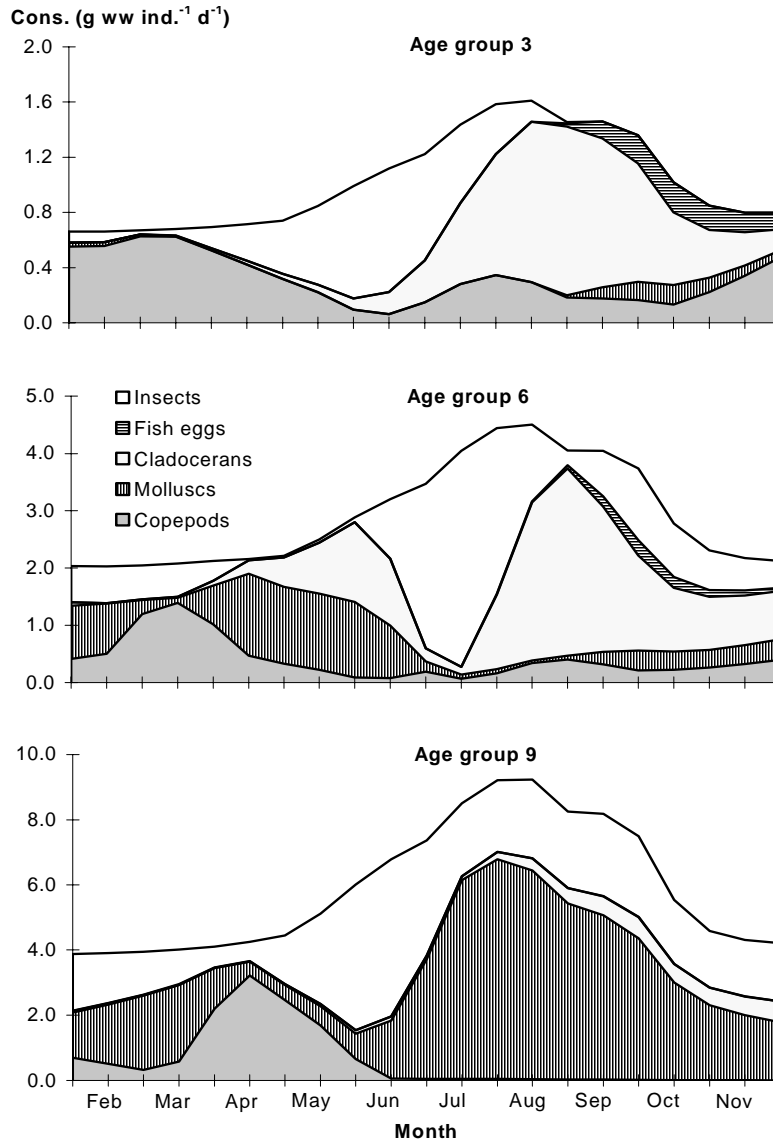


Figure 3. The estimated daily consumption of different food categories for individual Lake Kilpisjärvi whitefish in age groups 3, 6 and 9 (II).

3.1.2. Effect of ontogenetic diet shifts on infection with age

The plerocercoid infection usually commences in very young fish, while fry are uninfected as a result of their restricted diet (Fraser 1960). The diet of the whitefish larvae sampled in August comprised mainly cladocerans (*Bosmina*, *Holopedium*, I). Therefore no *D. ditremum*

plerocercoids were found in 0+ whitefish (III). The mean abundance and prevalence of *D. ditremum* infection increased abruptly at 2 years of age (Fig. 4). In the age group 2, 98% and in age group 3 all individuals were infected. In 1992-1993 the mean abundance in the age group 1 was (\pm SD) 12.3 ± 6.5 and in age groups 3 - 10 ranged from 87.4 ± 6.1 to 127.9 ± 83.1 (III). Also large whitefish preyed on copepods. In low water temperatures, at 4°C, when the food consumption was most restricted, copepods formed 90% of the total food consumption in age groups 2 – 3, and about 60% of the consumption in age groups 6 – 10 (III) maintaining high rate of parasite transmission. Copepods consumed by whitefish during the open-water season were most often *C. scutifer*, but also large-sized *Megacyclops* individuals were found.

The age-abundance curve levelled at age 3, and thereafter no accumulation in plerocercoid abundance was detected (linear regression, $p > 0.10$, $r^2 = 0.05$). The proportion of copepod food decreased with the age of the fish (2+ - 10+) from 11 to 1% in autumn and from 99 to 42% (Fig 3, II, III). The proportion of molluscs and insects increased in the diet with age. A clear diet shift was observed at the 9th year of age (Fig. 3). The largest individuals (9+ to 10+) fed upon large molluscs (*Lymnaea peregra*), 73% of the total consumption in late July. Similar ontogenetic diet shifts observed in Lake Kilpisjärvi whitefish (I), have been commonly observed in benthic coregonids (e.g. Bodaly 1979, Palomäki 1981, Heikinheimo *et al.* 2000). The observed infection pattern of *D. ditremum* was closely linked to the ontogenetic shifts in prey choice which phenomenon has been observed in whitefish also by Amundsen (1988). In Arctic charr of Takvatn, Norway, the lower infection rate in older age groups was also explained by the change in host diet and habitat (Knudsen & Klemetsen 1994).

For comparison to Lake Kilpisjärvi, the abundance of *D. ditremum* larvae in whitefish of the other mountain lakes studied, the rate of plerocercoid accumulation and the level of infection were lower. The abundance in different age groups reflected differences in the composition of diet between lakes and also the ontogenetic shift in the diet during the open water period from July to October 1993 (III). In Lake Kilpisjärvi and Lake in Pöyrisjärvi copepod proportions of 10%, during the main feeding season apparently maintained heavy infections of *D. ditremum* in whitefish. In Lake Pöyrisjärvi (39.2 ± 46.5) the age-abundance curve levelled after age 5 (III), and it was closely related with copepod proportion in the fish diet.

The parasite was strongly overdispersed in all lakes studied. The variance to mean ratio increased in Lake Kilpisjärvi sharply in age groups 2 - 3, and thereafter the trend was descending (III). In Lake Pöyrisjärvi the variance to mean ratio increased until age 5 years, and then decreased rapidly. Since the age-abundance curve did not descend within old fish, parasite induced mortality is not obvious. The decline is more likely explained by small sample size and change in the diet in the oldest fish. A variety of both abiotic and biotic factors may act to create dissimilarities between lakes with regard to spatial stability in fish parasite interactions (Kennedy 1970, Curtis 1983, Kristoffersen 1993).

Differences in the level of infection and in the transmission dynamics with age may be explained by differences in the lake type. Lake Kilpisjärvi is a deep, ultraoligotrophic lake having more pelagial and profundal areas, while Lake Pöyrisjärvi is a shallow, sandy-bottomed lake with plenty of benthic feeding habitats (III). For example, Bérubé & Curtis (1986) related the observed difference in *D. ditremum* infections in Arctic charr from two neighbouring lakes, to differences in shoreline contours and depth. Significantly higher parasite abundances were observed in the lake with poorer shoreline development and greater depth, and where the fish fed more intensively upon copepods.

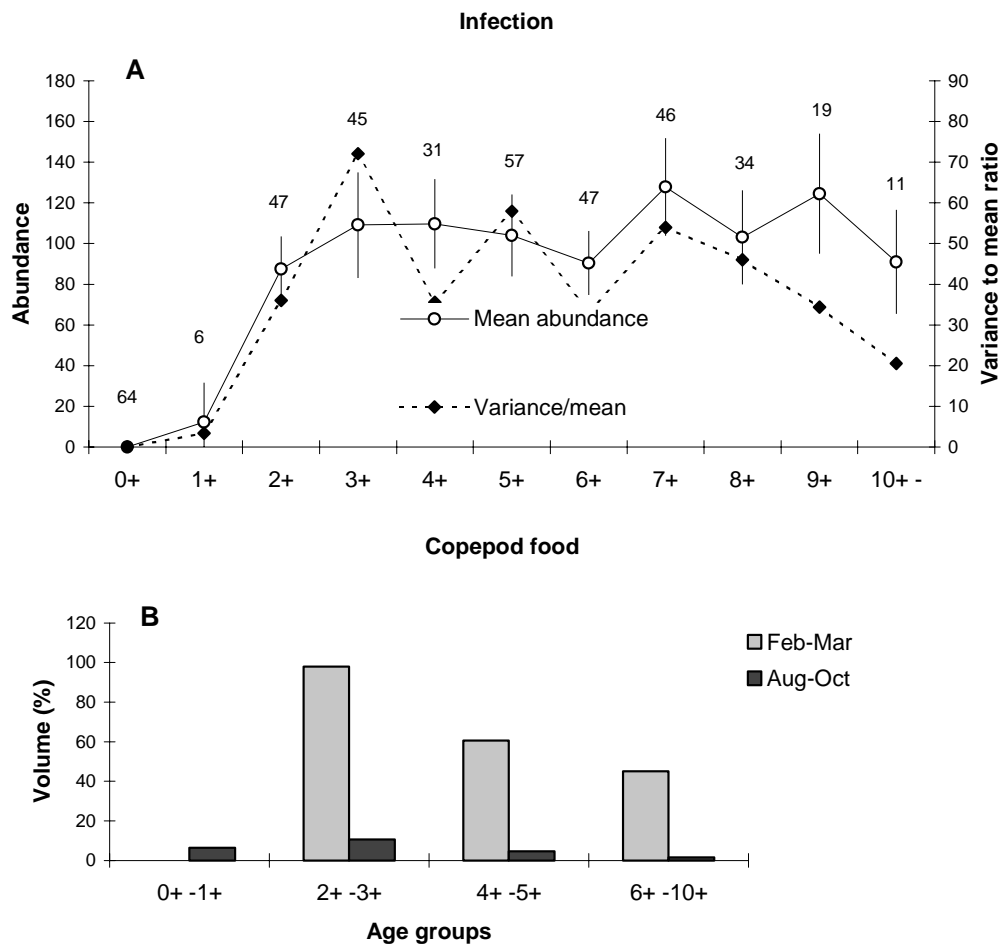


Figure 4. Mean abundance ($\pm 95\%$ confidence limits) and variance to mean ratio of *Diphyllobothrium ditremum* plerocercoids (A) and the mean copepod food proportion of stomach volume (B) in February-March and August-October in Lake Kilpisjärvi whitefish during 1992-1993 (II, III).

3.1.3. Effect of habitat use on the infection level in sympatric whitefish forms

In Lake Puolbatjavri there was also an obvious disparity in *D. ditremum* infection between the two whitefish forms with different habitat use and feeding habits (III). The stocked, lake-spawning, sparsely-rakered form (*C. lavaretus fera*) was caught more often in littoral zone and the river-spawning, medium-rakered (41 gillrakers) form (*C. lavaretus wartmanni*) more often in the profundal and in the pelagial. The sparsely-rakered form that fed mostly on zoobenthos and insects, harboured very few *D. ditremum* plerocercoids, while the other form feeding mostly insects and isopods, but also in some degree on copepods (1.9%), acquired heavy infection. Differences in abundance of *Diphyllobothrium* plerocercoids between two

sympatric whitefish forms observed during an intensive fishing project in a subarctic Lake Stuorajavri, Finnmark Norway, were also explained by differences in the diet, particularly by the copepod contribution to the autumn diets. The occurrence of plerocercoid cysts in pelagic form was only slightly reduced during the mass removal of whitefish, while there was more pronounced decrease in the infection of benthic whitefish (Amundsen 1988). These results suggest the connection of the *D. ditremum* infection on the pelagic food web. Also in Arctic charr, high infections of *D. ditremum* are often related to the choice of pelagic habitat (Henricson & Nyman 1976, Frandsen *et al.* 1989).

3.1.4. Rate of the parasite establishment

The mean abundance of *D. ditremum* in Lake Kilpisjärvi whitefish was 103.5 ± 71.3 plerocercoid larvae per host, with the highest number of larvae being 470 in a single fish. Important factors controlling the rate of parasite flow through the intermediate host-parasite system are the availability of the infective larvae, with the host's feeding habits and responses to the parasites acting as secondary controls (Kennedy 1970). However, the main factor for creating the increase in abundance of infection with age is the longevity of the plerocercoid in relation to the rate of infection (Halvorsen & Andersen 1984). To estimate population dynamic rates of *D. ditremum* in the host the catalytic model (Eq. 8) was fitted to the observed age-abundance curve in Lake Kilpisjärvi whitefish during 1992-1993 (III). The age 1.25 years was taken as the age at first infection occurs in March. There was no significant accumulation in abundance after 3 years of age (linear regression, $p > 0.10$), so the mean plerocercoid abundance in whitefish for the age groups 4 to 10 was taken as the asymptotic value ($A = 113.47$), where the death rate and rate of establishment of the parasite are in balance. The estimated death rate (u) from the data was 0.68. The rate of infection (λ) was 77.2 plerocercoids per fish per year and the estimated yearly loss of plerocercoids was 49.5%.

Most parasites in their intermediate fish hosts have a life span of at least a year. A mean life expectancy of 1.2 years was calculated here for the *D. ditremum* plerocercoids in whitefish (III). The life expectancy is short when compared to that of 2.3 years estimated by Halvorsen & Andersen (1984) for the same parasite species in Arctic charr, where the asymptotic abundance was as low as 13.2 plerocercoids per host, respectively. The difference in mean life expectancy of the plerocercoids in whitefish when compared to that of the Arctic charr

could be explained with high rate of parasite mortality due to crowding effects and well developed host resistance (Henricson 1977) or by parasite induced host mortality.

For better understanding of the host parasite interaction, it should be important to quantify the degree of host defence to be able to answer whether the out flow of the parasites observed is mainly due to parasite mortality caused by crowding effect (see Kennedy 1975) and host defence or due to parasite induced host mortality. *D. ditremum* and *D. dendriticum* have been considered to cause mortality in host fish (Henricson 1977, 1978, Halvorsen & Andersen 1984, Bérubé & Curtis 1986). The assumption has sometimes been based on the observation that age-specific parasite burdens and variance to mean ratio tend to level off or decline in the old ages, reflecting loss of parasites due to parasite-induced mortality in the oldest host (Henricson 1977, Halvorsen & Andersen 1984). Dispersion patterns such as those, mentioned above, may well be generated by factors such as age-related immune response (Anderson & Gordon 1982, Franzen *et al.* 1989). However, too little research has been focused to explore the resistance or tolerance of the host, or its ability to compensate the damage caused by parasites, when studying parasite-mediated selection in host populations (Goater & Holmes 1997). Rahkonen (1998) found some indication that resistant brown trout hosts obtained advantage by lowering the establishment rate of *D. dendriticum* plerocercoids, and that the parasites had effects on the feed intake, growth and mortality of the host. However, to be able to detect whether whitefish has developed host defences against *D. ditremum* infection, experiments where whitefish are exposed to *D. ditremum* infection should be needed.

As Henricson (1977) concluded from the case of Arctic charr, it may also be true in whitefish that due to the higher intensity and overdispersion of infection in whitefish there is reason to believe that the pathogenicity of *D. ditremum* is low and the lethal level thus higher, for example, when compared to *D. dendriticum*. It may reveal that the parasite is not new in its intermediate fish host. However, parasite numbers should not be used as a surrogate measure of host resistance Goater & Holmes (1997), because there are many other mechanisms which affect the number of parasites able to become established in a host (Rahkonen 1998).

In the present study the 0+ whitefish were sampled in August and, therefore, hardly old enough to acquire *Diphyllbothrium*. Generally, whether the absence of plerocercoids in 0+ fish is due to mechanisms preventing infection or caused by mortality of fish from infection with even single tapeworm larva (see, Halvorsen & Andersen 1984), as observed by

Rahkonen (1998) may bias results in very young fish and needs to be investigated more carefully.

3.2. Growth of the whitefish

3.2.1. Seasonal and lifetime growth patterns

The Lake Kilpisjärvi whitefish reached a mean total length of 20.3 cm and weight of 46.1 g at age 5. The growth rate was low showing the same length growth rate (22-25 cm at 5 year of age) as benthic whitefish in Lake Muddusjärvi (Kahilainen 1998) and in Lake Stuorajavri, in Finnmark (Amundsen 1988). The growth was slower than in large lakes and reservoirs in Lapland (Heikinheimo-Schmid & Huusko 1988, Salonen *et al.* 1996, Salonen *et al.* 1997). After age 5 the growth ceased most probably due to the difficulties in dietary shift from zooplankton to zoobenthos (I). In small lakes with simple prey-predator systems, compared with the complex systems in large ones, there is little chance of shifting from plankton to larger zoobenthos or even to small fish (Nilsson 1979, Raitaniemi 1999). The mean length of 8-year old fish was only 22.7 cm and weight 68.9 g. In whitefish intraspecific food competition inhibits growth and tends to prevent the shift to the next size category of prey, resulting in a situation in which several successive year-classes remain stunted (Salojärvi 1992). At age 9 the growth improved again, and the increase in weight was considerable (I, II, Fig. 5). The small whitefish is incapable of swallowing large prey such as molluscs and other large-sized zoobenthos. The importance of functional morphology in causing food segregation is widely known in other fish species (Werner 1977, Mittelbach 1984) in addition to whitefish (Hessen *et al.* 1986).

Fish that live in temperate or subpolar environments usually grow slowly or not at all during the winter months, but rapidly during the spring and summer (Wootton 1991). In Lake Kilpisjärvi the growth of the small fish (< 150 mm) commenced during the first half of July and that of the large fish about 1 week later (I), when the fish had begun to prey upon planktonic cladocerans. The weight varied over a wide range during the year (Fig. 5); the individual weight variation was large as well. Two growth peaks were observed during the year; the main weight maximum was observed prior to spawning in November and another lower maximum in early June before the ice break-up at water temperatures of about 4°C (II).

The yearly minimum (2.7°C) water temperature was observed in March, but the weight minimum of the whitefish in July. The main food consumption period of fish commenced in July, immediately after ice break-up and reached maximum values in early August at 10°C (II). Thereafter the total weight of fish increased rapidly, and the yearly weight maximum was reached immediately before spawning in late November and early December. Temperature has a controlling effect on the rates of both food consumption and metabolism. The optimum temperature for feeding of fish is that at which the highest consumption occurs (Wootton 1991). For whitefish the optimum temperature range is 8 - 10°C (Wells 1968, Elliott 1981).

Growth in weight, as described above, strongly reflects an annual reproductive cycle of the fish. Wide fluctuations in body composition, energy density and condition due to the effects of gonadal maturation and seasonal spawning cycles have been earlier documented in coregonids (Reshetnikov *et al.* 1970, Lizenko *et al.* 1975, Rudstam *et al.* 1994). In Lake Kilpisjärvi the rapid growth of the whitefish ovaries started in August. In late November, before spawning in early December the eggs constituted 12.9 % of the total body weight (II). The result agrees with those of other studies carried out on river-spawning whitefish of the Baltic Sea (Valtonen 1972, Lehtonen 1981).

The total weight loss during the winter season was largest in mature fish at 6 - 8 years of age, thus the net increase in weight was almost 0 g in age group 7 (Fig. 5). Another explanation for decreased growth rate is the spawning stress at the age of sexual maturity. The ceased growth of whitefish at the age of maturity has been observed by Amundsen (1988) in northern Norway. When the gonads of female Lake Kilpisjärvi whitefish matured rapidly in September, somatic tissues showed a sudden drop in energy density due to decreased food consumption (II, V). Similar energy loss of the soma throughout the period of low food consumption was observed in three-spined stickleback by Wootton *et al.* (1980).

Whitefish had two seasons associated with a marked decline in body condition (low somatic energy storage); first before the breeding season in September and another in winter during reduced feeding and low temperature (V). The reproductive investment of whitefish, particularly in females, is strongly dependent on energy reserves. It therefore seems likely that whitefish will be susceptible to the effects of food transmitted macroparasite infection in

winter, when food is limited and in the beginning of the breeding season, when reproduction imposes a drain on the nutrient reserves (see Tierney *et al.* 1996,

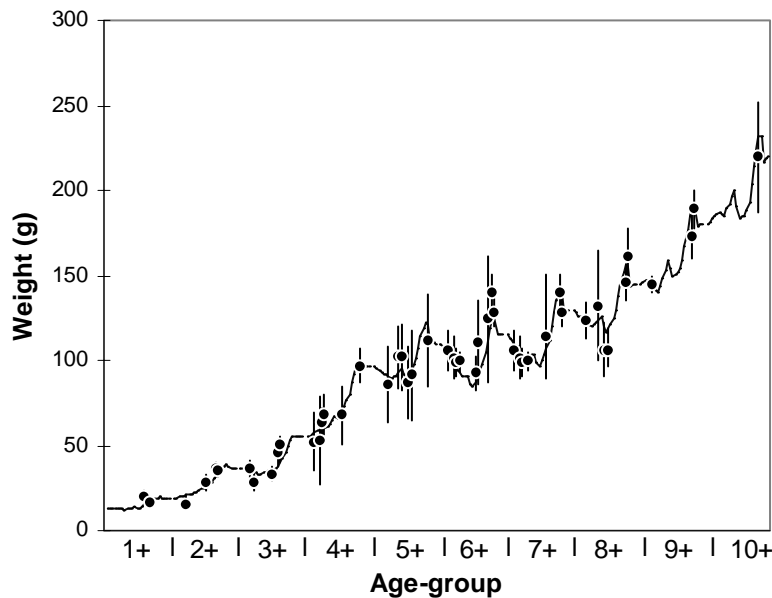


Figure 5. Observed and simulated weight of Lake Kilpisjärvi whitefish in the age groups 1 - 10 during the year 1993. The observed means with 95 percent confidence limits are indicated with solid dots. The estimates from the bioenergetics model are shown with solid line (II).

Paalavuo *et al.* 1998). The effect of the increased copepod proportion on the total food consumption of whitefish is antagonistic, including a source of prey with high energy content but also an increased risk of parasite transmission (II, III). The need of energy may lead the over-wintering whitefish to a “vicious circle” with the parasite. Even though the winter fasting in Lake Kilpisjärvi whitefish was not as complete as observed in broad whitefish (*C. nasus*) in Alaska, the results of the present study corroborates those by Fechhelm *et al.* (1995): an adaptive strategy of storing sufficient energy reserves during summer seems to be particularly critical to the growth, reproduction and survival of whitefish as well as other Arctic fish species.

3.2.2. Effect of *D. ditremum* infection on growth and condition

The abundance of *D. ditremum* plerocercoids had no significant influence on the length-at-age of Lake Kilpisjärvi whitefish (Table 2, VI). As length-at-age differed between 1992 and

1997, the possible influence of plerocercoid abundance on length-at-age was tested separately for the two years on age-classes 2-10 ($p > 0.10$, GLM). Also Poulin (2000), who studied variables influencing the relationship between metazoan parasites species of several families and the size of their fish host, emphasized that the relationship was often very variable and not as strong as often assumed in the literature.

Table 2. Influence of *Diphyllobothrium ditremum* plerocercoid abundance, age (5-10 and 2-4) and year (1992, 1997) on the length-at-age of whitefish in the Lake Kilpisjärvi. Year is categorical, and age and parasite abundance independent variables (VI).

Age 5-10, $r^2 =$ 0.58	SS	Df	F-value	$p <$
Age	6333	1	41	0.00
Year	8376	1	55	0.00
Age * year	5010	1	33	0.00
Abundance	128	1	0.83	ns
Error	19630	116		
Age 2-4, $r^2 = 0.72$				
Age	2144	1	13	0.00
Abundance	278	1	1.71	ns
Age*abundance	228	1	1.41	ns
Error	4217	26		

D. ditremum abundance had no significant effect on the residuals of the length-mass relationship, either ($r_s = 0.07$, $p > 0.10$, $n = 203$) (Fig. 6). The observations by Halvorsen & Andersen (1984) of *D. ditremum* in Arctic charr and by Rahkonen & Koski (1997) on the effects of *D. dendriticum* larvae in brown trout are in accordance with the results of this study on *D. ditremum*. In Lake Inari, the condition factor of brown trout seemed to increase along with the number of *D. dendriticum* plerocercoids indicating that the more the fish eats, the better condition it attains and the more larvae it accumulates.

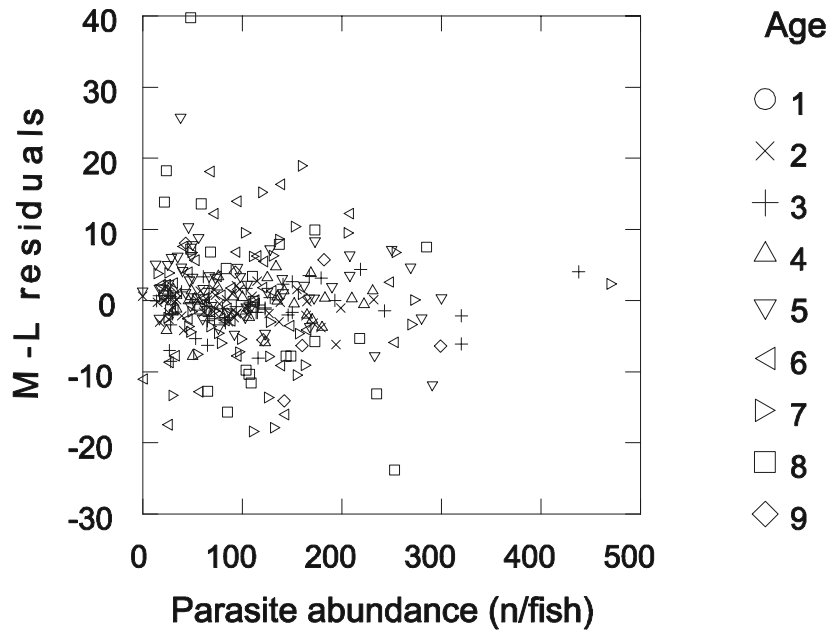


Figure 6. Correlation between the residuals of length-mass relationship and *Diphyllobothrium ditremum* plerocercoid abundance in whitefish of Lake Kilpisjärvi in 1992-97 (VI).

However, when the parasite is large when compared to the fish host or its inflammatory affect is pronounced as in three-spined sticklebacks infected with plerocercoids of *S. solidus*, the weight-length relationship indicated impaired body condition in infected fish in spring and autumn (Tierney *et al.* 1996).

3.3. Gonadal growth and energetics of reproduction

Fish reproduction involves a complex sequence of events. Before spawning it includes gonad growth and gamete maturation. Fishes of the temperate climate respond to regular cycles of temperature and day length. According to Munro (1990) these predicting factors primarily control the development and synchrony of breeding cycles. Synchronizing factors such as the presence of suitable mates serve as a cue causing final gamete maturation. These factors can be modified by secondary factors such as water quality, adult nutrition etc. The modifying factors are the causes of the intraspecific variations in breeding at different latitudes (Helfman *et al.* 1997).

In Lake Kilpisjärvi the whitefish females preparing to spawn lost their somatic energy in September, most probably because the food consumption decreases due to low water

temperature (II), but also due to energy allocation to the developing eggs (V). Expressed as relative energy, densities of ovaries increased towards the spawning season, while the somatic energy simultaneously dropped drastically in December, just before spawning. According to Dabrowski (1985), calculation of seasonal reproductive effort as the proportion of food consumed and reproductive investment is misleading in coregonids. Coregonids continued to feed during vitellogenesis, but the body stores are mobilised to a great extent for the purpose of energy increment of reproductive tissue, depending on environmental factors. Seasonal variation in the biochemical composition of coregonids has been reported by several authors (Dabrowski 1982, Dabrowski 1983, Dabrowski 1985, Ågren *et al.* 1987, Muje *et al.* 1988, Paalavuo *et al.* 1998). Coregonid gonads, especially eggs, are known to have high energy content. Relatively large amounts of resources derived from both food and somatic tissue are needed for gonadal development. The energy content of the gonads in relation to the body weight indicates the reproductive investment of fish.

One of the most frequently reported symptoms of parasitic infections is the depletion of energy stores (Walkey & Meakins 1970, Pennycuick 1971, Lemly & Esch 1984). According to Holmes & Zohar (1990) a parasitized host may suffer from a nutrient deficiency by one or more of the following mechanisms: a) direct nutrient drains (competition with the host for energy) or indirect damage to host tissues and thereby nutrient-requiring host defensive and repair responses, b) altered gastrointestinal functions such as absorption or gut motility, c) poor appetite (anorexia) and d) an impaired oxygen delivery to host tissues. The first and second mechanisms can be the most important reasons concerning *D. ditremum* infection in whitefish, where large number of plerocercoids penetrates into the stomach tissues. In many cases the encapsulated parasites almost totally occupy the stomach tissue.

At the individual level, the effects of parasites on the host are likely to be particularly marked in systems in which relatively large parasites infect small, short-lived hosts (Tierney *et al.* 1996) or in the systems in which the pathogenicity of the parasite is high. In the whitefish - *D. ditremum* host parasite system the effects of the small-sized plerocercoids in the long-lived, adult hosts are not as easily detectable. There are no earlier observations on depletion of energy stores caused by this parasite in whitefish, but Rodger (1991) found that a high number of *Diphylobothrium* larvae reduced abdominal fat in freshwater reared Atlantic salmon *Salmo salar* L. when compared with unaffected siblings.

3.3.1. Effects of *D. ditremum* infection on the ovaries

The effect of *D. ditremum* plerocercoids on the gonadal weight of female whitefish in Lake Kilpisjärvi was studied during the early development of ovaries in February-April (eq. 5, IV), at the time of the onset of yearly gonadal growth. At that time of the year the parasite abundance was a significant predictor of the weight of ovaries ($p < 0.001$). Simultaneously an increase in transmission of new plerocercoid cysts was observed (III). There are few observations of diminished fertility caused by the adverse effect of helminths on the reproduction of fishes. Plerocercoid infection of pseudophyllidean tapeworm *Schistocephalus solidus* has been found to cause sterility in sticklebacks *G. aculeatus* (Arme & Owen 1967, Mc Phail & Peacock 1983).

Before spawning (August-December) the parasite abundance had no significant effect on gonadosomatic index (gonad weight per fish weight) in female whitefish ($p = 0.984$), whereas the parasite abundance was a significant predictor for the relative energy density of gonads (VII). In the immature (idle) females the parasite abundance had a clear effect on the relative energy densities of gonads (model 1, $p < 0.001$). The relative energy densities of gonads were higher in mature than in immature (idle) females ($p = 0.011$). No significant interaction was observed, i.e., the curve shapes were not different. The parasite abundance did not have any effect on the somatic energy densities.

Fecundity of fish is one of the basic life history features, which determines the number of young born. Among the coregonid fishes, different whitefish forms, in contrast to vendace *C. albula* (L.), are plastic in their reproductive patterns (Sarvala *et al.* 1992). The absolute size-specific fecundity of Lake Kilpisjärvi whitefish ranged between 982 and 4490 eggs per fish and followed the same pattern as that estimated by Valtonen (1972) and Lehtonen (1981) on sea-spawning whitefish of the northern Baltic coast of Finland. In Lake Kilpisjärvi the rapid growth of the whitefish ovaries started in August. In late November before spawning the eggs constituted 12.9 % of the total body weight (II). In Åland and in Korsholm the percentage has been found to be 20% (Lehtonen 1981). Also in vendace of northern Finland, unfavourable conditions were found to be reflected in the size of ovaries (Lahti & Muje 1991).

Although there was a negative effect of plerocercoid abundance on the relative fecundity (regression, $p = 0.0116$, Fig. 7, V), the dry matter content of a single egg was positively

correlated to the plerocercoid abundance (regression, $p = 0.0023$). The lower number of eggs was compensated for with higher dry matter content. The sample size of was fairly low ($n = 12$), but trend was clear; the relative fecundity dropped before the abundance of 100 plerocercoids per fish. Sarvala *et al.* (1992) found that vendace individuals with the highest egg numbers had the smallest egg size and *vice versa*. During the formation of ovaries the egg numbers are determined first and then food conditions control the final size of eggs (Kamler 1992, Sarvala & Helminen 1995).

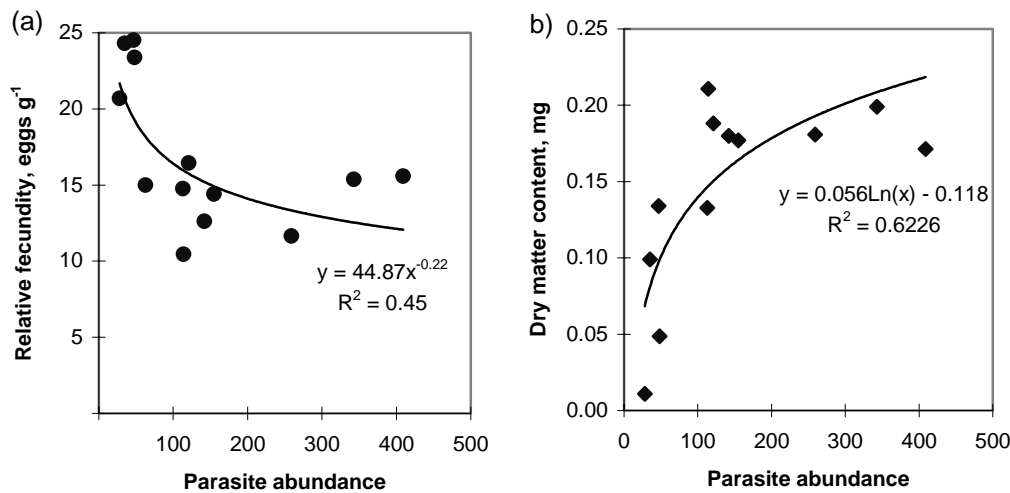


Figure 7. The relative fecundity (a) and relative dry matter content (b) of a single egg plotted against abundance of *Diphyllbothrium ditremum* plerocercoids in Lake Kilpisjärvi whitefish in December ($n = 12$).

The results mentioned above corroborate the results in paper V. Large eggs have been shown to produce larger fish larvae than small eggs (Bagenal 1978). Under natural conditions the survival of fish larvae depends on the size of eggs. Finally, the size of fully developed eggs of spawning whitefish in December obviously depends on the food supply in the preceding autumn.

3.4. Regulation in the whitefish population

The mechanisms regulating population size can be divided into density-independent and density-dependent processes (Neave 1953, Salojärvi 1991, 1992). Initial food abundance and temperature are the most crucial density-independent factors limiting growth in subarctic clear water lakes. Growth of whitefish has been shown to be sensitive to the trophic status of the lake (Ruhle & Gammeter 1998). For gape-limited fish species, such as whitefish, the growth depends on availability of suitable sized prey in every phase of the ontogenetic

growth. In general growth rates in whitefish populations have been shown to be density-dependent (Healey 1980, Jensen 1981, Mills & Chalanchuk 1988, Sarjamo *et al.* 1989, Salojärvi 1992, Salonen *et al.* 1996, Salonen *et al.* 1997).

According to Tolonen (1992) the growth rate of Lake Kilpisjärvi whitefish in 1982-83 had decreased when compared to the period of 1974-1978 observed by Tuunainen *et al.* (1979). In 1982-83 and 1992-93 the age-2-4 whitefish showed the same growth rate, but they had a greater length-at-age in 1992-93 than in 1982-83. For older fish both growth rates and length-at-age differed between the three study periods (VI). Simultaneously an improvement in condition of the fish was observed (Fig. 8, VI). Higher growth rate and length-mass relationship of the fish may indicate improved feeding conditions due to decreased food competition during the years 1983-1993.

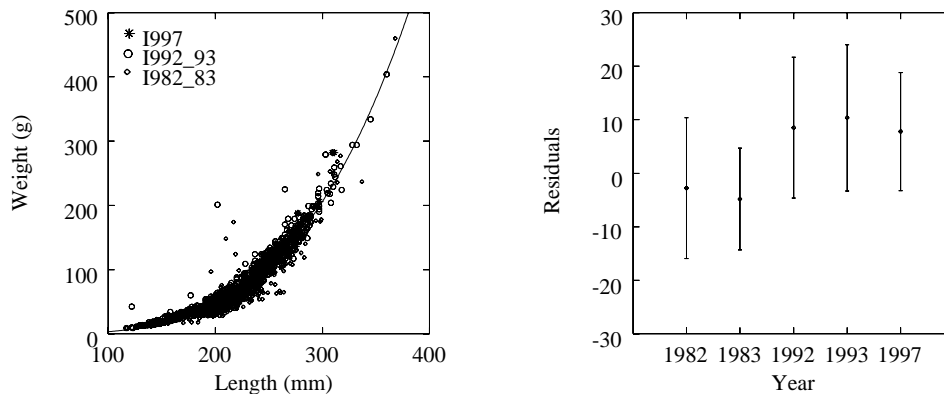


Figure 8. Length-mass relationship for the Lake Kilpisjärvi whitefish and residual deviation (mean \pm sd) over the studied years.

According to the theory of fisheries biology (Cushing 1981, Gulland 1983), the CPUE should decline as fishing effort increases, if no compensatory mechanisms operate. Compensatory processes tend to increase mortality or decrease reproduction as population size increases (Fig. 9). Observations of compensatory growth of whitefish have been common in many northeastern Finnish lakes, for example (Salojärvi 1988, 1992). In natural populations compensatory mechanisms can also operate in the opposite direction (Salojärvi 1991). In Lake Kilpisjärvi the significant decline in catch-per-unit-effort indicated that there was a decrease in population density during the period when the improvement in condition and

growth was observed (VI). The change was more pronounced in the numerical ($p < 0.01$, GLM) than in the weight ($p < 0.05$, GLM) of the CPUE.

Whitefish is the dominant fish species in the lake. Interference from predators, however, cannot be neglected, and it may have an effect on habitat use of whitefish populations (see Hessen *et al.* 1986). In Lake Kilpisjärvi Arctic charr have been observed to prey upon whitefish, especially in spring during the ice break-up (Tolonen, unpubl.). However, there was no evidence that the decrease in whitefish population density during the study period was caused by interspecific effects. The mean catches of other species were low, and did not differ between the years studied (VI). The most common of the other species was Arctic charr, with slightly higher (Mann-Whitney U-test, $p < 0.05$) catches in 1993 ($117 \text{ g net}^{-1} \text{ day}^{-1}$) than in 1983 ($20 \text{ g net}^{-1} \text{ day}^{-1}$). The mean catches of burbot, brown trout, and grayling were low; 5, 9, and $17 \text{ g net}^{-1} \text{ day}^{-1}$, respectively, and did not differ between the years (Mann-Whitney U-test, $p > 0.10$). Effect of interspecific competition with burbot may be almost negligible (VI, see also Tolonen *et al.* 1999). Thus the decrease in whitefish population density can hardly be explained with changes in the density of other species in the fish assemblage (VI).

The increase in the growth rate of the whitefish since the 1980s in Lake Kilpisjärvi can be attributed to lower population density and decreased intraspecific competition on food. This is in agreement with the results of Salojärvi (1988, 1991), Salojärvi & Huusko (1990) and Salonen *et al.* (1996) on the density-dependence of the growth in whitefish. Results in 1997 showed that the growth rate was again on the same level as observed in 1974-1978 by Tuunainen *et al.* (1979) (VI). Consequently growth of whitefish has been observed to decrease since early 1980s also in other lakes of northern Lapland where stockings have been carried out (Sarjamo *et al.* 1989, Lehtonen & Niemelä 1998), and to increase considerably after a decrease in population density (Amundsen 1988, Salonen *et al.* 1997).

Many authors have speculated about the role parasites may play in regulating the size of the host population (Anderson & May 1978, Adjei *et al.* 1986). Parasites can exert detrimental effects on their host population size, either directly by affecting survival and fecundity, or indirectly through increased susceptibility of predation and reduced competitive fitness (Anderson 1979). The basic assumptions in the models of Anderson & May (1979) are that the parasite increases the rate of host mortalities and that the mortality increases with the number of parasites per host (Fig. 9). In dense host populations the parasites are pathogenic

due to the impaired host resistance caused by poor nutritional condition and stress. Models have been used as implements when revealing the ability of the parasites regulating growth of their host populations, stabilizing effects of the parasites and factors leading to perturbations in host-parasite interactions (e.g. Kristoffersen 1993).

The prevalence of the *D. ditremum* infection in Lake Kilpisjärvi whitefish has been high since the 1960s, when stockings were sized. During the observation period 1982-1992 the whitefish population showed decreasing population density while the numbers of *D. ditremum* plerocercoids increasing trend (Table 3). However, no major change in abundance was found during the 1990s. The increasing trend in variance to mean ratio observed from 1980s may indicate increasing degree of stability in the system (III, VI).

Table 3. Summarised literature notes of the occurrence of *Diphyllobothrium ditremum* in Lake Kilpisjärvi whitefish; prevalence, mean number and variance-to-mean ratio of the plerocercoids according to age group and season from early 1960s to late 1990s (VI).

Year	Preval.%	Intensity (range)	s^2 / \bar{x}	Age group	Season	<i>N</i>
1964 ¹⁾	84	26.2 (1-70)	-	adult	summer	32
1982-83 ¹⁾	100	40-75(1-350)	-	1-12	Jul-Oct	473
1988 ²⁾	?	46-66 (?)	21-33	2-8	summer	?
1993 ³⁾	100	81 (4-298)	?	1-12	Jul-Sep	398
1992-93 ⁴⁾	98-100	103.5 ±71.3 (S.D.)	49.6	1-10	Feb-Dec	552
1997 ⁴⁾	100	110.9 ±80.0 (S.D.)	57.7	5-12	Mar-Apr, Aug-Dec	124

Sources: ¹⁾Tolonen (1992), ²⁾Haukisalmi (1989), ³⁾Gustafsson (1996), ⁴⁾III

The stabilizing effect of overdispersed parasite distributions upon the dynamics of host-parasite interactions has been emphasised by several workers (see, Crofton 1971, Anderson & Gordon 1982, Kristoffersen 1993).

Increase in numbers of food transmitted parasites in fish population have been observed, for example, when the feeding conditions of fish have been altered by changing prey animal availability in regulated lakes, such as Lake Inari (Rahkonen & Koski 1997). Intensive stockings have been found to cause stunting of the fish, increased interspecific or intraspecific competition on food and increased parasite infection. On other hand, in Lake Stuurajavri mass

removals of fish resulted in a dietary shift from zooplankton to benthic prey leading to a lower *D. ditremum* infection level among benthic whitefish (Amundsen 1988). Since *D. ditremum* is bound more in the pelagic food web, the infection level remained continuously high in the pelagic whitefish. This indicated a high degree of stability in the system (Kristoffersen 1993). Similar effect of persisting infection level due to stabilizing effect was presumably encountered in Lake Kilpisjärvi whitefish during the period of 1964-1997.

There was also a significant change in the gillraker counts between the periods 1974-1977 and 1982-1983 indicating change in the stock. Another change was observed between the periods 1982-1983 and 1992-1993 showing adaptation back to the gillraker count distribution observed in 1970s. The number of gillrakers is typical for the genotype of fish and does not change much during the individual growth of the fish and it is not susceptible for environmental factors (Svårdson 1979). However, the number of gillrakers in the whitefish population can alter for another during few generations (Svårdson 1957, Berg 1970). It seems probable that stocking with migratory whitefish have been resulted in a poorly adapted hybride stock in Lake Kilpisjärvi. Although the gillraker count does not directly determine the size of prey of whitefish (Sandlund *et al.* 1987, Langeland & Nost 1995, Mookerji *et al.* 1998, Heikinheimo *et al.* 2000), fish have some tendency to select prey they have learnt to use before. Due to changed habitat use and food competition, both short-term and long-term effects on the existing population of the species stocked and on the whole fish community, may be possible. At least theoretically, it is possible that the stocked population outcompetes the endemic one (Salojärvi 1992). In Lake Puolbmatjavri there was an obvious disparity in *D. ditremum* infection between two sympatric whitefish forms with different habitat use and feeding habits. The original, more pelagic whitefish form was heavier infected than the stocked, sparsely-rakered population. It shows that the habitat use had influence on the intensity of copepod feeding and finally on the level of the infection.

3.4.1. Role of *D. ditremum* induced mortality

Diphyllobothrium spp. plerocercoids are regarded as being able to cause mortality in their fish hosts (Henricson 1977, 1978, Chubb 1980, Halvorsen & Andersen 1984, Berube & Curtis 1986, Kristoffersen 1993, Rahkonen *et al.* 1996). Decreasing degree of overdispersion concomitant with a decline in abundance within older hosts has been suggested to indirectly

indicate parasite induced mortality of heavily parasitized individuals in natural populations (Henricson 1977, 1978, Anderson & Gordon 1982). Similar outflow on *D. dendriticum* was reported by Hickey & Harris (1947) and Fraser (1960). The method used has been criticized because the sample size tends to be small in older age groups, and the variance to mean ratio is strongly influenced by the number of individuals in the sample (Halvorsen & Andersen 1984, Pacala & Dobson 1988).

In Lake Kilpisjärvi whitefish the variance to mean ratio of *D. ditremum* increased sharply in age groups 1 - 3, and thereafter the trend was descending, but the age-abundance curve seemed to fluctuate around the level where the balance between host and parasite is attained (Fig. 4, see Kennedy 1970). In Lake Pöyrisjärvi whitefish (39.2 ± 46.5) the age-abundance curve levelled after age 5 and the variance to mean ratio decreased rapidly thereafter (III). Thus the evidence of parasite-induced mortality in these whitefish populations was ambiguous. Similar problems have been emphasized also by Halvorsen & Andersen (1984), Gordon & Rau (1982), Kennedy (1984) and Knudsen (1997).

D. dendriticum induced mortality has been shown not only correlate with the number of parasites but also with their location in the fish (Henricson 1978, Rahkonen 1998). There was no evidence of direct *D. ditremum* induced mortality in whitefish in the present study. The plerocercoid cysts were situated almost exclusively in stomach and oesophagus walls. In Lake Kilpisjärvi only 4.5% of the specimens analysed had cysts in the pyloric caeca (mean: 2.04) and in 2.1% a few cysts were attached in the intestine (mean: 1.3). No cysts were found in mesenteries, liver, musculature or other tissues of the host. Henricson (1977) reported about 4.6 % of *D. ditremum* plerocercoids occurring in other organs than stomach and pyloric caeca.

Holmes & Bethel (1972) concluded that parasites altered the behaviour of the intermediate host to make it more susceptible to predation. According to Arme & Owen (1967) secretory products released from plerocercoids of pseudophyllidean tapeworms have been found to cause reproductive sterility in fish hosts. The infected hosts were more vulnerable than the unaffected ones to predation by fish-eating birds. *Mergus* and *Gavia* species, the final hosts for *D. ditremum*, are effective fish-catchers when compared to gulls (*Larus* sp.), which serve for final hosts of *D. dendriticum*. Thus any dramatic altering of the behaviour of the intermediate fish host of *D. ditremum* is not necessary (Henricson 1977). This may explain

why the plerocercoids of *D. ditremum* do not need to migrate into vital organs of the fish host causing death of the host to ensure successful parasite transmission in the process (see Esch & Fernandez 1993).

The abundance of *D. ditremum* plerocercoids had no significant influence on length-at-age or condition (VI). As length-at-age differed between 1992 and 1997, the possible influence of plerocercoid abundance on length-at-age was tested separately for the two years. The results of this study support the assumption that whitefish possess well-developed resistance against *D. ditremum* (Halvorsen 1970, Bylund 1972) and the parasite therefore has little effect on the host (VI). On other hand, as Munro *et al.* (1983) suggested that disease may be having its greatest impact at the juvenile stage when natural mortality rates are known to be high. The relative increase in abundance was greatest in juvenile Lake Kilpisjärvi whitefish between age groups 1 and 2. If *D. ditremum* alone is able to cause acute mortality in whitefish it may occur among very young age groups, since the parasite burden had no effect on condition (VI). Also Bylund (1972) suggested that the impact of the plerocercoids could be most severe on young individuals. According to Adjei *et al.* (1986) helminths particularly in intermediate hosts, are most pathogenic at the time of infection when the larvae are penetrating through host tissue than when they are already encapsulated and relatively inert. However, the methods used in the present study do not prove the assumption. It may also be probable that the mortality rate in Lake Kilpisjärvi whitefish may be highest in early spring when the small newly attached plerocercoids rapidly increase in numbers and the energy stores, condition and host resistance of the fish are low (III, IV).

4. CONCLUDING SUMMARY

Whitefish in subarctic mountain lakes of Finnish Lapland harbored *D. ditremum* plerocercoids alone, although burbot and Arctic charr, for example, are infected by both *D. ditremum* and *D. dendriticum* of the tapeworm genus *Diphyllobothrium* (III). There were two periods of yearly transmission of *D. ditremum* in Lake Kilpisjärvi whitefish: the main period in September-October and another in March-April. The transmission reached the maximum in about one month since the mean copepod consumption peak was observed (III). The food consumption of whitefish during the ice-covered season was strongly reduced, but all sized individuals preyed almost exclusively on planktonic copepods, mainly over-wintering copepodids in late winter period from February to March (II). The energy densities of the

somatic tissue of the fish were at very low level in March showing urgent need of food supply (V) and the copepods appeared to represent the most energetic prey available (II). Thus the effect of the intensive copepod consumption appears to be antagonistic, including a source of prey with a high energy content but also an increased risk of parasite transmission.

In Lake Kilpisjärvi the numbers of *D. ditremum* plerocercoids per fish increased until 3 years of age (III). The variance to mean ratios were high, increasing up to 3 years of age, descending thereafter in the older age groups. The observed levelling of age-abundance curve was explained with ontogenetic diet shifts with age of fish and with plerocercoid mortality caused by intraspecific competition and host resistance. The proportion of molluscs increased and that of insects and crustaceans decreased in the diet with age (I, II). Intraspecific food competition and obvious crisis in dietary shift are the most probable explanations for the poor growth at 6 - 8 years age. Intraspecific food competition inhibits growth of the gape-limited whitefish by preventing shift to the next size category of prey. A clear diet shift was observed at the 9th year of age. The largest individuals fed increasingly on molluscs and less on copepods, which explained improved growth rate. In Lake Puolbmajavri, for comparison to the monomorphic whitefish of Lake Kilpisjärvi, there was an obvious disparity in *D. ditremum* infection between two sympatric whitefish forms with different habitat use and feeding habits. The original, more pelagic whitefish form was heavier infected than the stocked, sparsely-rakered form. It showed that the habitat use had a strong influence on the intensity of copepod feeding and on the level of the infection. Differences in the level of infection and in the transmission dynamics with age of fish were also explained by differences in the lake type. In the deep, ultraoligotrophic Lake Kilpisjärvi having more pelagial and profundal areas whitefish acquired heavy infection very young, while in the shallow, sandy-bottomed Lake Pöyrisjärvi with plenty of benthic feeding habitats, the infection rate was slower (III).

In Lake Kilpisjärvi whitefish high rate of new infection and yearly loss of plerocercoids per fish per year gave a mean life expectancy of 1.2 years for the *D. ditremum* plerocercoids, which is short when compared to that of 2.3 years, for example, estimated by other workers for the same parasite species in Arctic charr (III). The role of parasites in regulating the size of the whitefish population was discussed. In the 1970s catches decreased and in early 1980s also a clear increase in abundance of *D. ditremum* plerocercoids was observed. This was assumed to be an indication of perturbation in the host-parasite interaction caused by

stockings (VI). Decline in catch-per-unit-effort during the ten years of observation showed that the density of the whitefish population in Lake Kilpisjärvi had decreased in 1990s, simultaneously with an improvement in the growth and condition.

Population regulation occurs due to several different mechanisms, more than one of which may be acting at the same time (Fig. 9). Compensatory processes in population regulation tend to increase mortality or decrease reproduction as population size increases. Those processes in fish populations operate, for example, through reproduction (fecundity, egg quality), growth, interspecific competition, cannibalism, predation, diseases and parasitism. There are two possible ways *D. ditremum* plerocercoids may directly regulate the size of the fish population: first through suppressed fertility and secondly through parasite induced mortality. There was no clear evidence of the parasite-induced mortality in Lake Kilpisjärvi whitefish (III), while some effect on the reproduction was found (V). *D. ditremum* larvae had a clear negative effect on the relative energy density of ovaries in immature (idle year), but also in mature females. The result may indicate that the parasite does not necessarily cause idle years in the spawning cycle of whitefish. Negative effect of the parasite abundance on the relative fecundity was observed, as well. The negative effect on the fecundity was, however, compensated with a higher dry matter content of a single egg in the individuals with high parasite abundance (V). Since large eggs have been shown to produce larger fish larvae than small eggs, the survival of fish larvae depends on the size of eggs. The observed pattern is obviously one of the mechanisms acting through co-evolution (see Esch & Fernandez 1993), and creating the firm stability (see Kristoffersen 1993) in the host-parasite interaction between whitefish and *D. ditremum* in subarctic mountain lakes.

Since the absolute fecundity increases with the weight of the fish, somatic growth is important for future fecundity. However, neither growth nor condition (length-mass relationship) of the whitefish was found to be affected by the *D. ditremum* plerocercoid infection. The weight of whitefish varied over a wide range during the year. The most rapid weight increase was observed during the period from August to November which is partly due to the growth of the gonads (II). Results of the present study indicated that sufficient energy stores to be mobilised from the soma for the energy increment of gonads prior to the spawning period are necessary for achieving the yearly maturity (V). The results corroborate former observations on whitefish in the Arctic: the adaptive strategy of storing sufficient

energy reserves during summer seems to be particularly crucial to the growth, reproduction and survival of the whitefish (II). As observed also elsewhere in northern coregonids the period for accumulation of energy reserves in subarctic lakes may be too short for every year spawning, so idle years in reproduction cycle of whitefish females are necessary to make both somatic and gonadal growth possible.

After all, no clear relationship between the parasite abundance and condition of adult and juvenile whitefish was detected in the present study. On the contrary, the results support the assumption of the earlier workers that whitefish seems to be well adapted to sustain high abundance and prevalence of the parasite, which was explained with a high degree in stability of host-parasite interactions. Since adverse effects on the gonads were found, the parasite may have impact on the reproduction success of the fish. The possible impact of the parasite on the survival of the 0+ whitefish will be one of the future challenges in this field. Although it may be premature to conclude whether *D. ditremum* infection works as a main regulatory control on the whitefish population, the following scenarios could be possible. Intensive stockings may have promoted a perturbation in host-parasite interactions, and compensatory processes tend to keep the whitefish population within limits of the carrying capacity of the lake.

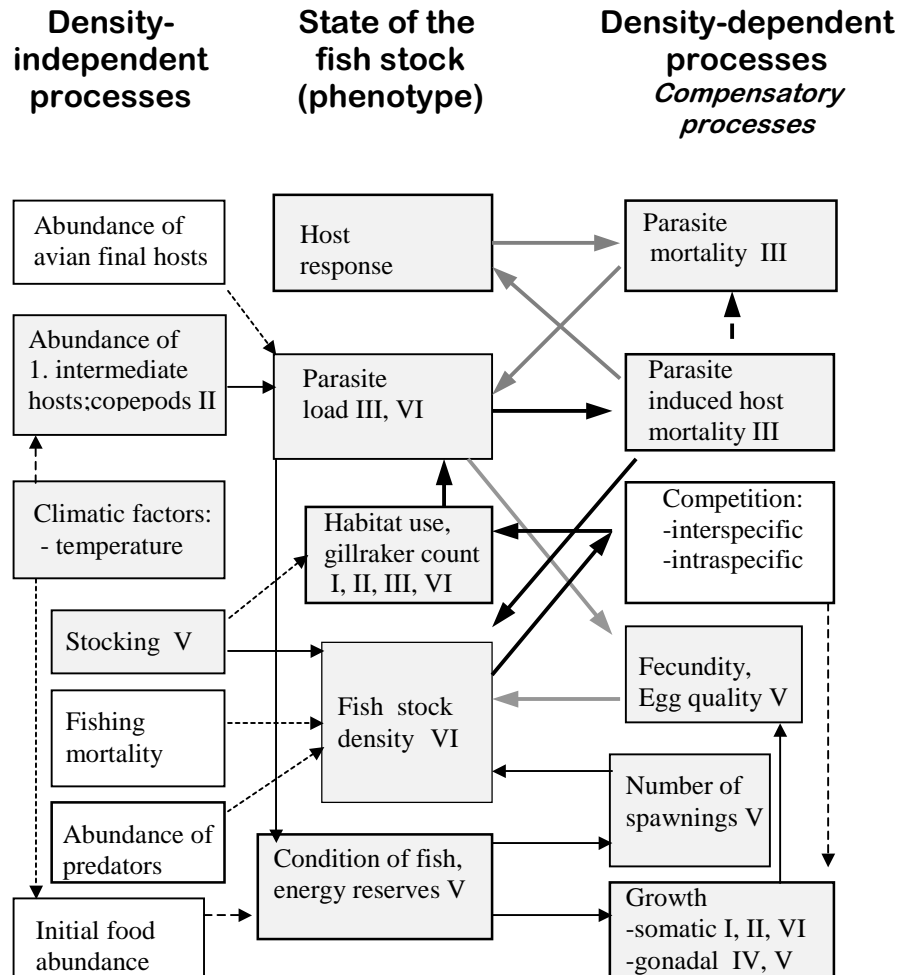


Figure 9. A simplified schematic presentation of the most important population regulation mechanisms including the host-parasite interaction in a whitefish population infected by a food transmitted parasite (*Diphyllbothrium ditremum*). The essential links concerning this study (shaded) are presented with solid arrows. Host-parasite interactions are shown with thick arrows. The classification of the density-dependent and density-independent processes is based on Salojärvi (1992) and references therein.

Acknowledgements

The field-work of the present study was performed with support and facilities from the Kilpisjärvi Biological Station. I express my warmest thanks to Henrik Wallgren, who encouraged me in my work from the very beginning. The aid of Urho Viik, Sulo Nikka, and

Ilkka Leinonen in experimental fishing and technical assistance of Oula Kalttopää, were much appreciated. I am deeply thankful to Bjørn Berland at the Parasitological Laboratory and to Egil Karlsbakk at the Department of Fisheries and Marine Biology, University of Bergen, for their guidance in my first steps of parasitological studies. Funds from NorFa Foundation and from Scandinavian Parasitological Society made possible my study trips to Norway and Iceland.

I wish to thank co-authors of the articles, and I am also grateful for critical comments on the earlier version of the manuscript to Tellervo Valtonen, University of Jyväskylä, Erkki Pulliainen, University of Oulu and Jyrki Lappalainen and Heikki Peltonen Department of Limnology and Environmental Protection, University of Helsinki. The referees: Ken MacKenzie and Riitta Rahkonen had valuable comments on this summary.

This study was supported by the University of Helsinki, by the Jenny and Antti Wihuri Foundation, by the Finnish Cultural Foundation, by the Oskar Öflund Foundation and by the sport-fishing society of Saanan Kiitäjät.

Tiivistelmä

Diphyllobothrium -suvun heisimadot ovat kalaa syövien lintujen ja nisäkkäiden suolensisäisiä loisia. Hankajalkaisäyriäiset toimivat niiden ensimmäisenä väli-isäntänä. *D. ditremum* ja *D. dendriticum* siirtyvät hankajalkaisista kalaan ja ovat plerokerkoiditoukkina kalojen kudoksissa. Kyseistä cestodi-sukua tutkittiin neljän järven siikakannoista, joista Kilpisjärven siika oli intensiivisemmän tutkimuksen kohteena. Kilpisjärven siikassa loisen esiintymistä tutkittiin vuoden ajoittain tapahtuvalla näytteen otolla vuosina 1992-93 ja 1997 sekä pitemmällä aikavälillä kirjallisuusviitteiden perusteella aina 1960-luvulta 1990-luvun loppupuolelle. Tutkimuksessa haluttiin selvittää, mitä *Diphyllobothrium* -suvun lajeja tunturijärvien siioissa esiintyy, ja miten siian vuodenajoittainen ja ontogeneettinen ravinnon vaihtuminen vaikuttaa *D. ditremum* loisen transmission dynamiikkaan eli rekrytoitumiseen. Haluttiin myös selvittää onko loisella vaikutusta siian kasvuun, kuntoon ja lisääntymiseen ja sitä kautta isäntäkalan populaation säätelyyn.

Tutkittujen tunturijärvien pohjasiiioissa tavattiin ainoastaan sukeltajasorsien heisimatoa *D. ditremum* eikä *D. dendriticum*-plerokerkoideja löydetty, vaikka lajia on tavattu meillä etelämpänä siioissa ja m.m. Kilpisjärvessä muissa kalalajeissa kuten tunturinieriässä ja mateessa. Kilpisjärvessä siian yksilökohtaiset *D. ditremum* toukkamäärät kasvoivat hyvin nopeasti kalan iän myötä, ja tasaantuivat tasolle 113 toukkaa per kala. Loisten kasaantumisen (aggregaatio) ilmentäjänä käytetty tunnusluku: hajonta per keskiarvo oli siialla verrattain korkea kaikissa tutkituissa järvissä. Loisabundanssin ja kasautumisen laskun vanhemmissa ikäryhmissä on perinteisesti katsottu indikoivan loisperäistä kuolevuutta isäntäpopulaatiossa.

Kilpisjärven siian kohdalla loisaggregaatio laski, mutta abundanssi ei, joten yksiselitteisesti ei voitu päätellä plerokerkoidi-infektion aiheuttavan kuolevuutta siikapopulaatiossa. Ottaen samanaikaisesti huomioon aikaisemmissa tutkimuksissa havaitun *D. ditremum*-plerokerkoidien aiheuttaman lievän vahingollisuuden isäntälajilleen, loisten kasaantumisilmiön väheneminen vanhoilla siiolla oli selitettävissä ravinnonkäytön asteettaisella muutoksella hankajalkaisravinnosta (*Eudiptomus*, *Cyclops*) hyönteis- ja pohjaeläinravintoon (chironomidi-toukat, *Pisidium*, *Gyraulius*, *Lymnaea*) eli ontogeneettisillä muutoksilla ravinto nichen (ekolokero) hyväksikäytössä kalan kasvaessa.

Siian infektoitumisaste näytti olevan enemmän riippuvainen järvityypistä ja habitaatin käytöstä kuin siikamuodon alkuperästä. Pöyrisjärvessä, jonka siikakanta on alkuperäinen, havaittiin hitaampi infektoitumiskehitys kuin Kilpisjärvessä, abundanssin saavuttaessa tasaantumisvaiheen vasta ikäryhmässä 6+. Ero Kilpisjärveen verrattuna oli selitettävissä vesikirppupainotteisella ruokavaliolla kalan ensimmäisen ikävuosien aikana infektiota kantavien hankajalkaisten tullessa kuvaan myöhemmin. Molemmissa edellä mainituissa järvissä havaittiin abundanssi-käyrän tasaantuminen ja kasaantumisindeksin lasku hankajalkaisravinnon osuuden laskiessa. Pulmankijärvessä (L. Puolbmajavri) kahden sympatrisesti elävän siikamuodon välillä havaittiin erilaisesta habitaatin käytöstä johtuva huomattava ero *D. ditremum* -infektoitumisasteessa. Istutettu harvasiivilähampainen enimmäkseen litoraalin pohjaeläimiä hyödyntävä muoto (*C. lavaretus fera*) oli vähemmän infektoitunut kuin alkuperäinen pelagiaali-alueella ja profundaalissa syönnöstelevä muoto (*C. lavaretus wartmanni*).

Seurattaessa *D. ditremum* populaation vuodenaikaista transmissio dynamiikkaa eli rekrytoitumista isäntäkalassa havaittiin kaksi pääasiallista tartuntahuippua: yksi syksyllä, syys- lokakuussa ja toinen keväällä maali-huhtikuussa. Ravinnonkulutus oli kevättalvella alhaisella tasolla. Myös isommat, jo karkeaa pohjaravintoa hyödyntämään pystyvät siikat söivät kevään tartuntahuippua edeltävänä ajankohtana pääasiassa hankajalkaisyriäisiä (*Eudiptomus*), joiden pohjassa talvehtivat kopepodiitti-vaiheet tuolloin palaavat vesimassaan ollen tuolloin ilmeisesti hyvin saatavilla. Korkean energiapitoisuuden ja pienen yksilökoon ansiosta hankajalkaisyriäiset ovat helposti sulavia ja näin ollen kylmänveden aikaan energieettisesti edullista ravintoa verrattuna kalkkikuorellisiin nilviäisiin niiden tarjoamasta suuremmasta kerta-annoksesta huolimatta. Kylmässä hidas suolentoiminta nollassi kalan isompia ravintokohteita valitessaan saaman hyödyn. Hankajalkaisravinnosta saatava nopea hyöty kostautuu lisääntyneen *D. ditremum*-infektion muodossa.

Siika menetti painoaan huomattavasti talvella. Vuotuinen suurin painolisäys ajoittui syyskesän ja syksyn intensiivisimmälle syönnöskaudelle, jolloin myös (sukurauhasten) gonadin painonlisäys oli nopeinta. Tulokset tukivat muualla arktisilla alueilla saatuja tuloksia: siika on sopeutunut nopeasti lisäämään lyhyenä syönnöskautena painoaan, mikä ominaisuus on elintärkeä sen kasvuille, lisääntymiselle ja eloonjäännille. Kyky energiavarojen nopeaan mobilisoimiseen somaattisesta kudoksesta gonadien energian tarpeisiin on subarktisille siiolle tärkeä sopeutuma vuotuisen kutukypsyuden saavuttamiseksi. *D. ditremum*-infektio näytti estävän ennen kaikkea immatuurien (lepovuotisten) yksilöiden gonadien suhteellisen energiapitoisuuden nousua, mutta maturoituvien yksilöihin korkeat loismäärät eivät näyttäneet vaikuttavan.

Useat tutkijat ovat esittäneet spekulatioita siitä, mikä on loisten merkitys isäntälajin kantojen säätelyssä. 1950-60-luvuilla alkaneet istutukset mahdollisesti aiheuttivat lisää loiskuormaa, mikä havaittiin 1990-luvun tilanteessa verrattuna 1960 infektion voimakkuuteen. 1990-

luvulle tultaessa siian kasvunopeus ja kunto paranivat, kun taas saaliit (CPUE) määrällisesti laskivat, eikä muiden kalalajien saaliissa tapahtunut merkitsevää muutosta. Näin ollen tiheydestä riippuvat tekijät ilmeisesti vaikuttivat siikakantaan. Populaation säätely tapahtuu eri mekanismien vaikutuksesta, joista useat eri tekijät voivat vaikuttaa samanaikaisesti. *D. ditremum* voi olla osallisena siian populaation säätelyssä kuolevuuteen ja lisääntymiseen vaikuttamalla. Tässä tutkittiin poikasvaiheen jälkeistä siikapopulaation tilaa. Yksiselitteisiä osoituksia loisperäisen kuolevuuden vaikutuksista ei tässä tutkimuksessa saatu. Loisen populaatiodynamiikkaa kuvaavalla mallilla laskettu verrattain lyhyt loisen keskimääräinen viipyminen isäntäkalassa selitettiin ankarasta lajinsisäisestä kilpailusta ja siialle ominaisesta tehokkaasta isäntävasteesta johtuvalla loiskuolleisuudella. Loisaabundanssin vaikutusta lisääntymiseen tutkittiin gonadin kasvuun sen kehityksen alkuvaiheessa keväällä, jolloin tulokseksi saatiin loisen inhiboiva vaikutus gonadien painoon. Gonadin kypsymiseen eli kutuvalmiuden saavuttamiseen loisella oli myös vaikutusta. Ovarioiden suhteellinen energiapitoisuus oli alhaisempi vaikeammin infektoituneilla yksilöillä. Myös suhteellinen fekunditeetti laski lois-abundanssin noustessa, mutta alhaisempi munamäärä korvautui coregonideille tyypilliseen tapaan yksittäisen mätimunän suuremmalla kuiva-ainepitoisuudella. Infektoituneimmat naarassiat näyttäisivät häviävän jälkeläisten tuottokyvyssä eli kärsivän fitnessin (biologisen kelpoisuuden) alenemisesta, mutta alentunut poikastuotto voi korvautua energiapitoisemmista munista kuoriutuvien isompien poikasten paremmalla elinkelpoisuudella.

Vuosina 1992-93 nuorten siikojen (1-4 vuotta) kasvunopeus oli sama kuin 10 vuotta aiemmin, mutta vanhemmissa ikäryhmissä oli havaittavissa kasvun nopeutumista. Silti mitään merkitsevää muutosta ei ollut tapahtunut loistiheyden ja kalan kunnon välisessä yhteydessä. Tämän tutkimuksen tulos siis tukee aiempien tutkijoiden oletuksia siitä, että pohjoisimpien järvien siikapopulaatiot ovat hyvin sopeutuneet kestämään korkeata *Diphyllbothrium* -infektioastetta.

References

- Adjei, E.L., Barnes, A. & Lester, R.J.G. 1986. A method for estimating possible parasite-related host mortality, illustrated using data from *Callitetrarhynchus gracilis* (Cestoda: Trypanorhyncha) in lizardfish (*Saurida* spp.). Parasitology 92: 227-243.
- Adlard, R.D. & Lester, R.J.G. 1994. Dynamics of the interaction between the parasitic isopod, *Anilocra pomacentri*, and the coral reef fish *Chromis nitida*. Parasitology 109: 311-324.
- Amundsen, P.-A. 1988. Effects of an intensive fishing programme on age structure, growth and parasite infection of stunted whitefish (*Coregonus lavaretus* L. s.l.) in Lake Stuurajavri, northern Norway. Finnish Fish. Res. 9: 425-434.
- Amundsen, P.-A. & Klemetsen, A. 1988. Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr *Salvelinus alpinus* (L.) in Takvatn, Northern Norway. J.Fish Biol. 33: 697-709.
- Amundsen, P.-A. & Kristoffersen, R. 1990. Infection of whitefish (*Coregonus lavaretus* L. s.l.) by *Triaenophorus crassus* Forel (Cestoda: Pseudophyllidea): a case study in parasite control. Can. J. Zool. 68: 1187-1192.
- Andersen, K.I., Ching, H. L. & Vik, R. 1987. A review of freshwater species of *Diphyllbothrium* with redescriptions and the distribution of *D. dendriticum* (Nitzsch, 1824) and *D. ditremum* (Creplin, 1825) from North America. Can. J. Zool. 65: 2216-2228.
- Andersen, K.I. & Gibson, D.I. 1989. A key to three species of larval *Diphyllbothrium* Cobbold, 1858 (Cestoda: Pseudophyllidea) occurring in European and North American freshwater fishes. Syst. Parasitol. 13: 3-9.

- Andersen, K.I. & Valtonen, E.T. 1992. Segregation and co-occurrence of the larval cestodes in freshwater fishes in the Bothnian Bay, Finland. *Parasitology* 104: 161-168.
- Anderson, R. M. 1979. The influence of parasite infection on the dynamics of host population growth. In: Anderson, R. M., Turner, B.D. & Taylor, L.R. (eds.), *Population Dynamics*. p. 245-281. Oxford: Blackwell Scientific Publications.
- Anderson, R.M. 1995. Evolutionary pressures in the spread and persistence of infectious agents in vertebrate populations. *Parasitology*: 111: 15-31.
- Anderson, R. M. & Gordon, D. M. 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* 85: 373-398.
- Anderson, R.M. & May, R.M. 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.* 47: 219-247.
- Anderson, R.M. & May, R.M. 1979. Population biology of infectious diseases. Part 1. *Nature* 280: 361-367.
- Anon. 1983. Hydrological data 1983. Monthly hydrological report. National Board of Waters, Helsinki 9: 1-4.
- Arme, C. & Owen, R.W. 1967. Infections of the three-spined stickleback, *Gasterosteus aculeatus* L., with the plerocercoid larvae of *Schistocephalus solidus* (Muller 1776) with special reference to pathological effects. *Parasitology* 57: 301-314.
- Bagenal, T.B. 1978. Aspects of fish fecundity. In: Gerking, S.D. (ed.) *Ecology of freshwater fish population*. p 75-101. Blackwell Sci. Publ., Oxford.
- Bagge, P. 1968. Ecological studies on the fauna on subarctic waters in Finnish Lapland. *Ann. Univ. Turku A II*: 40 Rep. Kevo Subarctic Sta. 4: 28-79.
- Beamish, R.J. & McFarlane, G.A. 1995. A discussion of the importance of the ageing errors, and application to walleye pollock: the world's largest fishery. In: Secor, D.H., Dean, J.M. & Campana, S.E. (eds.), *Recent Development in Fish Otolith Research*. The Belle W. Baruch Library in Marine Science 19. p. 545-565. University of South Carolina Press. Charleston.
- Berg A. 1970. A comparative study of food and growth and competition between two species of coregonids introduced into Lake Maggiore, Italy. In: Lindsey, C.C. & Woods, C.S. (eds.), *Biology of Coregonid Fishes*. Univ. Manitoba Press, Winnipeg, 311-346 pp.
- Bérubé, M. & Curtis, M. A. 1986. Transmission of *Diphyllbothrium ditremum* to Arctic Char (*Salvelinus alpinus*) in two Subarctic Quebec lakes. *Can. J. Fish. Aquat. Sci.* 43: 1626-1634.
- Bodaly, R.A. 1979. Morphology and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon Territory. *J. Fish. Res. Bd. Can.* 36: 1214-1222.
- Brown, E.A.R. & Scott, D.B.C. 1990. Anabolic adaptiveness in the two Scottish populations of powan, *Coregonus lavaretus* (L.). *J. Fish Biol.* 37: 251-253.
- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *J. Parasitol.* 83(4): 575-583.
- Bylund, G. 1972. Pathogenic effects of a diphyllbothriid plerocercoid in its host fishes. *Commentat. Biol. Soc. Sci. Fenn.* 58: 1-11.
- Bylund, G. 1975. Delimitation and characterization of European *Diphyllbothrium* species. Ph.D. thesis, Åbo Akademi, 23 p., Åbo.
- Bylund, G. & Andersen, K. 1994. Thirty years of *Diphyllbothrium* research and future trends. *Bulletin of the Scandinavian Society of Parasitology* 4: 47-56.
- Calow, P. 1985. Adaptive aspects of energy allocation. In: Tytler, P & Calow, P. (eds.), *Fish Energetics, New Perspectives*, Croom & Helms, London & Sydney. p. 13-31.
- Chubb, J.C. 1980. Seasonal occurrence of helminths in freshwater fishes. Part III. Larval Cestoda and Nematoda. *Adv. Parasitol.* 18: 1-120.
- Crofton, H.D. 1971. A model of host-parasite relationship. *Parasitology* 63: 343-364.
- Cummins K.W. & Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Verein. Limnol.* 18: 1-158.
- Curtis, M.A. 1983. Parasitism of Arctic char by *Diphyllbothrium ditremum* and *D. dendriticum* in relation to the food web structures of northern lakes. *Proc. Second ISACF workshop on Arctic char 1982*. ISACF Inf. Ser. 2: 11-18.

- Curtis, M.A. & Bylund, G. 1991. Diphyllbothriasis: Fish tapeworm disease in the circumpolar north. *Arct. Med. Res.* 50: 18-25.
- Cushing, D.H. 1981. *Fisheries Biology: A Study in Population Dynamics*. University of Wisconsin Press, Madison, Wisconsin.
- Dabrowski, K.R. 1982. Reproductive cycle of vendace (*Coregonus albula* L.) in relation to some chemical and biochemical changes in the body. *Hydrobiologia* 94: 3-15.
- Dabrowski, K.R. 1983. A note on the energy transformation in body and gonad of coregonid fish. *Arch. Hydrobiol.* 97(3): 406-414.
- Dabrowski, K.R. 1985. Energy budget of coregonid (*Coregonus* spp.) fish growth metabolism and reproduction. *Oikos* 45: 358-364.
- Dobson, A.P. & Hudson, P.J. 1992. Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *J. Anim. Ecol.* 61: 487-498.
- Einsele, W. 1943. Über die Wachstum der Coregonen in Voralpen Gebieten, insbesondere über die Verhältnis von Schuppen- und Längenwachstum. *Z. Fish.* 41: 1.
- Elgmork, K. 1962. A bottom resting stage in the planktonic freshwater copepod *Cyclops scutifer* Sars. *Oikos* 13: 306-310.
- Elliott, J.M., 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshw. Biol.* 2: 1-18.
- Elliott, J.M., 1979. Energetics of freshwater teleosts. *Symp. Zool. Soc. Lond.* 44: 29-61.
- Elliott J.M., 1981. Some aspects of thermal stress on freshwater teleosts. In Pickering, A.D (ed.), *Stress and Fish*. Academic Press Inc., London, pp. 209-245.
- Esch, G.W. & Fernandez, J.C. 1993. *A Functional Biology of Parasitism, Ecological and evolutionary implications*. Chapman & Hall, London. 330 p.
- Fechhelm, R.G., Griffiths, W.B., Wilson, W.J., Gallaway, B.J. & Bryan, J.D. 1995. Intra- and interseasonal changes in the relative condition and proximate body composition of broad whitefish from the Prudhoe Bay region of Alaska. *Trans. Am. Fish. Soc.* 124: 508-519.
- Frandsen, F., Malmquist, H. J. & Snorrason, S. S. 1989. Ecological parasitology of polymorphic Arctic char, *Salvelinus alpinus* L., in Thingvallavatn, Iceland. *J. Fish Biol.* 34: 281-297.
- Fraser, P.G. 1960: The occurrence of *Diphyllbothrium* in trout, with special reference to an outbreak in the West of England. *J. Helminthol.* 34: 59-72.
- Goater, C.P. & Holmes, J.C. 1997. Parasite mediated natural selection. In: Clayton, D.H. & Moore, J. (eds.), *Host-parasite evolution. General principles and avian models*: 9-29. Oxford University Press, Oxford.
- Gordon, D.M. & Rau, M.E. 1982: Possible evidence for mortality induced by the parasite *Apatemon gracilis* in a population of brook sticklebacks (*Culaea inconstans*). *Parasitology* 84: 41-47.
- Gulland, J.A. 1983. *Fish Stock Assessment. A Manual of Basic Methods*. John Wiley & Sons, New York.
- Gustafsson, T. 1996. *Diphyllbothrium ditremum* -heisimadon vaikutuksesta siian kasvuun, lisääntymiseen ja kuolleisuuteen subarktisisä Kilpisjärvässä. Pro gradu työ, Ekologian ja systematiikan laitos, Helsingin yliopisto, 34 p. (The effect of a tapeworm *D. ditremum* on growth, reproduction and mortality in subarctic Lake Kilpisjärvi, M. Sc. thesis. In Finnish).
- Hagen, H.K. 1970. Age, growth and reproduction of the mountain whitefish in Phelps lake, Wyoming. In: Lindsey, C.C. & Woods, C.S. (eds.). *Biology of coregonid fishes*, p. 399-415. Winnipeg.
- Halvorsen, O. 1970. Studies of the helminth fauna of Norway XV: On the taxonomy and biology of plerocercoids of *Diphyllbothrium* Cobbold, 1858 (Cestoda, Pseudophyllidea) from north-western Europe. *Nytt Mag. Zool.* 18: 113-174.
- Halvorsen, O. & Wissler, K. 1973. Studies of helminth fauna of Norway. XXVII. An experimental study of the ability of *Diphyllbothrium latum* L., *D. dendriticum* (Nitzsch) and *D. ditremum* (Creplin) (Cestoda, Pseudophyllidea) to infect paratenic hosts. *Norw. J. Zool.* 21: 201-210.
- Halvorsen, O. & Andersen, K. 1984. The ecological interaction between arctic char, *Salvelinus alpinus* L., and the plerocercoid stage of *Diphyllbothrium ditremum*. *J. Fish Biol.* 25: 305-316.
- Hansson, J. M. & Leggett, W. C. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. *Can. J. Aquat. Sci* 52: 280-286.
- Haraldstad, Ø. & Jonsson B. 1983. Age and sex segregation in habitat utilization by brown trout in a Norwegian lake. *Trans. Am. Fish. Soc.* 112: 27-37.

- Hario, M., Selin, K. & Soveri, T. 1992. Loisten osuudesta haahkan lisääntyvyyden heikkenemisessä. Suomen Riista: 38: 23-33 (Is there a parasite-induced deterioration in eider fecundity? In Finnish, with English summary).
- Haukisalmi, V. 1989. Voivatko loiset säädellä riistaeläinpopulaatioita. Suomen Riista 35: 72-82 (The regulation of game populations by parasites. In Finnish with English summary).
- Healey, M.C. 1980. Growth and recruitment in experimentally exploited whitefish (*Coregonus clupeaformis*) population. Can. J. Fish. Aquat. Sci. 37: 255-267).
- Heikinheimo-Schmid, O. 1982. Siian ravinnosta luonnontilaisessa ja säännöstellyssä järvessä. Riista- ja Kalatalouden Tutkimuslaitos, Kalantutkimusosasto. Monistettuja julkaisuja 4: 1-64 (In Finnish).
- Heikinheimo-Schmid, O. & Huusko, A. 1988. Management of coregonids in the heavily modified Lake Kemijärvi, Northern Finland. Finnish Fish. Res. 9: 435-445.
- Heikinheimo, O., Miinalainen, M. & Peltonen, H. 2000. Diet, growth and competitive abilities of sympatric whitefish forms in a dense introduced population: results of a stocking experiment. J. Fish Biol. 57: 808-827.
- Helfman, S.G., Collette, B.B. & Facey, D.E. 1997. The Diversity of Fishes. Blackwell Science. Malden, Mass. 528 p.
- Helminen, H., Sarvala, J. & Hirvonen, A. 1990. Growth and food consumption of vendace (*Coregonus albula* (L.)) in Lake Pyhäjärvi, SW Finland: a bioenergetics modeling analysis. Hydrobiologia 200/201: 511-522.
- Henricson, J. 1977. The abundance and distribution of *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in the char *Salvelinus alpinus* L. in Sweden. J. Fish Biol. 11: 231-248.
- Henricson, J. 1978. The dynamics of infection of *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in the char *Salvelinus alpinus* L. in Sweden. J. Fish Biol. 13: 51-71.
- Henricson, J. & Nyman, L. 1976. The ecological and genetical segregation of two sympatric species of dwarfed char *Salvelinus alpinus* (L.) species complex. Rep. Inst. Freshw. Res., Drottningholm 55: 15-37.
- Hessen, D.O., Skurdal, J., Vollestad, L.A. & Berge, D. 1986. Habitat use among size groups of monomorphic whitefish, *Coregonus lavaretus*. Hydrobiologia 137: 185-192.
- Hewett, S. W. & Johnson, B. L. 1992. A fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. UW Sea Grant Technical Report No. WIS-SG-92-250. University of Wisconsin-Madison, 79 p.
- Hickey, M.B. & Harris, J.R. 1947. Progress of the *Diphyllobothrium* epizootic at Poulaphouca Reservoir. Co. Wicklow. J. Helminthol. 22: 13-28.
- Hindar, K. & Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic Charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. Can. J. Fish. Aquat. Sci. 39: 1030-1045.
- Holmes, J.C. & Bethel, W.M. 1972. Modification of intermediate host behaviour by parasites. In: Canning, E.U. & Wright, C.A. (eds.) Behavioural Aspects of Parasite Transmission. Journal of the Linnean Society of London, Supplement 1: 123-149.
- Holmes, J.C. & Zohar, S. 1990. Pathology and host behaviour. In: Barnard, C.J. & Behnke, J.M. (eds.) Parasitism and host behaviour, p. 34-63. Taylor & Francis, London.
- Hristowski, N.D. 1992. Endohelminths in *Coregonus lavaretus* L. from Island Lake, Greece. Pol. Arch. Hydrobiol. 39: 667-670.
- Jacobsen O.J. 1974. Feeding habits of the population of whitefish, *Coregonus lavaretus* L. in Haugatjern - a eutrophic Norwegian lake. Norw. J. Zool. 22 (4): 295-318.
- Jensen, A.L. 1981. Population regulation in lake whitefish *Coregonus clupeaformis* (Mitchill). J. Fish Biol. 1: 557-573.
- Järnefelt, H. 1956. Zur limnologie einiger Gewässer Finnlands XVII. Ann. Zool. Soc. Vanamo 18: 2-15.
- Kahilainen, K. 1998. Sympatristen siikamuotojen kasvu, habitaatit ja yksikkösaaliit Muddusjärvessä. Pro gradu työ. Limnologian ja ympäristönsuojelun laitos, Helsingin yliopisto. 43 p. (Growth, habitats and catches of sympatric whitefish forms in Lake Muddusjärvi. M. Sc. thesis. In Finnish).
- Kamler, E. 1992. Early life history of fish. An energetics approach. Chapman & Hall, London. 267 p.

- Kennedy, C. R., 1970: The population biology of helminths of British freshwater fish. Symp. Br. Soc. Parasitol. 8: 145-159.
- Kennedy, C. R., 1975: Ecological Animal Parasitology. Oxford: Blackwell Scientific Publications.
- Kennedy, C. R., 1984: The use of frequency distributions in attempt to detect host mortality induced by infections of diplostomatid metacercariae. Parasitology. 89: 209-220.
- Knudsen, R. 1997. Relationships between parasite infection and feeding behaviour in Arctic charr (*Salvelinus alpinus* (L.)). Ph.D. thesis, University of Tromsø. 31 p.
- Knudsen, R. & Klemetsen, A. 1994. Infections of *Diphyllbothrium dendriticum*, *D. ditremum* (Cestoda) and *Cystidicola farionis* (Nematoda) in a north Norwegian population of the Arctic charr (*Salvelinus alpinus*) during winter. Can. J. Zool. 72: 1922-1930.
- Knudsen, R., Klemetsen, A. & Staldvik, F. 1996. Parasites as indicators of individual feeding specialization in Arctic charr during winter in Northern Norway. J. Fish Biol. 48: 1256-1265.
- Krebs, J.R. & Davies, N.B. 1991. Behavioural ecology: an evolutionary approach. 3rd ed. London Blackwell Science.
- Kristoffersen, R. 1989: Parasittene hos Takvassrøya. Ottar 3: 31-37. Trömsø Museum (in Norwegian).
- Kristoffersen, R. 1993. Parasites in northern salmonids: Effects of overpopulation and perturbations in systems with Arctic charr *Salvelinus alpinus* (L.) and whitefish (*Coregonus lavaretus* L. s.l.) in northern Norway. Ph.D. thesis. University of Tromsø. 82 p.
- Kuhlow, F. 1953. Über die Entwicklung und Anatomie von *Diphyllbothrium dendriticum* Nitzsch 1824. Zeitschrift für Parasitenkunde 16: 1-35.
- Lahti, E. & Muje, P. 1991. Egg quality and female condition in vendace (*Coregonus albula* L.) before and during spawning. Hydrobiologia 209: 175-182.
- Langeland, A. & Nost, T. 1995. Gill-raker structure and selective predation on zooplankton by particulate feeding fish. J. Fish Biol. 47: 719-732.
- Lazarro, X. 1987. A review of planktivorous fishes: The evolution, feeding behaviours, selectivities and impacts. Hydrobiologia 146: 97-167.
- Lehtonen, H. 1981. Biology and stock assessment of Coregonids by the Baltic coast of Finland. Finnish Fish. Res. 3: 31-83.
- Lehtonen, H. & Niemelä, E. 1998. Growth and population structure of whitefish (*Coregonus lavaretus* (L.)) in mountain lakes of northern Finland Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 50: 81-95.
- Lemly, A.D. & Esch, G.W. 1984. Effects of the trematode *Uvulifer ambloplitis* on juvenile bluegill sunfish, *Lepomis macrochirus*: ecological implications. J. Parasitol. 70: 475-492.
- Lizenko Y. I., Sidorov, V.S. & Potapova, O.I. 1975. Seasonal variations in the lipid composition of the tissues and organs of the large cisco (*Coregonus albula*) in Karelian lakes. J. Ichthyol. 15: 465-472.
- McCallum, H.I. 1989. Models to assess the potential of *Capillaria hepatica* to control population outbreaks of house mice. Parasitology 98: 425-437.
- McPhail, J.D. & Peacock, S.D. 1983. Some effects of cestode (*Schistocephalus solidus*) on reproduction in the threespine stickleback (*Gasterosteus aculeatus*): evolutionary aspects of a host-parasite interaction. Can. J. Zool. 61: 901-908.
- Miinalainen, M. & Heikinheimo, O. 1998. Siikamuotojen ravintokilpailu Vuokalanjärvässä. Helsinki. Finnish Game and Fisheries Research Institute, Kalatutkimuksia-Fiskundersökningar: 139. 39 p. (Food segregation between five whitefish (*Coregonus lavaretus* (L.)) forms in Lake Vuokalanjärvi. In Finnish with English abstract).
- Mills, K.H. & Chalanchuk, S.M. 1988. Population dynamics of unexploited lake whitefish (*Coregonus clupeaformis*) in one experimentally fertilized lake and three exploited lakes. Finnish Fish. Res. 9: 145-153.
- Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499-513.
- Mookerji, N., Heller, C., Meng, H.J., Bürgi, H.R. & Müller, R. 1998. Diel and seasonal patterns of whitefish *Coregonus* sp. in re-oligotrophic Lake Lucerne, Switzerland. J. Fish Biol. 52: 443-457.
- Muench, H. 1959. Catalytic models in epidemiology. Harvard University Press. Cambridge, Mass.

- Muje, P., Ågren, J., Lindqvist, O. & Hänninen, O. 1988. Fatty acid composition of vendace (*Coregonus albula* L.) muscle and its plankton feed. *Comp. Biochem. Physiol.* 92B: 75-79.
- Munro, A.D. 1990. General introduction. In: Munro, A.D., Scott, A.P. & Lam, T.J. (eds.), *Reproductional seasonality in teleosts: Environmental influences*. CRC Press, Boca Raton, FL. p. 1-11.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd. Can.* 9: 450-491.
- Nilsson, N.-A. 1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. *Rep. Inst. Freshw. Res., Drottningholm.* 58: 126-139.
- Oliva, M.E., Borquez, A.S. & Olivares, A.N. 1992. Sexual status of *Paralabrax humeralis* (Serranidae) and infection by *Philometra* sp (Nematoda: Dracunculoidea). *J. Fish Biol.* 40: 979-980.
- Paalavuo, M., Muje, P., Ågren, J. & Tambets, M. 1998. Energy content and fatty acid composition of vendace (*Coregonus albula* L.) gonads in four Finnish and Estonian lakes. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 50: 25-32.
- Pacala, S.W. & Dobson, A.P. 1988. The relation between the number of parasites/host and host age: population dynamics causes and maximum likelihood estimation. *Parasitology* 96: 197-210.
- Palomäki, R. 1981. Inarinjärven siikamuodot ja niiden ravinnonvalinta. Pro gradu työ. Biologian laitos, Jyväskylän yliopisto. 101 p. (The whitefish forms in Lake Inari and their food preferences. M. Sc. thesis. In Finnish).
- Palomäki, R., Jokela, J., Vuori, K.-M. & Puro, A. 1992. Prey preference and timing of the diet shifts of *Coregonus pidschian* and *C. lavaretus*: preliminary results of a field experiment. *Pol. Arch. Hydrobiol.* 39 (3-4): 351-359.
- Pennycuik, L. 1971. Differences in the parasite infection in three-spined sticklebacks (*Gasterosteus aculeatus* L.) of different sex, age and size. *Parasitology* 63: 378-388.
- Persson, L. 1983. Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. *Oikos* 41: 126-132.
- Pomeroy, P.P., 1991. A comparative assessment of temporal variation in diet of powan, *Coregonus lavaretus* (L.), from Loch Lomond and Loch Eck, Scotland, U.K. *J. Fish Biol.* 38 (3): 457-478.
- Poulin, R. 2000. Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *J. Fish Biol.* 56: 123-137.
- Price, P.W. 1990. Host populations as resources defining parasite community organisation. In: Esch, G.W., Bull, A.O. & Atto, J.M. (eds.), *Parasite Communities: Patterns and Processes*. p. 21-40.
- Pulkkinen, K. 1999. Transmission of *Triaenophorus crassus* from copepod first to coregonid second intermediate host and effects on intermediate hosts. *Biological Research Reports from the University of Jyväskylä* 76. 40 p.
- Pulliam H.R. 1974. On the theory of optimal diets. *Am. Nat.* 108: 59-74.
- Rahkonen, R. 1998. Interactions between a gull tapeworm *Diphyllobothrium dendriticum* (Cestoda) and trout (*Salmo trutta* L.). *Biological Research Reports from the University of Jyväskylä* 62. 43 p.
- Rahkonen, R., Aalto, J., Koski, P., Särkkä, J. & Juntunen, K. 1996. Cestode larvae *Diphyllobothrium dendriticum* as a cause of heart disease leading to mortality in hatchery-reared sea trout and brown trout. *Dis. Aquat. Organ.* 25(1-2): 15-22.
- Rahkonen, R. & Koski, P. 1997. Occurrence of cestode larvae in brown trout after stocking in a large regulated lake in northern Finland. *Dis. Aquat. Organ.* 31: 55-63.
- Raitaniemi, J. 1999. The growth responses of fish to differences in acidity-related lake characteristics and fish species composition. Ph.D. thesis. University of Helsinki and Finnish Game and Fisheries Research Institute, Helsinki. 23 p.
- Reshetnikov, J. S. 1967. Periodicity of reproduction in whitefish. *Vopr. Iktiolog.* 7: 1019-1031.
- Reshetnikov, Y.S., Paranyushkina, L.P. & Kirashko, V.I. 1970. Seasonal changes in blood serum protein composition and fat content in whitefishes. *J. Ichthyol.* 10: 804-815.
- Rodger, H.D. 1991. *Diphyllobothrium* sp. infections in freshwater reared Atlantic salmon (*Salmo salar* L.). *Aquaculture* 95: 7-14.
- Rudstam L.G., Binkowski, F. B. & Miller, M. A. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Trans. Am. Fish. Soc.* 123: 344-357.

- Ruhle C. & Gammeter, S. 1998. Alterations in the trophic status of Lake Walenstadt (Switzerland) and in the growth of its slow-growing whitefish (*Coregonus lavaretus* L.) Arch. Hydrobiol. Spec. Issues Advanc. Limnol 50: 109-120.
- Salojärvi K. 1988. Effects of the stocking density of whitefish (*Coregonus lavaretus* L. s.l.) fingerlings on the fish yield in Lake Peranka, Northern Finland. Finnish Fish. Res. 9: 407-416.
- Salojärvi, K. 1989. Validity of scale ages determined for whitefish checked by microtagging in Lake Oulujärvi, northern Finland. Aqua Fennica 19: 119-122.
- Salojärvi, K. 1991. Compensation in a whitefish (*Coregonus lavaretus* L. s.l.) population maintained by stocking in Lake Kallioinen, northern Finland. Finnish Fish. Res. 12: 65-76.
- Salojärvi, K. 1992. The role of compensatory processes in determining the yield from whitefish (*Coregonus lavaretus* L. s.l.) stocking in inland waters in northern Finland. Finnish Fish. Res. 13: 1-30
- Salojärvi, K. & Huusko, A. 1990. Results of whitefish (*Coregonus lavaretus* L. s.l.) fingerling stocking in lower part of Sotkamo water course, northern Finland. Aquaculture and Fisheries Management 21: 229-244.
- Salonen, E., Mutenia, A. & Salojärvi, K. 1996. Siian kalastus, istutukset ja pohjasiikakannan kehitys Inarinjärvellä vuosina 1980-1994. In: Inarinjärven pohjasiika -istutusten merkitys (Salonen, E., ed.) Helsinki. Finnish Game and Fisheries Research Institute, Kalatutkimuksia – Fiskundersökningar 113: 3-44. (Sparsely-rakered whitefish from Lake Inari: Results from stocking. In Finnish with English abstract).
- Salonen, E., Mutenia, A. & Kotajärvi, M. 1997. Lokan ja Porttipahdan peledsiika. Tekojärvien siikakantojen vaihtelu vuosina 1987-1996. Helsinki. Finnish Game and Fisheries Research Institute, Kalatutkimuksia - Fiskundersökningar 127. 34 p. (Peled in the Lokka and Porttipahta Reservoirs. In Finnish with English abstract).
- Sandlund, O.T., Naesje T.F. & Kjellberg G. 1987. The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco, *Coregonus albula*, whitefish, *Coregonus lavaretus* and smelt, *Osmerus eperlanus*. Arch. Hydrobiol. 110 (3): 357-363.
- Sarjamo, H., Jääskö, O. & Ahvonen, A. 1989. Inarin kunnan vesien kalakantojen käyttö- ja hoitosuunnitelma (Fisheries management plan for the Inari commune). Finnish Game and Fisheries Research Institute, Monistettu julkaisu 96: 1-187 (in Finnish).
- Sarvala, J., Helminen, H. & Hirvonen, A. 1992. Fecundity of vendace *Coregonus albula* L. in relation to year class variation in Lake Pyhäjärvi in SW-Finland. Pol Arch. Hydrobiol. 39 (3-4):341-349.
- Sarvala, J & Helminen, H. 1995. Significance of egg size variation in the year-class fluctuations of vendace *Coregonus albula* L. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 46: 187-194.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.
- Sharp, G.J.E., Pike, A.P. & Secombes C.J. 1989. The immune response of wild rainbow trout *Salmo gairdneri* Richardson to naturally acquired plerocercoid infections of *Diphyllbothrium dendriticum* (Nitzsch, 1824) and *D. ditremum* (Creplin, 1825). J. Fish Biol. 35: 781-794.
- Spratt, D.M. 1990. The role of helminths in the biological control of mammals. Int. J. Parasitol. 20: 543-550.
- Stewart, D. J. & Binkowski, F.B. 1986. Dynamics of consumption and food conversion of alewives: an energetic-modeling synthesis. Trans. Am. Fish. Soc. 115: 643-661.
- Svärdson, G. 1957. The Coregonid problem. VI. The palearctic species and their intergrades. -Rep. Inst Freshw. Res. Drottningholm 38: 267-356.
- Svärdson, G. 1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshw. Res. Drottningholm 57: 1-95.
- Tierney, J.F., Huntingford, F.A. & Crompton, D.W.T. 1996. Body condition and reproductive status in sticklebacks exposed to a single wave of *Schistocephalus solidus* infection. J. Fish Biol. 49: 483-493.
- Tolonen, A. 1992. Pohjasiian (*Coregonus lavaretus* (L.)) ravinto ja makroparasiitit sekä niiden yhteys kasvuun ja kutuvalmiuteen subarktisisä järvissä. Lisensiaatin tutkimus. Limnologian ja ympäristönsuojelun laitos, Helsingin yliopisto, 108 p. (Diet and macroparasites plus their effect on the growth and spawning preparedness in benthic whitefish of subarctic Lake Kilpisjärvi. Licentiate thesis. In Finnish).

- Tolonen, A. & Lappalainen, J. 1999. Origin of the large burbot (*Lota lota* (L.)) caught in an Arctic ice-fishing competition: a case study. *J. Appl. Ichthyol.* 15: 122-126.
- Tolonen, A., Kjellman, J. & Lappalainen, J. 1999. Diet overlap between burbot *Lota lota* L. and whitefish *Coregonus lavaretus* (L.) in a subarctic lake. *Ann. Zool. Fennici* 36: 205-214
- Tuunainen, P., Nylander, E., Alapassi, T. and Aikio, V. 1979. Kalastus ja kalakannat Tornionjoen vesistöissä. (Fisheries and fish stocks in Tornionjoki river system). Finnish Game and Fisheries Research Institute, Monistettuja julkaisuja 96, 187 p. (in Finnish).
- Valtonen, E.T. & Valtonen, T. 1979. Metazoan parasites of sea-spawning whitefish *Coregonus nasus* (Pallas) sensu Svärdsön in the Bothnian Bay. *Bothnian Bay Rep.* 2: 1-9.
- Valtonen, E.T., Brummer-Korvenkontio, H. & Rahkonen, R.A. 1988. A survey of the parasites of coregonids from three water bodies in Finland. *Finnish Fish. Res.* 9: 313-322.
- Valtonen, T. 1972. The maturity and gonadal development of *Coregonus nasus* (Pallas) sensu Svärdsön, in the Bay of Bothnia. *Aquilo Ser. Zool.* 13: 109-114.
- Vik, R. 1957. Studies on the helminth fauna of Norway, I. Taxonomy and ecology of *Diphyllobothrium norvegicum* n. sp. and the plerocercoids of *Diphyllobothrium latum* (L.). *Nytt Mag. Zool.* 5: 25-93.
- Vik, R. 1964. The genus *Diphyllobothrium*. An example of the interdependence of systematics and experimental biology. *Exp. Parasitol.* 15: 361-380.
- Walkey, M. & Meakins, R.H. 1970. An attempt to balance the energy budget of a host-parasite system. *J. Fish Biol.* 2: 361-372.
- Wells L., 1968. Seasonal depth distribution of fish in southern Lake Michigan. *U.S. Fish and Wildlife Service Fishery Bulletin* 67: 1-15.
- Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. *Am. Nat.* 111: 553-578.
- Werner, E.E. & Hall, D. J. 1977. Competition and habitat shift in two sunfishes (Centrarchidae), *Ecology* 58: 869-876.
- Werner, E.E. & Mittelbach, G.G. 1981. Optimal foraging: field test of diet choice and habitat switching. *Am. Zool.* 21: 813-829.
- Windell, J.T. 1971. Food analysis and rate of digestion. In: Ricker, W.E. (ed.), *Methods for Assessment of Fish Production in Fresh Waters*. IBP Handbook 3, Blackwell, Oxford.
- Wootton, R.J. 1985. Energetics of Reproduction. In: Tytler, P & Calow, P. (eds.), *Fish Energetics, New Perspectives*, Croom & Helms, London & Sydney. p. 231-254.
- Wootton, R. J. 1991. *Ecology of teleost fishes*. Chapman and Hall, London. 404 p.
- Wootton, R. J., Allen, J.R.M. & Cole, S.J. 1980. Energetics of the annual reproductive cycle in female sticklebacks *Gasterosteus aculeatus* L. *J. Fish Biol.* 17: 387-
- Ågren, J., Muje, P., Hänninen J., Herranen J. & Penttilä, I. 1987. Seasonal variations of lipid fatty acids of boreal freshwater fish species. *Comp. Biochem. Physiol* 88B: 905-909.