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Mortality of 0+ vendace (*Coregonus albula*) caused by predation and trawling

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Vendace (*Coregonus albula*) is the main fish caught in commercial lake fishery in Finland. It is also important in the diet of landlocked salmon (*Salmo salar m. sebago*). The vendace stock in lake Paasivesi has not recovered from a 10-year recession, and the number of stocked salmon has risen to a level where predation can contribute to the mortality of vendace. We constructed a model of the influence of salmon predation and commercial trawling on the mortality of 0+ vendace in this lake. Our analysis revealed that predation by salmon alone could cause a year-class failure with the present low level of vendace larvae in spring. With a high spring density, only a high trawling effort could thin the year-class to a low level. We recommended that in order to guarantee a high number of larvae in spring, the spawning stock biomass of vendace should be raised.

Introduction

Commercial fishery in Finnish lakes is mainly based on vendace (*Coregonus albula*) fishing. Trawling and winter seining are the most efficient methods used. Vendace is an important target-catch also in recreational fishery where gill netting is the most common method. Large fluctuations in year-class strength are typical of vendace stocks (Viljanen 1986, Salojärvi 1987). However, in the 1980s and 1990s there have been prolonged recessions of vendace stocks in many lakes (e.g. Valkeajärvi *et al*. 2002). In lake Paasivesi, the stock has not recovered as has happened in most nearby lakes in the water system, and the catches have remained low (Fig. 1). The reasons for the prolonged recession are generally still unknown. By comparing the influence of predator stocking and trawling on the mortality of 0+ vendace in Paasivesi, we tried to shed light on this problem.

In Finland, only the Vuoksi water system (Fig. 2) supported the stock of the endemic landlocked salmon (*Salmo salar m. sebago*). Salmon used to spawn in the upper parts of the water system e.g. in the Pielisjoki, and they used the lakes of the water system as feeding areas. The natural reproduction of this stock was completely destroyed due to damming of the spawning rivers in 1955 and 1971 (e.g. Kaukoranta *et al*. 2000). The landlocked salmon would have extirpated without a captive breeding program run since the beginning of the 1960s. The number of salmon stocked into the Pielisjoki increased rapidly

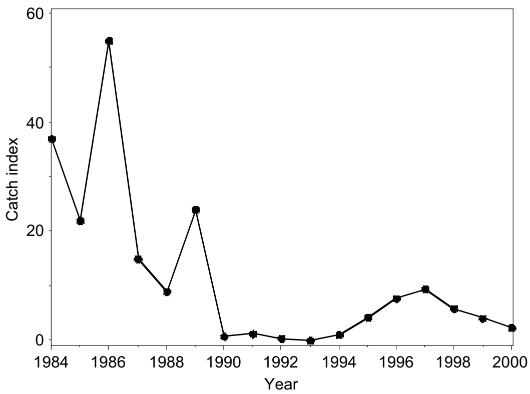

Fig. 1. Total commercial vendace trawl catch as an annual index in lake Paasivesi in 1984–2000.

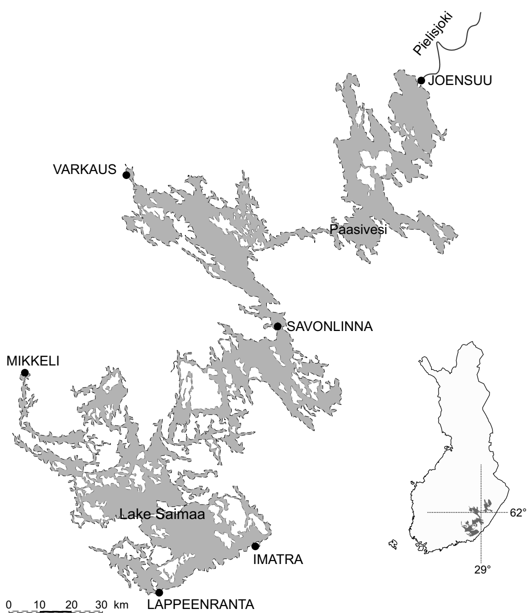

Fig. 2. Location of Vuoksi water system and Paasivesi.

during the 1990s and have lately been about 100 000 smolts per year (Fig. 3). The resulting predation pressure in Paasivesi has grown exceptionally high and the migration into the lake coincides with the transfer of vendace larvae into the pelagic area. During this time also the size of 0+ vendace is suitable for salmon predation. Landlocked salmon is known to feed mainly on pelagic vendace and smelt (*Osmerus eperlanus*) during its migration (Svärdson *et al.* 1988, Koivurinta *et al.* 2000). Lately, commercial fishermen in particular have speculated about the role of regular, large stockings of landlocked salmon

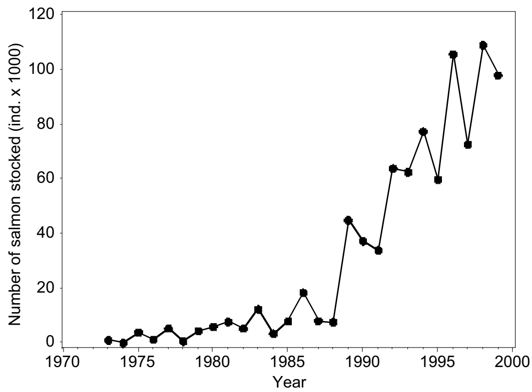

Fig. 3. Number of landlocked salmon smolts stocked in the Pielisjoki in 1973–1999.

on the prolonged vendace recession in Paasivesi. We know further that an extra mortality for 0+ vendace is caused by the filtering of small 0+ fish through the trawl cod-end (Suuronen *et al.* 1995).

In this paper, our goal is to estimate the mortality of 0+ vendace caused by stocked landlocked salmon and by trawl-fishery in Paasivesi. We also evaluate the effect of this mortality on the recruitment of vendace. Finally, we make suggestions for vendace and landlocked salmon management.

Material and methods

Study area

Paasivesi is a 110 km^2, oligotrophic, mesohumic and deep (mean depth 21 m) lake (Fig. 2). It is described in more detail e.g. by Jurvelius *et al.* (1984) and Huovinen *et al.* (1992).

About 30 fish species are found in Paasivesi. Vendace, European whitefish (*Coregonus lavaretus*), smelt, and perch (*Perca fluviatilis*) are the most common species in the pelagic area of the lake (Auvinen & Jurvelius 1994).

Commercial trawling has taken place in Paasivesi since 1981. Vendace was the most abundant species caught until the late 1980s (Jurvelius 1991). During the 1990s weak year-classes caused a declining trend in the vendace catches and the proportion of whitefish and smelt has increased in trawl catches. The fishing activity of the trawlers has depended not only on the catches but also on the market price of vendace and whitefish. The maximum number of two-boat trawling units in the lake was five in the late 1980s. From 1992 to 1997 the number of trawl pairs was one or two because of the poor catches, and since 1998 commercial trawling has been forbidden from the breaking up of the ice until the end of July.

Overall description of the model

The energy consumption of an individual salmon on each day of the simulation was calculated with the bioenergetics model (Hanson *et al.* 1997). This figure was multiplied by the number of salmon present in Paasivesi to determine the total consumption of the population. Based on diet analyses, the consumption of fish food and invertebrate food for each day was calculated.

The share of 0+ vendace in the diet of landlocked salmon was affected by the size and the density of 0+ vendace on each day. The growth of 0+ vendace and thus the size of vendace on each day of the simulation was density-dependent. We used the type II functional response (Holling 1959) and a length suitability curve to assess how salmon would react to changes in vendace density and size in their feeding behavior. Mortality of 0+ vendace passing through the trawl cod end was calculated for each day.

By adding together the mortality caused by salmon predation and by trawling on each day of the simulation, the number of survivors to the next day was calculated. The simulations were run from mid June to October. The number of 0+ vendace that survived until the end of the simulation when different runs were compared was the main result.

Abundance of migrating salmon present in Paasivesi

A total of 22 270 Carlin-tagged two-year-old landlocked salmon in 50 groups were stocked in 1973–2000. On average 400 smolts were tagged per group and the average tag return rate was 7.7%. To take into account the effect of unreported and lost tags for survival estimates, we used the correction coefficient of 2.9 obtained

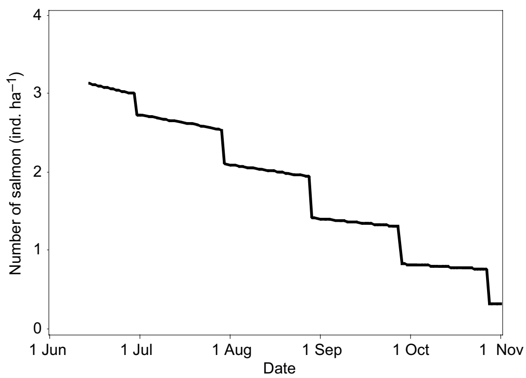

Fig. 4. Number of landlocked salmon in lake Paasivesi during their first growing season after stocking.

for brown trout (*Salmo trutta*) in the same water system (Kolari *et al.* 1998). Hence the true recovery rate of salmon would be about 20%. We assumed that an initial mortality of 80% takes place soon after stocking. We also estimated that 10% of the survivors would stop migrating or die during the 50 km journey from the river mouth to Paasivesi. Annually about 100 000 landlocked salmon smolts are stocked into the rivermouth of the Pielisjoki and thus the number of salmon smolts reaching the lake would be 18 000.

The migration pattern used in the model (Fig. 4) was based on tag recoveries. Salmon smolts were caught in Paasivesi as early as in the beginning of June, the mean date of returns in the first year was mid-September, and the latest tag returns came in late December. This pattern did not change much from year to year.

Salmon sampling and diet analysis

To study the diet of landlocked salmon, a total of 136 salmon were sampled in 1990–1992 by trawls and long lines. The total length (TL, mm) and weight (g) of each fish was measured. The stomachs were stored in ethanol until analyzed. If possible, prey fish were determined up to species level, and invertebrate prey were grouped together. Each species or group was weighed to the nearest 0.01 g wet weight. For model simulations, the diet was divided into the categories of fish prey and invertebrate prey and the importance of these categories in the diet was expressed as a mean share of the stomach

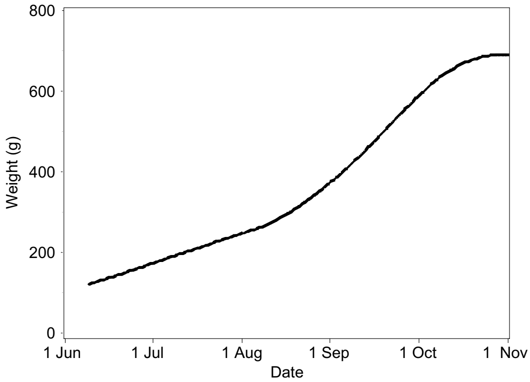

Fig. 5. Growth rate of landlocked salmon in lake Paasivesi during their first growing season after stocking.

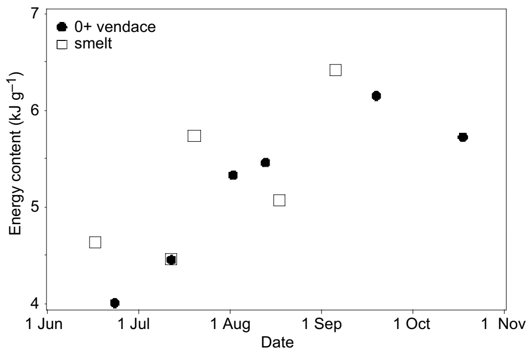

Fig. 6. Energy content of smelt and 0+ vendace during summer (data from O. Heikinheimo *et al.* unpubl. data).

contents. This was expressed monthly as a percent of total biomass in the sample for 2-year-old salmon. Unfortunately, no landlocked salmon were sampled from Paasivesi during periods of dense vendace stocks.

The ages of the salmon were determined from the scales of 68 fish. If a fish was not aged, it was included in age group 2 if it was shorter than 40 cm, which is the size landlocked salmon attain during the first growing season as determined from Carlin-tag recoveries. Hence, the diet material consisted of 107 two-year-old salmon, their mean weight being 186 g (S.D. = 123) and mean length 265 mm (S.D = 44). Food was found in the stomachs of 102 fish.

Bioenergetics modelling

We used the Wisconsin bioenergetics model 3 (Hanson *et al.* 1997) developed by Stewart *et al.* (1983) for lake trout (*Salvelinus namaycush*) to estimate the average individual daily consumption (grammes per day). We applied the parameters for salmonines (*Oncorhynchus* spp.) obtained from the study by Stewart and Ibarra (1991) and revised for brown trout by Vehanen *et al.* (1998). The parameter set for brown trout was used for landlocked salmon because of the similar ecology and life history of these species. The growth rate of both species is highly variable and dependent on the density of vendace stocks. The bioenergetics model was run for six and a half months, from mid-June to December. According to tag recoveries, salmon feed at this time in Paasivesi.

Information on landlocked salmon growth was derived from Carlin-tag recoveries of salmon stocked in the Pielisjoki. Mean lengths of salmon recovered within the first year after stocking (N = 1069) were calculated monthly. The average weight of salmon in each month (Fig. 5) was calculated with length-weight regression estimated from the data of test fishing.

Energy contents of 0+ vendace and smelt were obtained from samples from Ontojärvi (O. Heikinheimo *et al.* unpubl. data). The change in the energy contents during the growing season (Fig. 6) was taken into account in the bioenergetics calculations. Brown trout energy contents (Elliot 1976) were used for landlocked salmon predator energy contents.

The water temperature data used in the bioenergetics model was obtained from the Pielisjoki measuring station. Temperature data were averaged daily for the years 1979–1987.

Vendace larvae abundance in the beginning of the summer

The number of newly hatched vendace larvae varied between five and 50 million i.e. 500 to 5000 larvae ha^{-1} in Paasivesi during 1989–2001 (Fig. 7). We used these numbers and a four times higher number of 200 million (20 000 ha^{-1}) to simulate the spawning stock, this being much higher than the one at the moment. During the first three weeks after hatching, approximately two thirds of vendace larvae die in Paasivesi

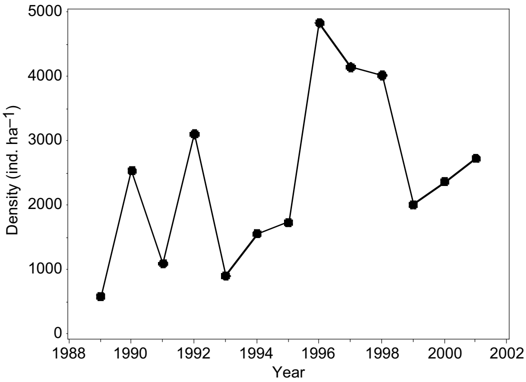

Fig. 7. Density of vendace larvae after hatching in lake Paasivesi in 1989–2001 (data from Karjalainen *et al.* 2000, J. Karjalainen unpubl.).

(Karjalainen *et al.* 2000). This mortality was used to estimate the number of three-week-old, approximately 20 mm long, vendace larvae in the middle of June, when the simulations were started.

Density dependent growth rate of 0+ vendace

Growth of 0+ vendace depends in most populations studied on the density of the year class (Karjalainen 1992, Helminen *et al.* 1993, Auvinen 1994, Auvinen & Jurvelius 1994). We used a growth model where the daily increment in length depended on the number of 0+ vendace present in the population. The growth was uniform for all individuals in the population. The length of vendace after the first growing season calculated with this model (Fig. 8a) was similar to that found in Paasivesi (Auvinen & Jurvelius 1994). The weight of vendace (Fig. 8b) depended on length, and it was calculated separately for vendace up to 45 mm in length (W_1 data from Karjalainen (1992) and H. Auvinen unpubl.) and above 45 mm (W_2, H. Auvinen unpubl.) with Eqs. 1 and 2, respectively:

$$W_1 = (3.18L^{3.67}) \times 10^{-7} \quad (1)$$
$$W_2 = (9.9L^{3.39}) \times 10^{-7}, \quad (2)$$

where W is the weight in g and L is the length in mm.

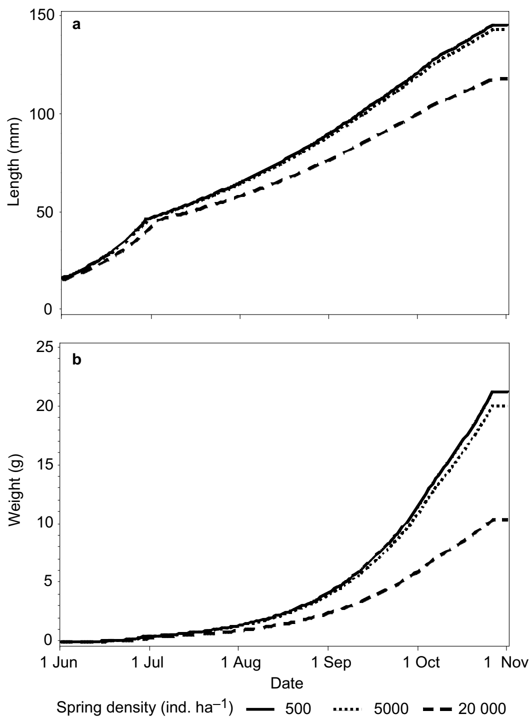

Fig. 8. The growth pattern of 0+ vendace with three different spring densities and with present salmon stocking and one trawl pair. — **a**: growth in length. — **b**: growth in weight.

Mortality of vendace larvae when passing through the cod end of trawls

Suuronen *et al.* (1995) studied the mortality of 0+ vendace when passing through the cod-end of trawls. Survival of escapees was related to e.g. season and time of day. Their results were used to estimate the mortality of 0+ vendace caused by trawls during the trawl fishing season in Paasivesi. They found that average mortality rates of fish in the morning, afternoon and evening hauls (30%–40%) were significantly lower than those during the dark hours (70%–80%). Trawlers in the study area usually operate from late afternoon to sunset. We used therefore mortality values that were ca. 25% lower than the mean values in Suuronen *et al.* (1995) (Fig. 9).

We assumed that 0+ vendace were evenly distributed to the upper layers of the 5500 ha deep area of the lake and thus vulnerable to trawling operations. The number of 0+ vendace going through the trawl cod-end was calculated

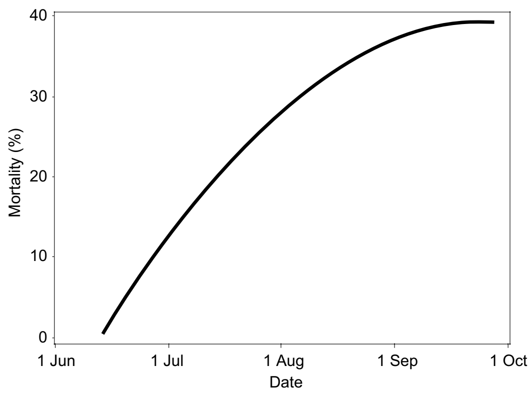

Fig. 9. Mortality of 0+ vendace passing through the cod end of a trawl. Estimated values for trawl hauls between afternoon and sunset. Original data from Suuronen *et al.* (1995).

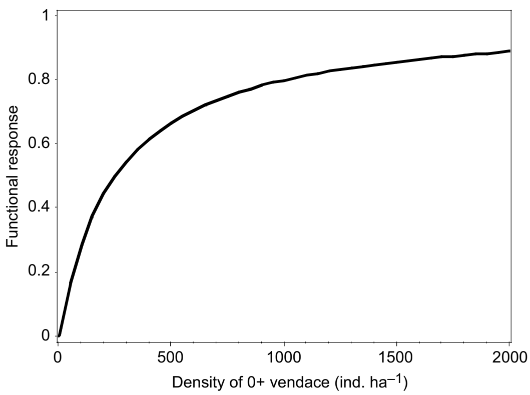

Fig. 10. Functional response of landlocked salmon on 0+ vendace density, with the maximum consumption scaled to 1.

on the basis of average vendace density and trawling area for each day. The area swept by a trawl per hour was estimated to 35 ha and the number of trawling hours per trawler was set at four hours on five days a week.

Vendace as salmon food

The amount of fish prey consumed by the landlocked salmon population on each day calculated by the bioenergetics model was used as the starting point when estimating the predation mortality of 0+ vendace. Vendace is a dominant species in the diet of landlocked salmon during a dense vendace population (Koivurinta *et al.* 2000).

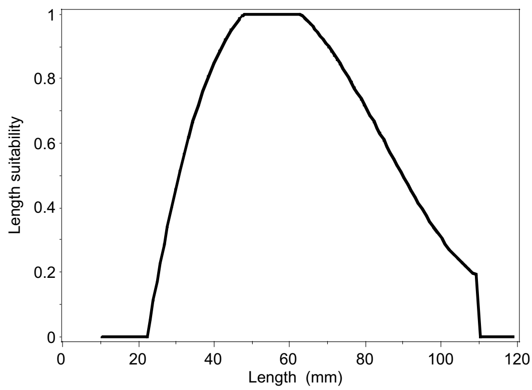

Fig. 11. Length suitability of 0+ vendace as salmon food.

The share of vendace in the diet was assumed to be affected by the density (functional response) and size of 0+ vendace (length suitability) on each day. The effect of the density of 0+ vendace on the predation of salmon on 0+ vendace was estimated with a type II functional response equation (Fig. 10; Holling 1959). A curve for the suitability for 0+ vendace as salmon food (S) was drawn by hand based on the data by Hyvärinen *et al.* (2000), which are consistent with the observations of brown trout in Puruvesi (I. Kolari unpubl. data) (Fig. 11).

The number of 0+ vendace eaten by the salmon population on each day was calculated with the equation:

$$T_i = N_i S_i M_i / (N_i + D) W_i \quad (3)$$

where T_i is the number of 0+ vendace eaten by the salmon population on day i, N_i is the number of 0+ vendace per hectare on day i, S_i is the length suitability value for day i, M_i is the mass of fish food eaten by the salmon population on day i (from the bioenergetics model), D is the half saturation constant or the number of 0+ vendace per hectare when the consumption is half the maximum, and W_i is the mass of a 0+ vendace on day i. We used $D = 250$ adopted from Heikinheimo *et al.* (2002). The value of S varied between 0 and 1. If the length of 0+ vendace reached 110 mm then S was set to 0. An example of a combined effect of the functional response and length suitability on salmon food selection is shown in Fig. 12.

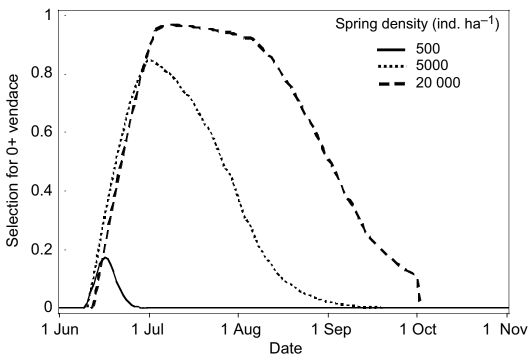

Fig. 12. Combined effect of 0+ vendace density and length on selection of vendace as fish food of landlocked salmon with present salmon stocking, one trawl pair and three spring densities of vendace larvae and the maximum consumption scaled to 1.

To test the sensitivity of the model, runs with functional response types II and III and half saturation rates ranging from 150 to 750 were performed. Also runs with two alternative values for the length suitability with values of 25% lower and higher than that in Fig. 11 were made. The equation for functional response type III was:

$$T_i = N_i^2 S_i M_i / (N_i^2 + D^2) W_i \quad (4)$$

with the same symbols for variables as in Eq. 3.

Results

The two-year-old landlocked salmon in Paasivesi already fed on fish in June, a couple of weeks after stocking. In June, fish prey accounted for half of the stomach contents, the rest being invertebrates (Fig. 13). Coregonidae, which could not be identified as separate species, represented the largest fraction of fish prey. In June, salmon ate some vendace, even when vendace stocks were sparse. Towards the end of the summer, the proportion of invertebrates declined and vendace disappeared. In August–October, landlocked salmon ate almost solely smelt, since vendace stock was low. The model predicted similar results. During its first year in the lake, in June–December, the food consumption of a two-year-old landlocked salmon was 2.2 kg, of which 1.9 kg was fish.

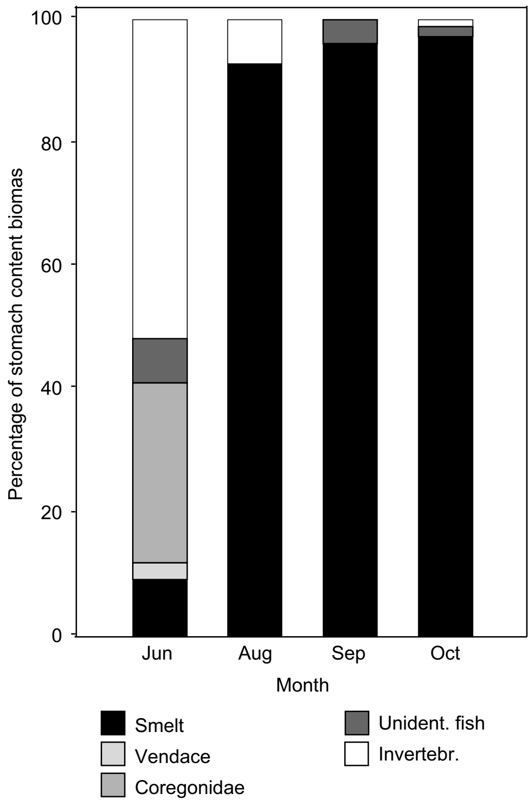

Fig. 13. The composition of two-year-old landlocked salmon diet in lake Paasivesi during 1990–1992.

The 0+ vendace mortality model simulations showed that with the lowest observed vendace larvae density in 1989–1997, about 500 larvae ha^{-1} in spring, predation by salmon can alone cause a drop to zero density in a few days (Fig. 14a). Even if the number of stocked salmon was only 25% of the present, the autumn density of vendace would not exceed 100 fish ha^{-1} even without trawl fishery. The same survival rate of larvae would be attained with intermediate trawling effort and no stockings (Fig. 15a).

At a density of 2500 larvae ha^{-1} in spring, a satisfactory level vendace recruitment to fishery (500 ha^{-1} in autumn) cannot take place with present stocking numbers of landlocked salmon (Fig. 15b). With half of the present stockings this goal could be reached, however, without any trawling.

At the highest densities observed in 1989–1997, i.e. 5000 larvae ha^{-1} in spring, a sufficient number of vendace can be recruited to fishery

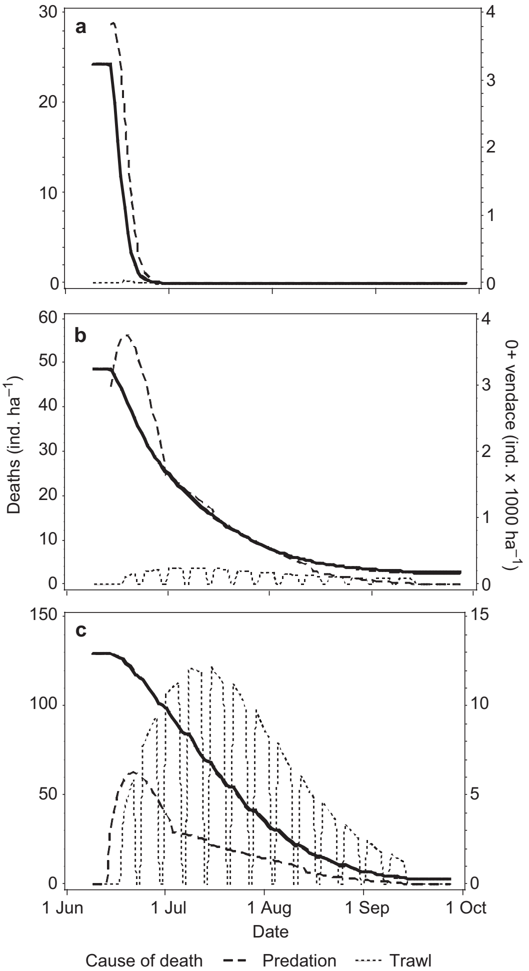

Fig. 14. Density of 0+ vendace (solid line) during the growing season and causes of death (dotted lines). — **a**: spring density of 500 ha^{-1}; — **b**: 5000 ha^{-1}; — **c**: 20 000 ha^{-1}.

with the present stocking numbers of landlocked salmon, and a low trawling effort. The year-class can still be depleted with an intermediate trawling effort (Fig. 15c). At this springtime density, predation is still the most common reason for mortality (Fig. 14b).

With high larval densities, i.e. 20 000 larvae ha^{-1} in spring, only an extremely high trawling effort can deplete the year class (Figs. 14c and 15d).

The use of functional response type III instead of type II did not cause a drastic change in the survival rate of 0+ vendace. With the low initial number of vendace in spring, the type II functional response resulted in no survivors but the type III response saved 11 vendace. With medium spring density, the number of survivors was 182 and 102, respectively. With the high spring density, the number of survivors was the same for both functional response types.

The half saturation constant in the functional response equations was given values from 150 to 750 individuals per hectare. This had a clear effect on the number of survivors in the cases of low (500 0+ vendace ha^{-1}) and medium (5000 0+ vendace ha^{-1}) initial numbers of 0+ vendace. Especially with the low initial density of vendace, high half saturation rate values with functional response type III resulted in higher survival, e.g. with the half saturation constant of 550 about 45 vendace would survive until winter.

The length selection factor was given values 25% above and below the one used in the model runs. With low initial density (500 larvae ha^{-1}) all length selection values resulted in 0 survivors. In the medium initial density (5000 larvae ha^{-1}) the differences were the greatest; from 212 survivors to 895 survivors. In the high initial density the values ranged from 7200 to 8600.

Discussion

Our results suggest that the predation by landlocked salmon stocked in the water system is a significant contributor to the mortality of 0+ vendace in Paasivesi. The 100 000 salmon stocked annually in the Pielisjoki equals the estimated number of natural smolt production (Kaukoranta *et al.* 2000). This number is also required to ensure a sufficient number of spawners (25–50 mating couples) for the founder population of a new brood stock generation according to the principles adopted for maintaining genetic diversity in a fish stock. According to the tagging data only 0.04% of released fish reach maturity and migrate back to the stocking area (Pursiainen *et al.* 1998). The genetic point of view supports the large annual stockings of landlocked salmon; however, this principle sometimes conflicts with the interests of commercial fishery.

Concern about the effects of large stocking of salmonid predatory fish on prey fish populations have been expressed in the Great Lakes (Jones

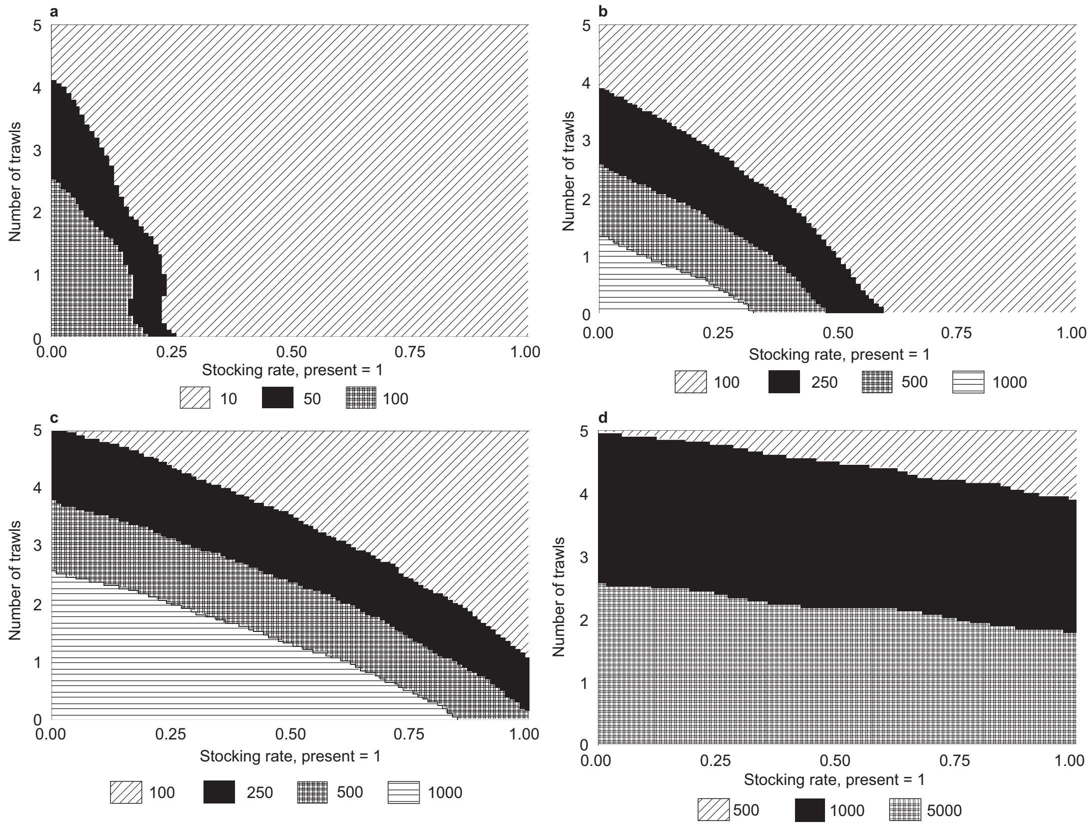

Fig. 15. Resulting density of 0+ vendace in autumn with varying number of trawls and stocking rate with varying spring densities of vendace larvae. — **a**: spring density of 500 ha^{-1}; — **b**: 2500 ha^{-1}; — **c**: 5000 ha^{-1}; — **d**: 20 000 ha^{-1}.

et al. 1993, Kitchell *et al.* 1994, Rand & Stewart 1998). In some Finnish lakes brown trout have been assumed to be involved in maintaining prolonged low-density periods in vendace stocks (Helminen *et al.* 1997, Valkeajärvi *et al.* 1997, Vehanen *et al.* 1998). The mean stocking density of brown trout in these lakes (0.5–1 smolt ha^{-1}) is, however, much lower than the density of landlocked salmon (3.3 smolts ha^{-1}) entering Paasivesi every year. Predator abundance commonly accounts for much of the uncertainty related to population-level predation estimates (Beauchamp *et al.* 1995, Hartman & Brandt 1995, Cartwright *et al.* 1998). Salmon migration through Paasivesi could be more rapid than we expected, especially during a period of low vendace density. However, only a few days were needed to deplete the whole vendace year-class if the spring density of prey was low.

In Paasivesi smelt was the most important prey species for landlocked salmon in the beginning of the 1990s, when vendace stock was sparse. Landlocked salmon were observed to have fed on vendace only in the beginning of the growing season. We did not have any data on the feeding of two-year-old salmon from a period of high vendace density in Paasivesi. The type II functional response (Holling 1959) was assumed in our model. This type of dependence is plausible because salmon was observed to select vendace even during periods of very low vendace density. Landlocked salmon is more confined to pelagic vendace than brown trout and obviously due to habitat preferences of both prey and predator species, salmon is known to prefer vendace to smelt as prey and feed almost solely on vendace if it is possible (Svärdson *et al.* 1988, Hyvärinen *et al.* 2000, Koivurinta *et al.* 2000). The energy content of smelt is no lower than that of vendace. Shifting from vendace to smelt could result in foraging in inappropriate light or temperature conditions, making foraging less efficient than when salmon forage for vendace. Smelt and vendace are spatially segregated and, for example, show different vertical migrations in lakes (Jurvelius 1991).

The growth rate of landlocked salmon has been observed to be dependent on the population size of vendace (Koivurinta *et al*. 2000). A two-year-old landlocked salmon smolt attained on average a length of 41 cm and a weight of 700 g during the first growing season in Paasivesi. In lake Puula, central Finland, introduced landlocked salmon grew much faster and attained a size of 1.5 kg and 50 cm in the first summer, when the vendace stock was dense. During the same period in lake Päijänne, central Finland, where the vendace stock was low, the growth rate of introduced landlocked salmon was much slower, and landlocked salmon were only 300 g in weight and 31 cm in length at the end of their first summer in the lake (Koivurinta *et al*. 2000). However, we could not find any difference in the growth of tagged salmon living in periods of varying vendace stock densities in 1979–1996, and we used food consumption based on the average growth rate as the maximum consumption level.

The sensitivity tests revealed that the functional response type III with low initial vendace density would result in a higher number of survivors than in model runs with type II functional response. The uncertainty of the real response type is, however, not crucial for the conclusions.

According to hydro-acoustic studies, the density (fish ha^{-1}) of adult vendace is greatest in the south-west part of Paasivesi (Jurvelius & Marjomäki 2001). Commercial trawling is concentrated almost totally in this area. There is no reason why predatory salmon should not live in the same area. Exploratory trawling has shown that 0+ vendace live mostly in the uppermost 10 m depth layer (Jurvelius 1991). Hauling of commercial trawling takes place in the uppermost 15 m, and young salmon are known to live in the surface layer of the water column. In the experimental trawling in 1990–1992 the number of salmon caught in the surface hauls in Paasivesi varied between 0.4 and 2.6 fish ha^{-1} (J. Jurvelius unpubl. data). The spatial compatibility of salmon predation and trawling is good. In this respect there is no incongruity in comparing predation and trawling.

Hydro-acoustic studies have shown that the distribution of vendace is patchy i.e. they live in schools in Paasivesi (Jurvelius & Auvinen 1989, Jurvelius & Marjomäki 2001). Schooling is known to provide protection against predation. Hence we can suppose that the energy cost of a salmon predator is larger while vendace are patchily distributed than evenly distributed. This might cause an under-estimation of the influence of salmon predation. On the other hand, trawling and salmon predation are known to break up vendace schools (A. Pesonen pers. comm.). Hence the effect of vendace schooling on the predation of salmon and trawl fishing is not exactly known.

In addition to landlocked salmon an average of 3000 brown trout are stocked annually in Paasivesi. Neither their predation on vendace nor the possible predation by perch (Auvinen 1994, Helminen & Sarvala 1994, Huusko *et al*. 1996, Jaatinen *et al*. 1999, Heikinheimo 2001), whitefish (Salojärvi 1991), pike-perch (*Stizostedion lucioperca*) (Vehanen *et al*. 1998) and smelt (Sterligova *et al*. 1988) were taken into account in the 0+ vendace mortality model.

The trawling-induced escape mortality of 0+ vendace is one of the most widely discussed topics in lake fisheries management in Finland. In many cases trawling has been seen as the only threat to the vendace population in lakes (Salmi *et al*. 2000). However, our study shows that predation by stocked salmon can be a serious factor in the prevention of the recovery of vendace stocks after periods of low recruitment.

The vendace spawning population biomass directly affects the number of hatching larvae (Viljanen 1988, Karjalainen *et al*. 2000). According to the model calculations, the initial number of hatching larvae greatly affects the development of the density of the cohort. However, a dome-shaped stock-recruitment curve has been suggested for vendace lake populations (Valtonen & Marjomäki 1988, Auvinen 1994). Therefore the spawning stock should preferably be kept at an intermediate level rather than increased to an extremely high level. Vendace shows clear density-dependency in its population dynamics (e.g. Hamrin & Persson 1986), and periods of low recruitment may be started with a couple of year-class failures caused by intra-specific factors preventing the onset of new strong year-classes (Auvinen 1994).

It is obvious that a strong vendace stock is beneficial for the growth and survival of landlocked salmon entering the lakes either naturally or by stocking (Koivurinta *et al*. 2000). Therefore also for the benefit of the landlocked salmon stocking program, stocking practices for salmon could be further developed. If the vendace stocks in the lakes situated near the stocking place in the Pielisjoki are low in density, a period of lower stocking numbers should be considered. It is highly likely that in natural conditions the number of landlocked salmon smolts varies considerably each year, as do, for example, Baltic salmon smolts (Lindroth 1965).

In fisheries management the maintenance of the endangered landlocked salmon in the water system is considered highly important by the fisheries authorities. Thus our first suggestion is that the vendace fishing effort should be reduced for a couple of years in this lake. If this does not increase the recruitment of vendace, also the number of stocked salmon could be considered. When both of these restrictions are in effect at the same time, the conditions for good vendace survival should be met. A recovery of the vendace stock should favour both fisheries and landlocked salmon enhancement.

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