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# Relations between diet, growth, visceral lipid content and yield of the stocked brown trout in three small lakes in northern Finland

Teuvo Niva

*Niva, T., University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 Jyväskylä, Finland; and Finnish Game and Fisheries Research Institute, Taivalkoski Game and Fisheries Research, Ohtaoja, FIN-93400 Taivalkoski, Finland*

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Diet, growth, visceral fat accumulation and a consecutive yield of the stocked brown trout (*Salmo trutta* L.) (four age groups, initial weight range 29–373 g) were studied in three small Finnish lakes in 1991–1996. The average growth rate and visceral lipid content were significantly greater in lakes and years when the trout fed mainly on small fish, such as vendace (*Coregonus albula* L.), ninespine stickleback (*Pungitius pungitius* L.) and one-summer-old perch (*Perca fluviatilis* L.) than their insectivorous conspecifics. The stocked trout initially foraging unpreferred food items shifted rapidly to feed on small fish when their stocks became abundant. Piscivorous trout increased their visceral lipids prior to winter whereas in insectivorous fish these decreased gradually during the growth season which probably caused increased overwinter mortality. Therefore, relative yields were significantly higher for piscivorous than insectivorous trout. On the other hand, the largest trout at release showed the poorest performance irrespective of the quality of the foraging environment.

## 1. Introduction

Natural reproduction of the Finnish sea-run stocks of the brown trout (*Salmo trutta* L.) collapsed mainly due to river damming in the 1950s. The freshwater resident stocks have decreased more slowly, and this decline has been caused by several human activities such as river channelization, and overfishing (Huusko & Yrjänä 1996, Vehanen 1998). Today, the only indigenous wild stocks of the brown trout which have retained their vitality exist in the Koutajoki river system, northeastern Finland (Huusko *et al.* 1990). Culturing and releasing smolt-sized trout into lakes have been the main tool for stock management of the brown trout in Finland during the last three decades. In the 1990s, approximately one million 2- or 3-year-old brown trout have been annually stocked into Finnish freshwaters.

As in Finland, degradation of the environment and intensified fishery have reduced wild salmonid stocks all over the world (Mills 1989, Cowx 1994). Consequently, artificial breeding and stocking activities for mitigation of salmonids have increased enormously, followed by numerous studies on the ecology of stocked fish in a new natural environment. Only few studies, however, have been designed so as to empirically assess the relative influences of several simultaneously operating factors affecting growth and survival of stocked salmonids. In a seminal paper, Bilton *et al.* (1982) suggested the existence of "optimum release windows" that provide optimal conditions for post-smolts to survive through an abundance of forage organisms present in the sea. More recently, optimal size and time for smolt release have been suggested to be stock specific (Labelle *et al.* 1996), relative to pre-smolt growth rate (Bohlin *et al.* 1993), and that they may vary annually (Mathews & Ishida, 1989). Moreover, imprinting and accurate homing of hatchery released juvenile salmon have been suggested to be determined by their endocrinological state (e.g., parr-smolt transformation) at the time of release (Quinn 1993). Several authors have suggested that considerable interannual variation in the environment (food supply, predation etc.) affects the growth and survival of stocked salmonids more than variation in hatchery-related factors (Fisher & Pearcy 1987, Green & Macdonald 1987, Gunn *et al.* 1987, O'Gorman *et al.* 1987, Holtby *et al.* 1990, Brodeur *et al.* 1992, Unwin 1997). In Finland, high yields of stocked brown trout have been caught in lakes with proportionally high yields of vendace (*Coregonus albula* (L.)) (Vehanen 1995, Vehanen & Aspi 1996). As vendace is a common prey for the brown trout (Järvi 1915, Lind 1978), these results suggest that food supply may control the stocking success of the brown trout, but the mechanism by which the food supply affects the consecutive yield remains unsolved.

Energy allocation between maintenance, growth and storage lipids may be the most important life history response of juvenile salmonids to their seasonal environment (Gardiner & Geddes 1980, Higgins & Talbot 1985, Cunjak 1988, Heggenes & Saltveit 1989, Riehle & Griffith 1993, Bull & Metcalfe 1997, Berg & Bremset 1998, *see* also Jokela 1997). Storage lipids may be used for feeding activities during the growth season, but they are usually maximized at the onset of winter. Storage lipids are mobilized during the winter, and overwinter survival of the fish is tightly dependent on the ability of fish to regulate energy reserves prior to winter (Bull *et al.* 1996). Combination of low growth rate and decreasing storage lipids imply a period of negative energy balance, which is likely to result in an increased overwinter mortality, certainly resulting in a decreased yield. Consequently, the aim of the present study was to estimate the quantitative effects of interannual variation in the diet (reflecting the food supply) on growth, fat accumulation and yield of the stocked brown trout. The study was conducted as a field experiment, designed so that sources of variation from genetics and hatchery treatment were kept minimal for trout at release. In addition, the lakes chosen for the study were similar in respect to area, mean depth, water quality, resident fish species composition, fishing practice and stocking rate. Four age groups of brown trout were used in the experiment to study size-mediated effects on predator–prey interaction between the brown trout and its prey fish species (Olson 1996). Variation in the food supply, particularly in vendace stocks (Salojärvi 1987, Viljanen 1988, Sandlund *et al.* 1991, Helminen *et al.* 1993), may be considerable across lakes and years, and therefore, the experiment was executed in three lakes and over five years.

## 2. Materials and methods

### 2.1. Fish material and tagging

All fish used in the study were grand offspring of wild parents belonging to a migratory strain of the brown trout found above the Jyrävä falls in Kitkajoki, the tributary of Koutajoki, a river in northeastern Finland (*see* review by Huusko *et al.* 1990). Throughout the text, the age of brown trout is determined and abbreviated as follows: brown trout are born in late spring, and the fish of a particular cohort are called one summer old (1-S-O) during their first growth season, one year old (1-Y-O) during the following spring before their second growth season, etc. The F2-cohorts, including approximately 20 000 of 2-Y-O fish each, were cultured under natural photoperiod (66°N, 29°E) at the hatchery of the Finnish Game and Fisheries Research Institute in Kuusamo prior to tagging. During the growth season, commercial food pellets were supplied continuously with automatic feeders during daylight hours.

Any trout with anomalies in developmental features or serious tissue damage were excluded from tagging. Four age groups (weight range 29–373 g) of juvenile trout were identified either by binary coded wire (CW) or visible implant (VI) tags (Northwest Marine Technology, Inc., Shaw Island, Washington 98286, USA) in 1991–1995. Schedule for tagging was determined by the experimental protocol presented in Appendix 1. Because the CW tags are batch coded, length of 100–150 fish were measured first, and then only the fish within one standard deviation of the mean length were tagged. The VI tags were individually coded and therefore size-sorting was not needed. On average, each group of tagged fish was kept in a separate tank for 63 days (range 32–111 d) before inspection of the tags. At inspection, individual length (mm) and weight (g) of the fish with readable VI tags were measured (*see* Niva 1995). All the CW tagged fish were inspected individually for tag retention, which was always > 95%. During the inspection, length (mm) and weight (g) of 150–200 randomly selected fish from each CW tagged group were measured to calculate mean length and weight at release.

The number of tagged fish was proportional to the area of each experimental lake, according to the age group. Stocking densities were 2.01 (S.D. = 0.10) fish per hectare for 2-Y-O and 3-S-O fish, and 1.03 (S.D. = 0.12) fish per hectare for 3-Y-O and 4-S-O fish. The 2-Y-O and 3-Y-O fish were released between 2 and 18 June, and the 3-S-O and 4-S-O fish between 29 September and 20 October.

## 2.2. Stocked lakes and sampling of trout

The fish were released into the lakes located near the hatchery ca. one week after inspection. The lakes Kylmäluoma (KYL), Iso-Porontima (IPO) and Ylioudonjärvi (YLI) were chosen because they well represent northern Finnish lake environments typically inhabited by this stock of brown trout (Table 1). All the lakes are situated at the uppermost part of their respective watercourses, i.e. the fish could migrate only downstream. At KYL, there was a fish farm at the river outlet, which excluded migration of the stocked trout. The lakes were thermally stratified in summer and winter, and ice-covered from late October to late May.

Five local fishermen on each lake were equipped with measuring instruments and trained to measure and store samples of the trout they caught. A total of 1 532 tagged fish (6% of the released fish) were caught between 1991 and 1996 (*see* Appendix 1). Weight (g) and length (mm) of each fish were measured, and the date of capture was recorded. In addition, head and viscera of the fish caught were stored at –18°C until analyzed. Almost all fish (95%) were caught with gill nets which were usually set in the evening and examined and emptied in the following morning. There were no breaks in sampling because the sample collectors fished throughout the year. Only in late May and late October was fishing terminated for a short time due to a weak ice cover. The mesh size used was recorded for 1 075 trout. To control for gill net selectivity, I analyzed fish size variation between different mesh sizes. Sample proportions (%) were calculated for different mesh sizes, according to the lake.

## 2.3. Laboratory measurements

The tag was recovered from the head, and all food items from inside the mouth, esophagus and stomach were removed in the laboratory. Food items were identified to species (fish) and family (invertebrates), and each taxonomic group was weighed to the nearest 0.01 g (wet weight), and the number of prey fish was counted by species. The average weight of prey fish was calculated within stomachs.

**Table 1.** Physical and chemical characteristics of the three study lakes (KYL = Kylmäluoma, IPO = Iso-Porontima, YLI = Ylioudonjärvi) in 1991–1996. Temperature and oxygen content were measured annually from 15, 10, 5 and 1 meter depth (also range order) during late March or early April (winter) and during late July or early August (summer). The ranges of pH and total phosphorus were from corresponding summer measurements at 1 meter depth.

| | KYL | IPO | YLI |
|---|---|---|---|
| Area, $km^2$ | 3.73 | 3.45 | 2.32 |
| Mean (max.) depth, m | 9.0 (27) | 9.5 (41) | 7.0 (19) |
| Shore type | Sand | Gravel | Gravel |
| pH | 6.5–7.1 | 6.8–7.4 | 6.3–7.1 |
| Tot.P, $\mu g\ l^{-1}$ | 7–10 | 6–12 | 7–10 |
| T, °C, summer | 7.3–15.5 | 7.5–14.5 | 7.7–15.7 |
| T, °C, winter | 3.6–0.9 | 2.7–0.4 | 3.4–1.0 |
| $O_2$, mg $l^{-1}$, summer | 9.4–9.8 | 9.6–10.2 | 6.7–9.9 |
| $O_2$, mg $l^{-1}$, winter | 8.6–12.0 | 8.2–12.0 | 4.2–12.2 |

The weight of prey fish and invertebrates in the stomach was expressed as a percentage of the overall weight of the stomach contents (prey item weight/total weight of a stomach contents) (Hyslop 1980).

Next, the viscera (minus food and genitals) were homogenized and dried at 110°C overnight. The lipids were extracted and purified with a mixture of chloroform and methanol (2:1) (Blight & Dyer 1959). The total lipid content was analyzed with the colorimetric sulpho-phospho-vanillin method (Frings & Dunn 1970). The coefficient of variation of the colorimetric method was 6.5%, comparable to 3.5% or 6.0% reported by Frings and Dunn (1970) and Barnes and Blackstock (1973), respectively. Individual fat reserves were expressed as a percentage of dry weight to control for variation in body size (Bull & Metcalfe 1997).

## 2.4. Data analysis

Annual mean percentages of the most important prey items (vendace, perch, ninespine stickleback, unidentifiable fish, and invertebrates) were calculated for each age group and lake. Prey percentages were analyzed mainly qualitatively because estimating growth from food consumption quantitatively has been found equivocal in field studies (Hewett & Johnson 1992 and references therein).

The present data consisted of 1 532 recaptured fish from 50 tagging groups. Of these, 897 fish from 48 groups were caught during their first, 101 fish from 28 groups were caught during their second and 20 fish from five tagging groups were caught during their third growing season. Therefore, I focused the following analysis only on the two first growing seasons.

Interannual, within-season, lake- and age-specific variation in the growth rate and visceral lipid content of the trout were analyzed with the analysis of variance (ANOVA). Only fish caught during their first growing season were selected for the analysis. As the trout released in June grew until December, only fish that were caught from July to December were selected. As the trout released in fall (October) started their growth during the next summer (according to data set of 408 fish that were caught during their first winter and spring), only the trout caught from the next July to December (i.e. approximately 9–13 months after release) were selected. The remaining data set ($n = 897$) was strongly unbalanced due to a high number of observations from particular tagging groups in IPO. I randomly sampled a reduced data set (10%–50% of observations) from these groups. Finally, a total of 488 fish were selected for analysis. Growth rate of each fish was calculated using equation (Bagenal 1978):

$$\mathrm{SGR} = \frac{\ln W_{t1} - \ln W_{t0}}{t_1 - t_0} \tag{1}$$

where SGR is the specific growth rate (% day$^{-1}$), $W_{t0}$ and $W_{t1}$ are the body weight of the fish at the start (release) and the end of the growth period, respectively, and $t_1 - t_0$ is the length of that period in days. The growth rates for all the fish released in fall were calculated so that their first growth season was fixed to start on 1 June. An ANOVA model with four factors is complicated by multi-level interactions. Therefore, I analyzed each age group separately.

Absolute weight increase of the fish from growth season to another is a fundamental phenotypic life history characteristic of any given population of brown trout. In the present study, age-specific weight was measured both at the hatchery and lakes. Mean fish weights at the end of their first and second growing season were crosstabulated according to fish age at release (hatchery), stocked lake and fish age at recapture (Table 2).

## 2.5. Estimating relative yields

A relative yield (yield per thousand fish released) data are widely used to estimate overall stocking success of salmonids, and often mark-recovery data are used to estimate relative contributions of marked groups to the catch for a specific area and time (Bernard *et al.* 1998 and references therein). In the present study, each trout population living in a given lake and year was mixed with separate (up to 12 in KYL, 8 in IPO and 10 in YLI) groups identified by tags. I estimated the relative yield for each tagging group using a slightly modified version of a common approach discussed by Geiger (1990). First, data on annual total yields of the brown trout were gathered by sending catch questionnaires to households which had bought licenses to fish in the lakes. On average in 1991–1996, the numbers of households interviewed annually were 33 for KYL, 24 for YLI and 36 for IPO. Each inquiry was mailed up to three times to nonrespondents resulting in a high cumulative recovery rate (mean 87%, range 78%–98%). Second, assuming that the proportion of a particular tagging group in the annual sample (collected by the local fishermen) was random, the annual total yield (estimated from questionnaires) was partitioned according to the corresponding proportions of tagging groups present in the annual sample. These annual yield estimates of each tagging group were summed for the total yield estimate and related to thousand released fish, resulting in the gross relative yield (GRY, kg). If the stocked fish are caught soon after release due to high fishing pressure, it is self evident that increasing fish weight at release will increase GRY directly, resulting in an illusion of a 'high' relative yield. In the present study, between-age differences in fish weight at release were over five-fold, and 82% of the fish released in spring and 91% of the fish released in autumn were caught before their second growth season. To control for fish size at release, I also calculated the release-weight of the tagging group related to thousand fish (e.g., tagging groups with an average fish weight of 50 and 350 g weighed 50 and 350 kg at release, respectively). Then the release-weight of the tagging group was subtracted from the GRY, and this estimate is termed here the net relative yield (NRY, kg). Variation in the NRY were analyzed by analysis of variance with stocking lake and age of fish at release as factors. Values of GRY are presented in Appendix 1.

Annual total yields of other fish species were also estimated from the catch questionnaires described above, and the annual sum of fishing days were divided by the lake area to estimate the fishing effort.

## 3. Results

### 3.1. Fisheries and yields

Fishing efforts were on average 2.9 day ha$^{-1}$ for KYL, 3.0 for YLI and 3.1 for IPO (ANOVA, $F$ = 0.02, df = 2, $p$ = 0.33). They were 3.8–4.7 day ha$^{-1}$ during the open water months, and 1.5–1.9 day ha$^{-1}$ during the ice-covered months. Annual percentages of the gillnet catch of the total yield of the brown trout were always > 90. It is, hence, likely that a decrease in densities of the stocked brown trout caused by fisheries was approximately at the same level in all lakes. Of the trout samples, 72%–91% were caught with gill net mesh sizes between 31–50 mm (from knot to knot), and overlap in the trout size captured by different mesh sizes was considerable (Table 3).

Yields of different fish species varied considerably across the lakes and years (Fig. 1). A very high yield of vendace was caught in IPO in 1993. Also in YLI in 1991 and in IPO in 1992 the vendace yield was relatively high. The yields in KYL and IPO were strongly dominated by planktivorous species, whitefish (*Coregonus lavaretus*) and vendace. Their proportion of the total yields ranged from 71% to 93% in 1991–1996. In YLI, the proportion of these species in the total yield was 71% in 1991, and thereafter annually 62%, 64%, 29%, 14% and finally 4% in 1996. Decrease in the yield of whitefish and vendace in 1993–1996 in YLI coincided with increase in the yield of perch (*Perca fluviatilis* L.) and trout, particularly in 1995 (28%). On average, only 5.9% of the total yields were from stocks of pike (*Esox lucius* L.) and burbot (*Lota lota* L.), potential predators of the brown trout. It is noteworthy that 93% of the trout sampled were tagged, meaning that the proportion of resident population of brown trout in the lakes was negligible compared to stocked fish.

### 3.2. Diet of trout

Percentages of empty stomachs were 20 in KYL ($n$ = 438), 13 in YLI ($n$ = 263) and 16 in IPO ($n$ = 831). Excluding the empty stomachs, percentages

**Table 2.** Mean total weight (W, g) of juvenile brown trout at the hatchery and in the three study lakes (KYL, YLI and IPO) according to age of the fish (2-Y-O = two years old; 3-S-O = three summers old; etc.). Standard deviations (S.D.) of each mean weight represent interannual (not individual) variation calculated using annual mean weights of specific set of tagging groups (hatchery $n$ = 14–15; wild $n$ = 2–5). For example, for the 2-Y-O trout at release that were recaptured in IPO at the end of their first growing season, at the age of 3-S-O, S.D. of 25 g around the mean fish weight of 314 g were calculated using corresponding mean weights of individual fish of each tagging group stocked into IPO in 1991–1995. Table cells without observations are indicated with asterisk.

| | | Age at hatchery | | | |
|---|---|---|---|---|---|
| Age | Lake | 2-Y-O W (S.D.) 47 (12) | 3-S-O W (S.D.) 127 (16) | 3-Y-O W (S.D.) 146 (23) | 4-S-O W (S.D.) 305 (48) |
| 3-S-O | KYL | 162 (42) | | | |
| 3-S-O | YLI | 149 (35) | | | |
| 3-S-O | IPO | 314 (25) | | | |
| 4-S-O | KYL | 454 (139) | 483 (267) | 309 (53) | |
| 4-S-O | YLI | 554 (206) | 501 (154) | 347 (63) | |
| 4-S-O | IPO | 991 (334) | 785 (104) | 679 (59) | |
| 5-S-O | KYL | * | 615 (465) | 872 (496) | 605 (254) |
| 5-S-O | YLI | * | 903 (334) | 960 (255) | 715 (365) |
| 5-S-O | IPO | * | 2 350 (212) | 2 413 (265) | 843 (71) |

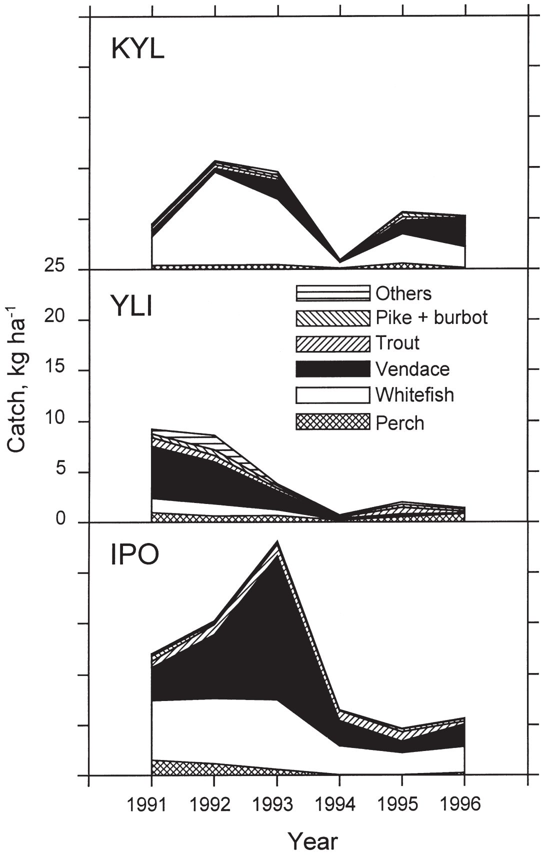


**Fig. 1.** Annual species-specific yields calculated as the total catch (kg) per area of the lake (ha) according to surveys. Category "Others" include mostly roach (*Rutilus rutilus* L.), bream (*Abramis brama* L.), and ruffe (*Gymnocephalus cernuus* L.).

of piscivorous trout were 23 in KYL, 52 in YLI and 91 in IPO. Correspondingly, percentages of trout that had fed on invertebrates were 87 in KYL, 62 in YLI and 22 in IPO, meaning that in all the lakes only a small proportion (10%–14%) of fish had a mixed diet.

In KYL during the whole study period, the stocked trout of all sizes fed mainly on invertebrates such as Trichoptera and Ephemeroptera larvae, and adult Hymenoptera (Fig. 2), probably due to low abundance of suitable-sized fish prey. However, the proportion of vendace and unidentified fish prey was > 50% in 1992 and 1996 for 3-S-O trout.

In YLI, invertebrate prey was dominant from 1991 to 1994, except in the 2-Y-O and 3-Y-O trout where the proportion of fish prey was > 60% in 1991 and 1992 (Fig. 2). Usually the maximum summer water temperature of the lakes studied was 15–17°C, but in summer 1995 it was 20°C. Probably due to this, a very strong year class of perch was born in YLI (but not in KYL and IPO). The trout fed heavily on the 1-S-O perch in 1995 and in winter 1996 in YLI (Fig. 2). The average weight of prey perch was 0.46 g at that time. It is noteworthy that 58 out of 77 fish captured in 1995 and 1996 in YLI were at their second or third growth season. These fish had been feeding on invertebrates earlier, in 1993 and 1994, but shifted to feed strongly on perch in 1995.

In IPO, a very strong year-class of vendace was born in 1991. The proportion of vendace in the diet of stocked brown trout was high in 1991 but thereafter decreased sharply, coinciding with an increase in the proportion of ninespine stickleback (*Pungitius pungitius* L.) in the diet (Fig. 2). The mean weight of vendace prey found in the stomachs of the trout was 1.2 g in 1991, 2.8 g in 1992, 4.2 g in 1993, 12.8 g in 1994 and 23.1 g in

**Table 3.** Proportion (%) of trout samples caught by different mesh sized gill nets in the three study lakes (on the left). Median and mean fish length and weight, their standard deviation and the average fish length and weight at 10 and 90% percentiles, and the number of trout (on the right).

| Mesh size (mm) | Lake | | | Fish length (weight) at capture, mm (g) | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | KYL | YLI | IPO | Median | Mean | S.D. | P10% | P90% | *N* |
| < 20 | 12 | 1 | 0 | 283 (219) | 295 (277) | 55 (200) | 242 (132) | 370 (512) | 51 |
| 21–30 | 15 | 0 | 0 | 294 (244) | 289 (257) | 41 (126) | 230 (131) | 334 (375) | 66 |
| 31–40 | 68 | 2 | 64 | 311 (315) | 316 (357) | 46 (177) | 260 (189) | 370 (550) | 575 |
| 41–50 | 4 | 70 | 27 | 345 (419) | 343 (473) | 60 (272) | 268 (195) | 410 (769) | 281 |
| > 51 | 1 | 27 | 9 | 410 (815) | 412 (912) | 84 (563) | 307 (278) | 516 (1615) | 102 |

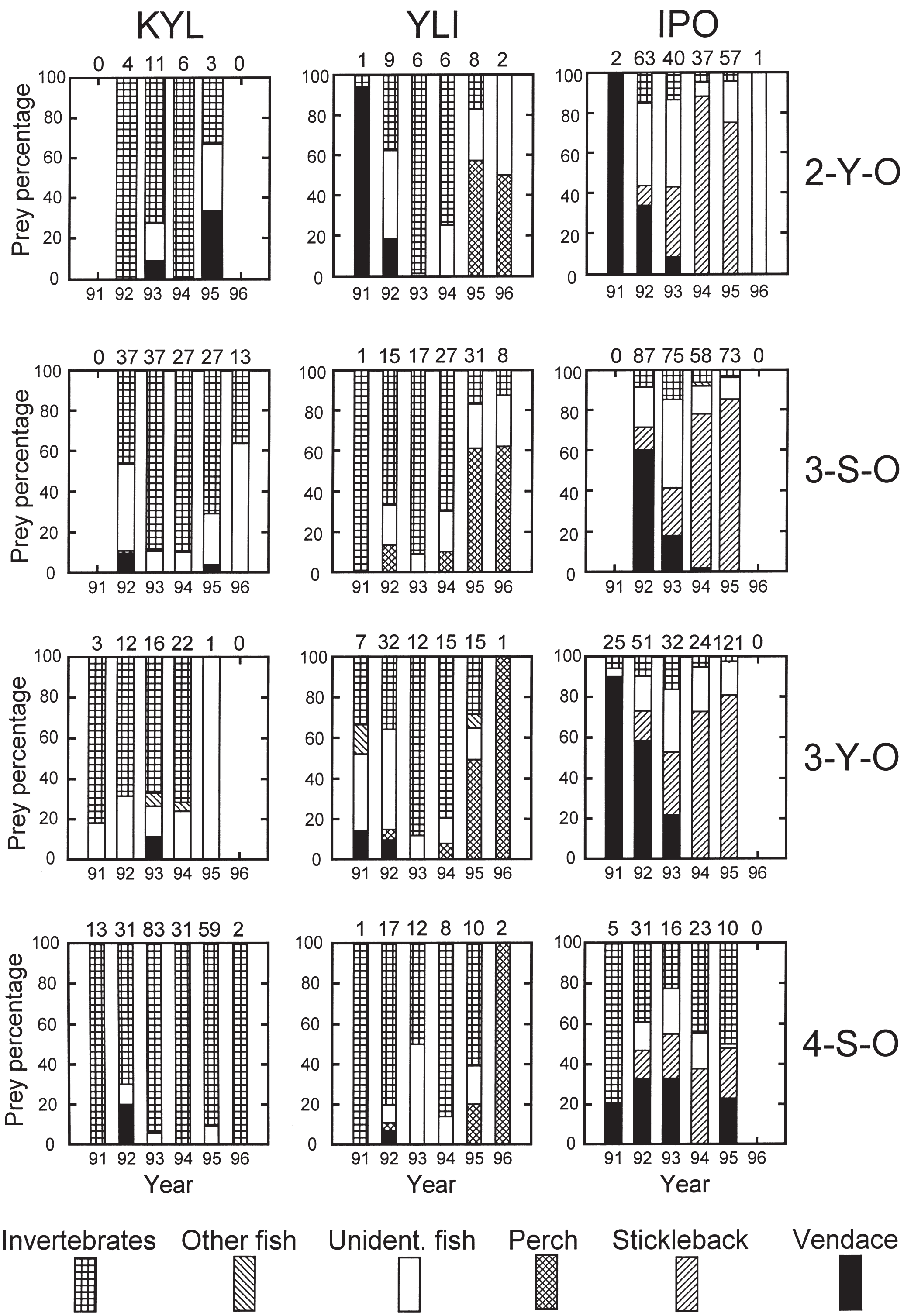


**Fig. 2.** Proportion (%) of different prey items in relation to overall stomach contents of the 2-Y-O, 3-S-O, 3-Y-O and 4-S-O brown trout in 1991–1996 among the three study lakes (KYL = Kylmäluoma, YLI = Ylioudonjärvi, IPO = Iso-Porontima). Numbers above the bars indicate the numbers of trout analyzed.

1995. The corresponding weights for ninespine stickleback were 0.18 g in 1991, 0.28 g in 1992, 0.37 g in 1993, 0.33 g in 1994 and 0.50 g in 1995. There was a tendency of the 2-Y-O trout to shift sooner to feed on sticklebacks than older trout did, and surprisingly, the diet shift among the 4-S-O brown trout was obscure and these fish did not, as expected, gain benefit from their size by feeding larger vendace in 1992 and 1993 (for details *see* Niva & Julkunen 1998).

### 3.3. Phenotypic variation in trout weight

Phenotypic variation in absolute weight of the trout of any given age was enormous (Table 2). At the hatchery, the 2-Y-O trout weighed on average 47 g, and after two growing seasons, at the age of 4-S-O, on average 305 g. When the 2-Y-O fish were stocked into natural lakes, however, their average weights as 4-S-O were 454 g in KYL, 554 in YLI and 991 g in IPO. From another viewpoint, average weight of the 4-S-O trout in IPO was 991 g for 2-Y-O trout at release; and 785 g and 679 g for the 3-S-O and 3-Y-O trout at release, respectively. More generally, weights of the fish in the lakes were often negatively correlated with the fish age at release, suggesting that increased time spent in the wild resulted in improved growth. All these comparisons indicate a substantially greater growth in the wild than in the hatchery. Finally, fish weights in IPO were considerably greater than in YLI or KYL. Weight differences between YLI and KYL were smaller, but in six out of seven cases the rank order of weights was YLI > KYL.

### 3.4. Interannual and within-season patterns in growth rate and lipid content of viscera

#### *3.4.1. Two-year-old fish at release*

Growth rate of the 2-Y-O trout was significantly affected by lake, and year and month of capture (ANOVA, $r^2 = 0.83$, Table 4). The mean SGR of 0.83% in KYL was significantly lower than those of 1.7% in YLI and 1.6% in IPO (Tukeys test, $p < 0.05$). The year was significant because the low average growth rate in 1993 was caused simply by the fact that five out of six fish from KYL were captured in 1993 (Fig. 3). A within-season variation (month of capture) in SGR was significant, decreasing from 2.4% in July to 1.1% in November and December. The ANOVA model explained 88% of the variation in visceral lipid percentage in the 2-Y-O trout, and in addition to highly significant main factors, the LAKE × MONTH interaction was also significant (Table 4). The average lipid content of 40% in the fish in in IPO was significantly higher than those of 16% in YLI or 11% in KYL. YEAR was significant because in IPO, the average lipid content in the fish increased from 33%–34% in 1991 and 1992 to 54% in 1995 (Fig. 3). The LAKE × MONTH interaction was significant because in IPO, the lipid content in

**Table 4.** Analysis of variance table of the growth rate (SGR, % day$^{-1}$, on the left) and visceral lipid percentage (VLP, % of dry weight, on the right) of the 2-year-old brown trout at release during the first growing season (July–December) with respect to stocking lake, year and month of recapture. Corresponding between-year and within-season patterns in SGR and VLP are presented in Fig. 3.

| | SGR, $r^2 = 0.83$ | | | | VLP, $r^2 = 0.88$ | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Lake | 2 | 1.16 | 19.7 | 0.000 | 2 | 1 169.5 | 44.7 | 0.000 |
| Year | 3 | 0.56 | 9.6 | 0.000 | 3 | 280.6 | 10.7 | 0.000 |
| Month | 5 | 0.93 | 15.8 | 0.000 | 5 | 251.3 | 9.6 | 0.000 |
| Lake × Year | 1 | 0.01 | 0.1 | 0.722 | 1 | 0.0 | 0.0 | 0.990 |
| Lake × Month | 1 | 0.00 | 0.0 | 0.966 | 1 | 1 46.3 | 5.6 | 0.022 |
| Year × Month | 6 | 0.08 | 1.4 | 0.242 | 6 | 67.3 | 2.6 | 0.029 |
| Lake × Year × Month | 1 | 0.00 | 0.0 | 0.919 | 1 | 66.5 | 2.5 | 0.117 |
| Error | 54 | 0.06 | | | 54 | 26.2 | | |

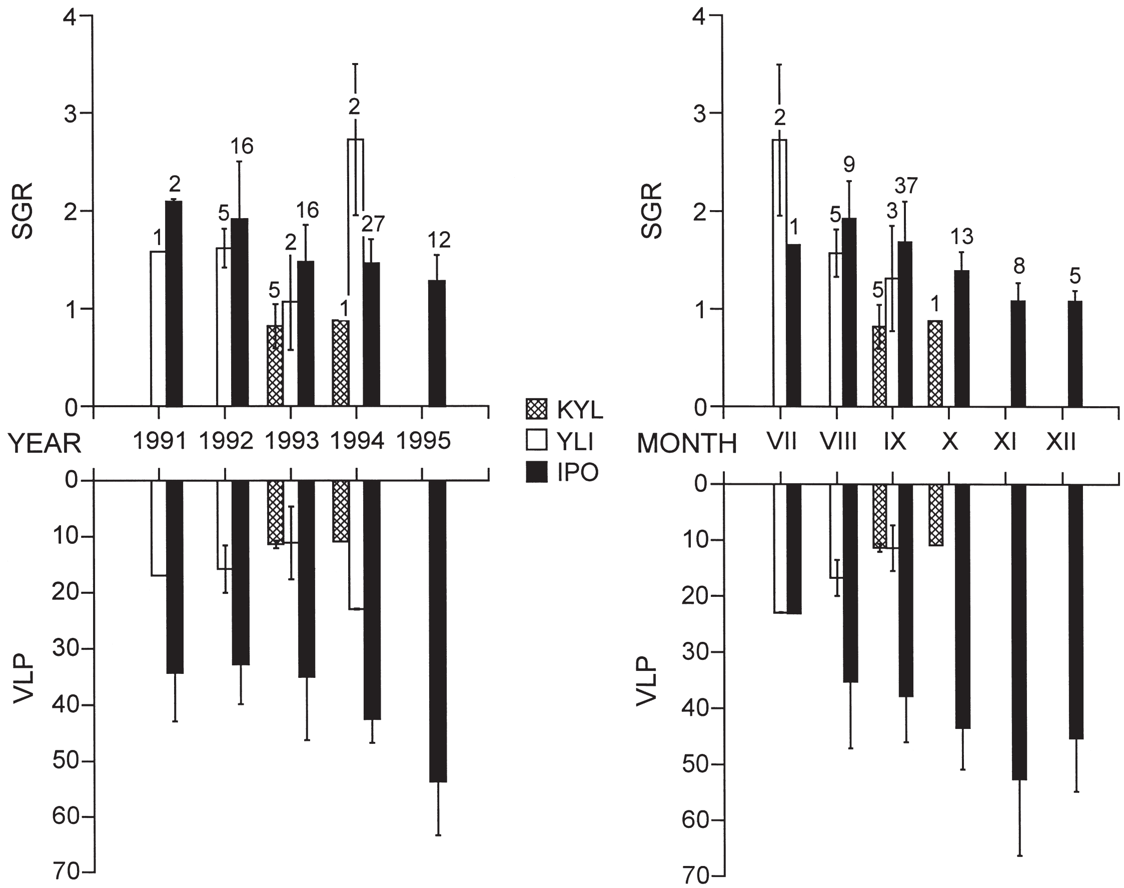


**Fig. 3.** Interannual (on the left) and within-season (on the right) mean (± S.D.) specific growth rates (SGR, % day$^{-1}$) and mean (± S.D.) visceral lipid percentage (VLP, % of dry weight) of the brown trout released at the age of 2 years into the three study lakes (KYL, YLI and IPO) in 1991–1995. Numbers above the bars indicate the number of fish which were selected for ANOVA analysis. Results of ANOVA corresponding this figure are presented in Table 4. Notice that fish caught in 1995 were not considered in the ANOVA.

the fish increased from 23% in July to 53% in November, whereas in YLI and KYL the content decreased from 23% in July to 11% in September and October (Fig. 3).

### *3.4.2. Three-summer-old fish at release*

The growth rate of the 3-S-O trout was significantly affected by the lake, year and month of capture and all their interactions (Table 5). The mean SGR of 1.0% in KYL and 0.97% in YLI were significantly lower than that of 1.5% in IPO (Tukey's test, $p < 0.05$). The YEAR × LAKE interaction was significant because the interannual variation in SGR was relatively small in IPO, but in YLI and KYL SGR decreased from 1.1%–1.2% in 1992 to 0.73%–0.79% in 1993 and 1994, and finally because in 1995 SGR was 1.3%–1.5% in all the lakes (Fig. 4). In IPO, the SGR was highest in July and thereafter it decreased until November. In contrast, in KYL and YLI the growth rate was not dependent on the month of capture, resulting in a significant LAKE × MONTH interaction. A total of 88% of the variation in the visceral lipid percentage in the 3-S-O trout was explained by the ANOVA model (Table 5). The lipid content in the fish was on average 35% in IPO but only 19% in YLI and 17% in KYL. Interannual changes in the lipid contents followed remarkably different patterns in IPO than in KYL or YLI. In IPO, the mean lipid content in the fish increased

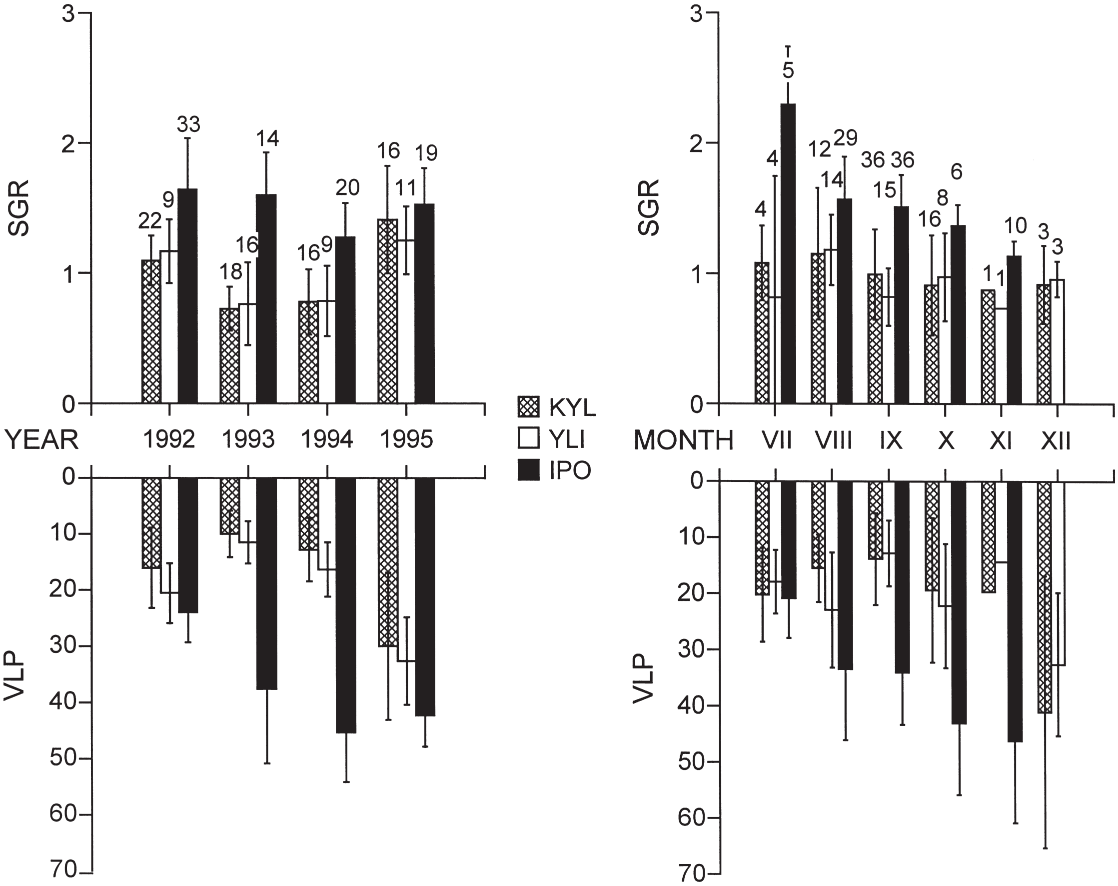


**Fig. 4.** Interannual (upper and lower panels on the left) and within-season (upper and lower panels on the right) mean (± S.D.) specific growth rates (SGR, % day$^{-1}$) and mean (± S.D.) visceral lipid percentage (VLP, % of dry weight) of the brown trout released at the age of 3 summers into the three study lakes (KYL, YLI and IPO) in 1992–1995. Numbers above the bars indicate the number of fish which were selected for ANOVA analysis. Results of ANOVA corresponding this figure are presented in Table 5.

**Table 5.** Analysis of variance table of the growth rate (SGR, % day$^{-1}$, on the left) and visceral lipid percentage (VLP, % of dry weight, on the right) of the 3-summer-old brown trout at release during the first growing season (July–December) with respect to stocking lake, year and month of recapture. Corresponding between-year and within-season patterns in SGR and VLP are presented in Fig. 4.

| | SGR, $r^2$ = 0.81 | | | | VLP, $r^2$ = 0.88 | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Lake | 2 | 2.83 | 58.2 | 0.000 | 2 | 2 855.3 | 89.9 | 0.000 |
| Year | 3 | 1.24 | 25.4 | 0.000 | 3 | 783.1 | 24.6 | 0.000 |
| Month | 5 | 0.47 | 9.6 | 0.000 | 5 | 137.6 | 4.3 | 0.001 |
| Lake × Year | 6 | 0.37 | 7.5 | 0.000 | 6 | 374.7 | 11.8 | 0.000 |
| Lake × Month | 9 | 0.12 | 2.5 | 0.012 | 9 | 144.9 | 4.6 | 0.000 |
| Year × Month | 13 | 0.16 | 3.3 | 0.000 | 13 | 114.4 | 3.6 | 0.000 |
| Lake × Year × Month | 10 | 0.09 | 1.9 | 0.046 | 10 | 61.8 | 1.9 | 0.043 |
| Error | 154 | 0.05 | | | 151 | 31.8 | | |

significantly from 24% in 1992 to 42% in 1995 (Fig. 4). In KYL and IPO, the values first decreased from 16%–21% in 1992 to 10%–13% in 1993 and then increased to 30%–33% in 1995 (Fig. 4). Also within-season patterns in the lipid contents were different in the fish in IPO than in KYL or YLI. Mean lipid percentages were 18–21 in July in the fish in all the lakes. Thereafter, they increased to 46 in IPO in November, whereas in YLI and KYL the mean lipid percentages were 13–23 from August to October, and then increased to 33–41 in November (Fig. 4).

### *3.4.3. Three-year-old fish at release*

The growth rate of the 3-Y-O trout was significantly affected by the lake, year and month of capture, and LAKE × MONTH and YEAR × MONTH interactions (Table 6). Mean SGRs of 0.54% in KYL, 0.73% in YLI and 1.2% in IPO differed significantly from each other (Tukey's tests, $p < 0.05$). In all the lakes SGRs were higher in 1991 and 1992 than in other years (Fig. 5). In YLI and IPO, SGRs were at their maximum in July or August, and decreased thereafter until November or December (Fig. 5). In KYL, however, growth rate was not dependent on month. The visceral lipid percentage of the 3-Y-O trout was mainly affected by the lake and month of capture (Table 6). The average lipid content of 43% in the trout in IPO was significantly higher than those of 21% in YLI and 22% in KYL (Tukey's test, $p < 0.05$). The month was a very important factor because within-season changes in the lipid content followed a similar pattern in all the lakes: lipid percentages decreased from July to September and October, and thereafter they increased. However, in IPO the lipid percentages in the trout were at a considerably higher level than these in other lakes.

### *3.4.4. Four-summer-old fish at release*

The growth rate of the 4-S-O trout was significantly affected by the lake but not by any other factor (Table 7, Fig 6). Average SGR of 1.2% in IPO was significantly higher than that of 0.71% in KYL or 0.57% in YLI (Tukeys test, $p < 0.05$). The visceral lipid percentage in the 4-S-O trout was significantly affected by the lake and year of capture (Table 7). The average lipid content in the trout in IPO was 38%; a significantly higher than value those of 21% and 23% recorded in the trout in YLI and KYL, respectively. In 1992, the mean lipid content ranged between 18%–24% in the fish in all the lakes. In 1993 and 1994, the lipid content was greater in the trout in IPO than YLI and KYL, but in 1995 this was true only between IPO and YLI (Fig. 6). Within-season changes in lipid percentages in the 4-S-O trout were not found (Fig. 6).

**Table 6.** Analysis of variance table of the growth rate (SGR, % day$^{-1}$, on the left) and visceral lipid percentage (VLP, % of dry weight, on the right) of the 3-year-old brown trout at release during the first growing season (July–December) with respect to stocking lake, year and month of recapture. Corresponding between-year and within-season patterns in SGR and VLP are presented in Fig. 5.

| | SGR, $r^2$ = 0.80 | | | | VLP, $r^2$ = 0.85 | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Lake | 2 | 1.82 | 31.8 | 0.000 | 2 | 1935.3 | 36.5 | 0.000 |
| Year | 3 | 1.04 | 18.2 | 0.000 | 3 | 360.4 | 6.8 | 0.000 |
| Month | 4 | 0.29 | 5.1 | 0.001 | 4 | 931.4 | 17.6 | 0.000 |
| Lake × Year | 6 | 0.03 | 0.5 | 0.830 | 6 | 188.5 | 3.6 | 0.003 |
| Lake × Month | 7 | 0.15 | 2.6 | 0.018 | 7 | 112.3 | 2.1 | 0.050 |
| Year × Month | 10 | 0.15 | 2.6 | 0.008 | 10 | 102.4 | 1.9 | 0.051 |
| Lake × Year × Month | 6 | 0.03 | 0.5 | 0.806 | 5 | 63.4 | 1.2 | 0.317 |
| Error | 87 | 0.06 | | | 87 | 53.0 | | |

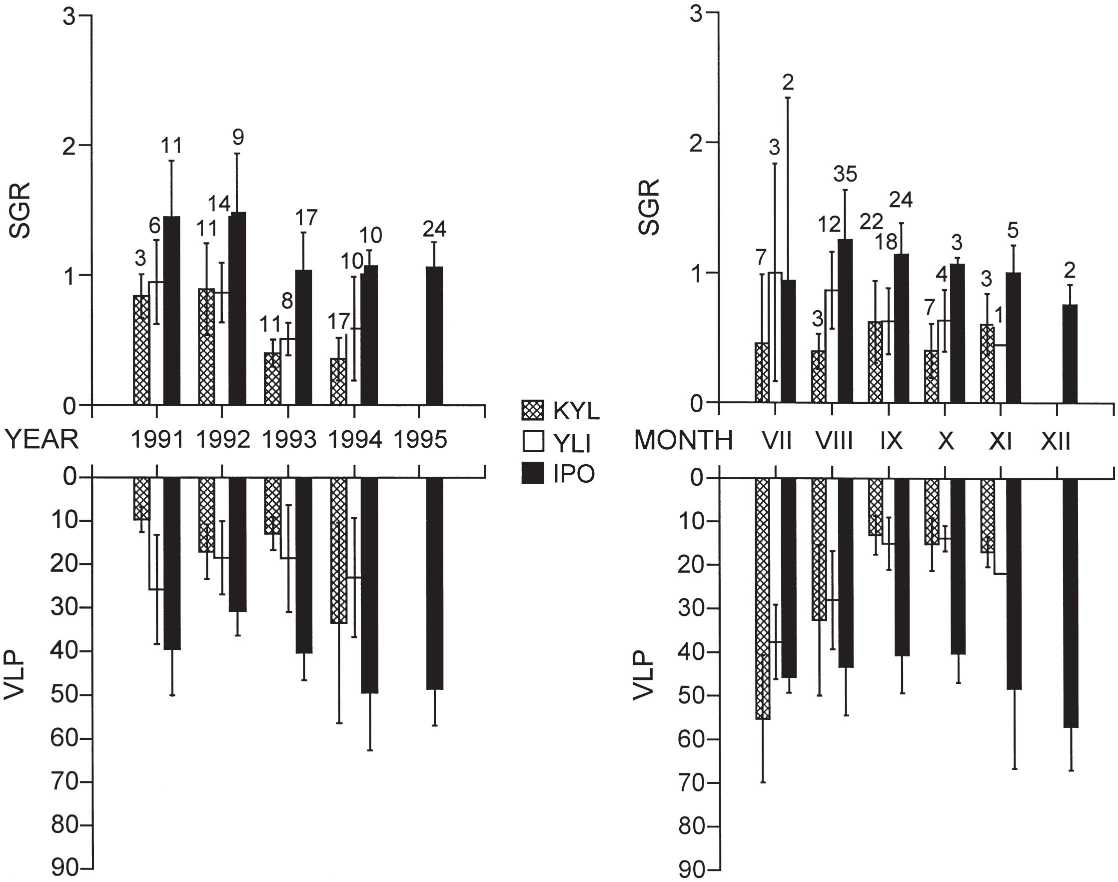


**Fig. 5.** Interannual (upper and lower panels on the left) and within-season (upper and lower panels on the right) mean (± S.D.) specific growth rates (SGR, % day$^{-1}$) and mean (± S.D.) visceral lipid percentage (VLP, % of dry weight) of the brown trout released at the age of 3 years into the three study lakes (KYL, YLI and IPO) in 1991–1995. Numbers above the bars indicate the number of fish which were selected for ANOVA analysis. Results of ANOVA corresponding this figure are presented in Table 6. Notice that fish caught in 1995 were not considered in the ANOVA.

**Table 7.** Analysis of variance table of the growth rate (SGR, % day$^{-1}$, on the left) and visceral lipid percentage (VLP, % of dry weight, on the right) of the 4-summer-old brown trout at release during the first growing season (July–December) with respect to stocking lake, year and month of recapture. Corresponding between-year and within-season patterns in SGR and VLP are presented in Fig. 6.

| | SGR, $r^2$ = 0.67 | | | | VLP, $r^2$ = 0.88 | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Lake | 2 | 1.39 | 8.1 | 0.004 | 2 | 550.9 | 7.0 | 0.007 |
| Year | 3 | 0.11 | 0.7 | 0.586 | 3 | 293.6 | 3.7 | 0.033 |
| Month | 5 | 0.09 | 0.5 | 0.764 | 5 | 36.9 | 0.5 | 0.794 |
| Lake × Year | 4 | 0.10 | 0.6 | 0.685 | 5 | 114.1 | 1.5 | 0.260 |
| Lake × Month | 3 | 0.02 | 0.1 | 0.966 | 4 | 47.3 | 0.6 | 0.667 |
| Year × Month | 5 | 0.09 | 0.5 | 0.756 | 6 | 35.7 | 0.5 | 0.832 |
| Lake × Year × Month | 1 | 0.00 | 0.0 | 0.928 | 1 | 8.9 | 0.1 | 0.741 |
| Error | 16 | 0.17 | | | 16 | 78.7 | | |

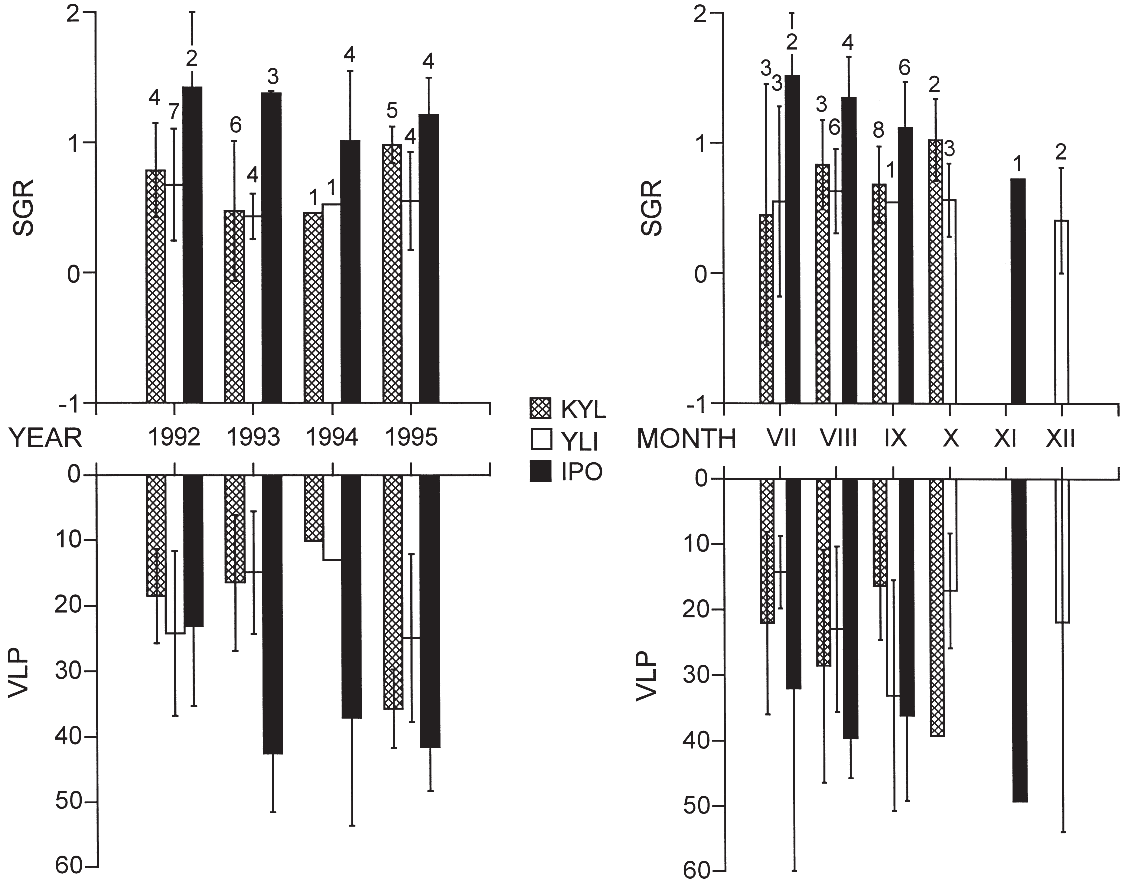


**Fig. 6.** Interannual (upper and lower panels on the left) and within-season (upper and lower panels on the right) mean (± S.D.) specific growth rates (SGR, % day$^{-1}$) and mean (± S.D.) visceral lipid percentage (VLP, % of dry weight) of the brown trout released at the age of 4 summers into the three study lakes (KYL, YLI and IPO) in 1992–1995. Numbers above the bars indicate the number of fish which were selected for ANOVA analysis. Results of ANOVA corresponding this figure are presented in Table 7.

### 3.4. Relative yield of brown trout

A stocking success of the brown trout, in terms of the net relative yield (NRY), was strongly dependent (ANOVA, $r^2 = 0.76$) on a lake (df = 2, $F$ = 13.6, $p < 0.001$) and age of fish at release (df = 3, $F = 24.1$, $p < 0.001$) and their interaction (df = 6, $F = 3.2$, $p = 0.012$). The NRY was positive only in IPO for the 2-year, 3-summer and 3-Y-O trout (Fig. 7). In all other cases, the NRYs were negative, and the decrease in the NRY was associated with the increase in age (size) of the trout at release. The NRYs were smallest for the 4-S-O trout in all the lakes.

## 4. Discussion

### 4.1. Methodological aspects

Most trout samples in the present study were collected from gillnet catches. A gillnet is a size selective gear, and gillnet selectivity efficiencies have been found essential for correcting estimates on abundance and size structure of a fish population if sampled with gillnets. Gillnet selectivity efficiencies have usually been determined in studies that apply short-term sampling strategy on a very large fish population with unknown size structure (e.g., Kurkilahti *et al.* 1998). As stated

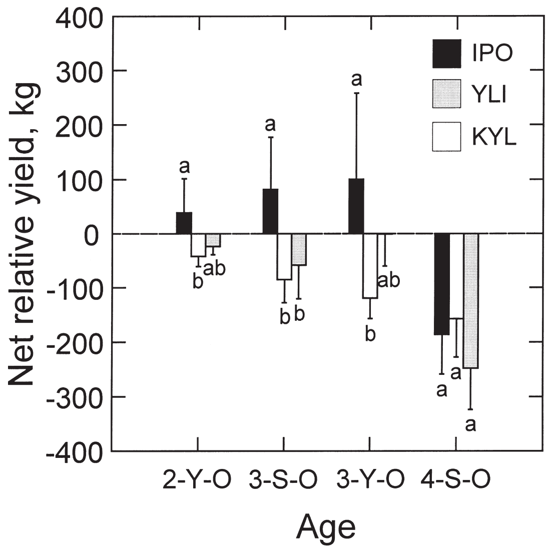


**Fig. 7.** Net relative yield (yield related to 1000 released fish minus weight of the fish at release) for four age groups (2-Y-O = two years old, 3-S-O = three summers old, 3-Y-O = three years old and 4-S-O = four summers old) of the brown trout stocked into three study lakes (IPO = Iso-Porontima, YLI = Ylioudonjärvi, KYL = Kylmäluoma), northeastern Finland in 1991–1996. Statistically significant between-lake differences in the mean net relative yield are indicated by different letters for each age groups separately (Bonferroni test, $p < 0.05$).

before, this was not the case in sampling trout in the present study. Excluding the short periods in late May and October, gillnetting was an everyday exercise in the studied lakes. When sampling with gillnets over a long term (i.e. over several growth seasons in the present study), the probability of a growing individual to be caught with a gillnet of any given mesh size is likely to change all the time (Rudstam *et al.* 1984). Therefore, it is possible that a considerably high overlap in the trout size caught with gillents of different mesh sizes was due to this unstudied phenomenon. Although the exact bias for abundance and size distribution of the trout caused by gillnet selectivity remains unknown, it is quite evident that sampling was equally biased across lakes.

The lipid contents were measured only in visceral tissues because buying the whole fish from fishermen would have been very costly. Storage reserves in the body of many salmonids are larger than that in the viscera. In general, it is reasonable to assume that a fish does not mobilize lipid energy from one tissue and store lipids into another at the same time, and that a fish does not exchange stored lipid energy from one tissue to another. The filling order of different storage targets is poorly understood in wild salmonids, but we know that when reserve lipids are mainly in the muscle tissue, these probably start to be mobilized as soon as food intake ceases (Love 1980, Miglavs & Jobling 1989). In the present study, some decreases in the visceral lipid content were rapid and extreme (from 60% in early June to 10% in late August) suggesting that they matched the corresponding changes in the body lipids. It is, however, important to notice that visceral lipid percentages were used more as indices for fat accumulation than quantitative energetic measurements.

As showed by Palermo (1990, *see* also Bergman et al. 1992), the unknown and usually highly variable reporting rate of the recovered tags is likely to confuse yield estimates (and the recovery rate itself) in studies based on voluntary tag recoveries. In the present study, the tags were recovered by the selected local fishermen, equipped and educated for sampling. Lake- and year-specific variation in the proportion of fish sampled of the total yield of brown trout was, therefore, controlled for, allowing unbiased estimates of relative yield.

### 4.2. Relations between diet, growth and fat accumulation

The growth rate and visceral lipid content of the stocked brown trout were tightly dependent on their diet (reflecting food supply) in the particular lake and year. In lakes and years when the stocked trout fed mainly on small fish, such as vendace (IPO 1991–1993, possibly YLI 1991), ninespine stickleback (IPO 1993–1995), and perch (YLI 1995–1996), their growth was significantly faster than in lakes and years when the trout fed mainly on invertebrates (KYL 1991–1994, YLI 1992–1994). Also the average lipid content of viscera was significantly greater in the piscivorous than insectivorous trout.

Within-season patterns in the growth and lipid content differed also remarkably among the lakes. In IPO, the growth rate of the trout during the first growing season was highest in July and August, and decreased somewhat thereafter until December. This seasonal decrease in the growth rate coincided with the increase in content of visceral lipids which were maximized during early winter, usually in November. In contrast, in YLI and especially in KYL, low growth rates of the trout were independent of seasons, but the lipid content of the viscera decreased strongly during the summer. This suggests that these trout used visceral energy reserves accumulated during their hatchery period for life support and foraging.

The diet mediated patterns described above were weaker in the 4-S-O trout than in younger fish. For instance, the diet shift from vendace to ninespine stickleback was hardly noticible in the 4-S-O trout in IPO (Fig. 2, *see* also Niva & Julkunen 1998). In YLI in 1995, the proportion of perch in the diet of the 4-S-O trout was lower than in the diet of younger trout. Only some individuals captured more than one year after release showed similar feeding behaviour as younger fish. Overall, the growth rate of the 4-S-O trout at release was slower than in the three youngest age groups. This was not just due to initial age or size of the fish itself, because the 3-S-O and 3-Y-O fish grew faster between ages 4-S-O and 5-S-O than the 4-S-O trout at release. Most males among the 4-S-O trout were precocious during the inspection of tags, but, unfortunately, this was not recorded in a systematic manner. It is, however, likely that early maturation of trout affected their feeding behavior negatively, as found for precocious male salmon parr (Rowe & Thorpe 1990).

### 4.3. Factors associated with net relative yield (NRY)

Net relative yields of the stocked brown trout were significantly higher in IPO than in KYL and YLI for the three youngest age groups, but not so for the 4-S-O trout that showed the lowest relative yield in all the lakes. Invertebrate food, low growth rate and depletion in visceral lipids were characteristic of the stocked brown trout in KYL and YLI in most years. Because a negative NRY means a decrease in fish biomass, it is reasonable to conclude that negative NRYs were associated with increased natural mortality of the stocked brown trout in the studied boreal lakes. Correspondingly, positive values of NRY were associated with feeding on small fish, good growth and high levels of storage lipids at the onset of winter (predicting relatively low overwinter mortality). The first summer at sea has been found critical for the overwinter survival of post-smolt coho salmon (*Oncorhynchus kisutch*) (Holtby *et al.* 1990) and chinook salmon (*O. tshawyscha*) (Unwin 1997), and for juvenile salmon (*Salmo salar* L.) in the river environment (Gardiner & Geddes 1980). The present results suggest that for juvenile brown trout stocked into boreal lakes, natural mortality may take place or start in August and September because the visceral lipid content was at a minimum during this time.

### 4.4. Diet preference and food competition

The stocked trout shifted twice from unpreferred food items towards preferred food in the same lake. First, in IPO the trout shifted from large vendace to feed on ninespine stickleback in 1993 (Niva & Julkunen 1996). The growth indicator (specific growth rate) used in the present paper indicated that the diet shift caused decrease in the growth rate in 1993, without a further increase in its in 1994 and 1995 (compare Niva & Julkunen 1996). On the other hand, visceral lipid percentages were significantly higher in 1994 and 1995 than in 1991 and 1992, which may indicate that vendace and stickleback provided energetically similar resources which were allocated differentially. Second, in YLI the trout shifted from invertebrates to feed on 1-S-O perch in 1995. As noticed before, 75% of the fish captured in YLI in 1995 were at their second or third growth season, i.e. these fish fed on invertebrates in 1993 and 1994. The diet shift enhanced growth of the trout dramatically in 1995. For instance, the 3-S-O trout (127 g at release) stocked in 1992, weighed at the age of 5-S-O on average 628 g (S.D. = 342, $n = 5$), but in December 1995, 1 825 g (S.D. = 272, $n = 4$). All these findings suggest a causal relation between abundance of small fish prey and growth of juvenile brown trout during the first year after release in boreal lakes. This is exactly the same result as O'Gorman *et al.* (1987) found between brown trout and alewife (*Alosa pseudoharengus*) in Lake Ontario.

An interspecific food competition and/or predation on stocked trout are certainly important factors which may reduce stocking success of salmonids (Gunn *et al.* 1987). The present study was designed so that impacts from these factors were minimized by choosing study lakes in which native fish fauna were dominated by planktivorous species and where stocks of potential predators were small. An annual stocking rate in the present study was ca. 6 fish per hectare, while it averaged 1.1 in 34 Finnish lakes studied by Vehanen (1995). Therefore, the intraspecific food competition was probably strong in lakes and years when the trout were forced to feed on invertebrates. It is possible that a relatively good growth rate in KYL and YLI in 1991 and 1995 were partly due to lower fish densities during these years as compared with 1992–1994. On the other hand, the previously used high stocking rate was doubled in 1995 in IPO. As a result, the trout fed strongly on stickleback, and their growth rate and increase in storage lipids were at the same level as in previous years. Hence, it remains open for further studies what the maximum stocking density is when suitable-sized prey fish are very abundant.

### 4.5. Management implications

Small vendace, ninespine stickleback and 1-S-O perch were the fish species highly preferred by the stocked brown trout in the three small boreal lakes studied. Vehanen (1995) and Vehanen and Aspi (1996) concluded that high catches of vendace and whitefish, for example, implies sufficient food resource for brown trout. This conclusion was not supported by the present study. First, whitefish was the dominant species in the yields (especially in KYL), but only one trout (out of 1 532) had actually been feeding on whitefish. Second, fish < 1 g were common in the diet of the stocked trout, but these stocks were not caught with any fishing gear. Third, the size of vendace in recruitment (IPO 1993) was considerably larger than preferred by the brown trout (IPO 1991 and 1992). The present results suggest that the abundance of vendace stock should be estimated before it is recruited to fisheries, in order to adjust stocking rate of brown trout successfully. Because larval survival is suggested by several authors to be the primary determinant of year-class strength of vendace (Salojärvi 1987, Viljanen 1988, Helminen & Sarvala 1994, Huusko *et al.* 1996, Helminen *et al.* 1997), modeling mortality would allow a valid empirically based tool for adjusting the stocking rate of brown trout in relation to prey abundance.

In conclusion, stocking smolt-sized (100–200 g) trout into a lake where highly abundant and small (< 4 g in average) fish stocks are present is recommended for management of brown trout stocks in boreal lakes. Stocking large (> 200 g) post-smolt brown trout in the belief that they are superior in foraging large fish prey seems to be an unwarranted management practice, according to the results of the present study.

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**Appendix 1.** Age at release (2-Y-O = two-year-old, 3-S-O = three-summer-old, 3-Y-O = three-year-old, 4-S-O = four-summer-old), year of release, tag type (CW = binary coded wire tag, VI = visible implant tag), mean weight at release (W, g), number of stocked fish (SF), number of recaptured fish (RF) and gross relative yield (GRY, kg, *see* Materials and methods) for brown trout stocked into KYL, IPO and YLI in 1991–1995.

| | | | KYL | | | | IPO | | | | YLI | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age | Year | Tag | W | SF | RF | GRY | W | SF | RF | GRY | W | SF | RF | GRY |
| 2-Y-O | 1991 | CW | 37 | 750 | 5 | 10 | 41 | 688 | 7 | 22 | 45 | 560 | 7 | 21 |
| 2-Y-O | 1992 | CW | 34 | 738 | 6 | 5 | 29 | 687 | 82 | 139 | 30 | 454 | 8 | 11 |
| 2-Y-O | 1993 | CW | 57 | 776 | 9 | 3 | 57 | 696 | 27 | 84 | 57 | 458 | 11 | 47 |
| 2-Y-O | 1994 | CW | 62 | 760 | 4 | 5 | 56 | 710 | 32 | 51 | 57 | 470 | 6 | 14 |
| 2-Y-O | 1995 | CW | – | – | – | – | 45 | 1 045 | 52 | 124 | – | – | – | – |
| 3-S-O | 1991 | VI | 124 | 731 | 33 | 72 | 123 | 726 | 71 | 200 | 135 | 466 | 13 | 36 |
| 3-S-O | 1992 | CW | 119 | 748 | 39 | 22 | 122 | 697 | 93 | 319 | 136 | 464 | 46 | 146 |
| 3-S-O | 1993 | CW | 142 | 721 | 29 | 12 | 153 | 665 | 57 | 194 | 148 | 427 | 21 | 57 |
| 3-S-O | 1994 | CW | 108 | 760 | 40 | 55 | 104 | 700 | 72 | 121 | 108 | 460 | 19 | 63 |
| 3-Y-O | 1991 | CW | 154 | 375 | 5 | 21 | 152 | 345 | 26 | 495 | 155 | 330 | 25 | 228 |
| 3-Y-O | 1992 | VI | 118 | 370 | 15 | 43 | 123 | 350 | 50 | 204 | 130 | 230 | 20 | 112 |
| 3-Y-O | 1993 | VI | 134 | 386 | 13 | 14 | 132 | 355 | 32 | 194 | 138 | 243 | 16 | 107 |
| 3-Y-O | 1994 | VI | 177 | 380 | 21 | 29 | 185 | 350 | 27 | 191 | 180 | 240 | 21 | 91 |
| 3-Y-O | 1995 | CW | – | – | – | – | 125 | 1 040 | 118 | 133 | – | – | – | – |
| 4-S-O | 1991 | VI | 314 | 396 | 20 | 86 | 305 | 300 | 9 | 104 | 346 | 297 | 12 | 61 |
| 4-S-O | 1992 | VI | 263 | 299 | 66 | 179 | 269 | 334 | 36 | 156 | 288 | 239 | 11 | 59 |
| 4-S-O | 1993 | VI | 251 | 383 | 59 | 90 | 254 | 354 | 14 | 82 | 261 | 237 | 18 | 93 |
| 4-S-O | 1994 | VI | 369 | 380 | 74 | 211 | 369 | 350 | 26 | 109 | 373 | 240 | 9 | 63 |