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UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Ecology of stocked brown trout (*Salmo trutta* L.) was studied in three boreal lakes, north-eastern Finland. The field experiment was designed so that sources of variation from genetics and treatment at the hatchery of trout were kept minimal. In addition, the study lakes were similar with respect to area, depth, water quality, resident fish species composition, fishing effort and stocking rate. Hence, feeding, energetics and yield of stocked trout were hypothesised to be affected by seasonal and interannual fluctuation in abundance and size of vendace (*Coregonus albula* L.). Another large field data was collected to study relationship between larval mortality and subsequent recruitment of vendace.

Stocking success of brown trout, in terms of growth and net relative yield, was tightly dependent on the proportion of small fish prey in the diet of trout. When the trout fed strongly on small (< 4 g) fish prey, such as vendace, nine-spined stickleback (*Pungitius pungitius* L.), and perch (*Perca fluviatilis* L), their growth was fast, and they also increased storage lipids. When the trout fed mainly on invertebrates their growth was poor, and a strong depletion in storage lipids during the first growing season probably increased owerwinter mortality. Size of trout at release and season of stocking were less significant factors, except the trout released at post-smolt stage showed the poorest success independently of the quality of the foraging environment.

Variation in the vendace recruitment was found to be caused mainly by variation in larval mortality during the three weeks after ice-break. Predator-prey interaction between trout and vendace was sensitive to prey growth, because growth of vendace caused a diet shift from vendace to stickleback. At the individual level, growth rate of the trout at the hatchery predicted poorly growth rate in the lakes, suggesting that growth was determined by environment-specific set of traits.

Key words: Brown trout; diet; growth; predation; stock-recruitment; stocking; tagging; vendace.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by Roman numerals I–V.

I Niva, T. Relations between diet, growth, visceral lipid content and yield of stocked brown trout in three small lakes in northern Finland. Annales Zoologici Fennici 36, in press.

II Karjalainen, J., Auvinen, H., Helminen, H., Niva, T., Sarvala, J. & Viljanen, M. Unpredictability of fish recruitment: interannual variation in young-of-the-year vendace (*Coregonus albula* (L.)) abundance. Submitted.

III Niva, T. & Julkunen, M. 1998. Effect of population fluctuation of vendace (*Coregonus albula*) on the diet and growth of stocked brown trout (*Salmo trutta*). Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 50: 295–303.

IV Niva, T. 1995. Retention of visible implant tags by juvenile brown trout. J. Fish Biol. 46: 997–1002.

V Niva, T. & Jokela, J. Phenotypic correlation of juvenile growth rate between different consecutive foraging environments in salmonid fish: a field experiment. Manuscript.

1 INTRODUCTION

After the last ice age, the brown trout (*Salmo trutta* L.) inhabited most river systems in Europe (Elliott 1994). Recent anadromous (sea-run) and freshwater resident life history types have probably derived from the ancient anadromous population(s) of brown trout (Hindar et al. 1991). In Finland, unknown but probably large proportion of the freshwater resident stocks adopted fixed migratory life history type (Gross 1987, Dodson 1997), resembling anadromous brown trout both in morphology and migration pattern (Krueger & May 1987). More specifically, in spring most parr (young trout living in a stream) that have reached length of 20–25 cm with weight of 90–150 g overcome a complex smoltification process, by which the parr transform into the migratory smolt stage (Hoar 1988, Pirhonen & Forsman 1998). Smolting age vary from two to five years, depending on the latitude of the stream and individual growth variation within a cohort. The smolts migrate during a relatively short period in late spring (Pirhonen et al. 1998) to a neighboring large lake where they forage and grow 2–5 years until first maturity at the weight of 1.5–4 kg (Lind 1978, Huusko et al. 1990). Mature fish, at least 5 years old, migrate to their home stream to spawn. Weight of the repeat spawners may be up to 10 kg, and size and age at maturity has known to be fairly similar in the Finnish sea-run and lake-run stocks of brown trout (Järvi 1940, Huusko et al. 1990).

Natural reproduction of the Finnish sea-run stocks of brown trout collapsed mainly due to river damming in the 1950s. The lake-run stocks have reduced more slowly and this decay has been caused by several human activities. River channelization, forestry drainage and recently peat mining have reduced area and quality of stream beds suitable for eggs and juvenile stages of brown trout. Cheap and very effective nylon gillnets came on the market during the 1960s. Thereafter increasing proportion of the total yields of the inland lake fishery have been caught by gillnets. Most target fish species for the gillnet fishery are small-sized, and hence relatively dense mesh sizes (< 50 mm) have been popularly used in Finland. As a result, juvenile brown trout < 1 kg have been caught by gillnets, and the exploitation rate of the recent Finnish lake-run stocks of brown trout have obviously been close to 100 % since the only indigenous stocks which have retained their vitality exist in the Koutajoki river system — no doubt due to fact that the smolts of these stocks migrate across the boundary between Finland and Russia to enter their feeding areas at the Lake Pyaozero, a large Russian lake characterized by low fishing pressure (Huusko et al. 1990). During the last three decades, culturing and releasing smolt-sized trout into lakes have been the main tool for stock management of brown trout in Finland. In the 1990s, approximately one million 2- or 3-year-old brown trout have been annually stocked into the 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, hatchery production and releasing young salmonids have increased enormously, followed by numerous studies on the ecology of cultured fish in relation to environmental shift. The loss of genetic variability due to artificial breeding (e.g. Allendorf & Ryman 1987) and the genetic structure of natural and hatchery stocks of salmonid populations (e.g. Koljonen 1989) have been studied intensively during the last decades. Unfortunately, the relationship between electrophoretic characters and the life-history characters that are sensitive to selection, and therefore important to local adaptation, is not at all clear (Hard 1995 and references therein). Some more ecologically oriented studies have been designed so that they 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 abundance of forage organisms present in the sea. More recently, optimal size and time for smolt releasing (migration) 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). Several authors have suggested that considerable interannual variation in the (marine, lake) environment (food supply, predation etc.) may control for growth and survival of stocked salmonids more than that of hatchery-related factors (Green & Macdonald 1987, Gunn et al. 1987, O'Gorman et al. 1987, Fisher & Pearcy 1988, Holtby et al. 1990, Brodeur et al. 1992, Unwin, 1997). These results sustain the former notation by Bilton et al. (1982) that "size and time at juvenile release and success of adult returns are viewed as initial and final aspects of a biological system whose central components as yet are imperfectly understood".

The present study was planned in winter 1990/1991 according to the ideas viewed in the previous paragraph, and it was aimed to improve stocking success of brown trout in Finland. The vendace (*Coregonus albula* L.) is commonly known to be predated by brown trout in Finnish lakes (Järvi 1915, Lind 1978), and pronounced year-class fluctuations are common in vendace stocks (Salojärvi 1987, Viljanen 1988). Hence, the general hypotheses of the study was that year-to-year changes in the abundance of vendace (food supply) is the most important factor determining stocking success of juvenile brown trout in Finnish lakes (Paper I).

Particularly, predator-prey interaction between brown trout and vendace was hypothesized to be affected by relative sizes of both species in a given year (Tonn & Paszkowski 1986, Wilbur 1988, Osenberg & Mittelbach 1989). This is to say that large brown trout at release should be more capable to feed on large vendace than their smaller conspecifics, predicting higher growth rate and consecutive catch for large- than small-sized trout at release (Papers I and III). More generally, many hatchery-oriented managers believe that stocking success of salmonids is higher for stocks or individuals that show relatively high growth rate at the hatchery than that of slow-growing stocks or individuals. This hypotheses, which obviously predict that growth rate at the hatchery is positively correlated with growth rate in the wild, was tested in Paper V.

In the course of the study, there was an increasing evidence that predator-prey interaction between brown trout and vendace was tightly dependent on the growth of the prey vendace (see Rice et al. 1993, Olson 1996a,b, Paper III). Because growth of vendace is density dependent (Viljanen 1988), interannual changes in the year-class strength of vendace affect directly its growth rate which, in turn, may strongly affect vulnerability of vendace for brown trout in a given year. Therefore, our capability to predict year-class strength of vendace would be very useful not only for adjusting commercial vendace fishery but also for adjusting timing, fish size and rate of stocking brown trout. The survival at the larval stage 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). However, only very few attempts have been made to estimate the larval and juvenile mortality in field. Therefore, we analyzed large field data collected from seven Finnish lakes in 1989–1998 to detect if this critical larval phase determines the recruitment of vendace (Paper II). In short, scopes of the separate papers of the present thesis overlap considerably. At the end of present summary they are coupled in order to discuss the applied value of the results at the national level.

2 MATERIALS AND METHODS

2.1 Study areas

All brown trout used in the study belonged to the lake-run strain of brown trout found above the Jyrävä falls in the River Kitkajoki, the Koutajoki watercourse, northeastern Finland (Huusko et al. 1990). All the study on brown trout (Papers I, III, IV and V) was done in north-eastern Finland (66° N, 29° E) in three small lakes. The Lakes Kylmäluoma (KYL), Iso-Porontima (IPO) and Ylioudonjärvi (YLI) were chosen for the study because they represent the boreal lake environment typically inhabited by this stock of brown trout (Table 1 in Paper I).

Data on vendace was collected from seven large (area 32–230 km^2), oligo-mesotrophic (total phosphorus 5–20 µg/l) Finnish lakes located at 60-66°N, and 22–30°E (Paper II). Relevant data on vendace in the three 'trout' lakes was available only in IPO (Paper III).

2.2 The study design: brown trout

All the brown trout used in the field experiment were maternal half-sibs (in detail in Paper V), and each of the five F2-cohorts was cultured under natural photoperiod (66 °N) in a single large stock of which the trout were randomly assigned to one of the three stocking lakes, and the number of stocked fish was always proportional to the area of each stocking lake. This procedure, resulting in three comparable groups of brown trout at release, was replicated annually for four age group of trout, identified by internal tags (Table 1, Papers I and IV). The lakes chosen for the study were similar with respect to area, mean depth, water quality, resident fish species composition and fishing effort (Paper I). Therefore, interannual and between-lake variation in the food supply of the stocking lakes were hypothesized to cause measurable phenotypic responses to diet, growth, fat accumulation and consecutive yield of stocked brown trout with respect to one hatchery-related factor, the age (size) of trout at release.

As pointed out in many textbooks (e.g. Laird & Stott 1978), it is very important that the tag would have little or no effect on the fishes' behaviour, growth, survival, or liability to capture by predators or fishing gear. Therefore, only very small internal tags were used in the study (Bergman et al. 1992). Numerous studies on the binary coded wire tag (CW) have shown that it is harmless for the fish (Buckley & Blankenship 1990). Another tag type used, the visible implant tag (VI), arrived on the market just when I started the study in 1991. I evaluated its suitability for juvenile brown trout (Paper IV), and Paper V was based on its individual code. At the population level, unknown and usually highly variable reporting rate of the recovered tags is likely to confuse any yield estimate (and the recovery rate itself) in studies based on voluntary tag recoveries (Palermo 1990, Bergman et al. 1992). In the present study, the tags were recovered by the selected local fishermen which were equipped and educated for sampling. Lake- and year-specific variation in the proportion of sampled fish of the total yield of brown trout was under control allowing relative yield estimates unbiased by the sampling design itself. In short, it is improbable that any given measure or estimate of the present study were markedly biased by the tags.

The fish were released into the stocking lakes located near the hatchery ca. one week after inspection of the tags. Five local fishermen on each lake were equipped with measuring instruments and trained to measure and store samples of the trout they caught. Weight and length change, stomach contents and total lipid content of the viscera were measured from 1532 trout captured on average 225 (M.D. 174, S.D. ± 187, range 0–1288) days after release (Table 1).

Relative yield (yield per thousand fish released) was calculated for each tagging group to estimate overall stocking success. Details of the methods listed above are presented in separate papers.

2.3 The study design: vendace

The survival at the larval stage 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). However, only very few attempts have been made to estimate the larval and juvenile mortality in field. Therefore, we analysed large field data collected from seven Finnish lakes in 1989–1998 to detect if this critical larval phase determines the recruitment of vendace.

Total number of newly hatched vendace larvae was estimated following a uniform sampling procedure and equipment (Karjalainen et al. 1998) in all lakes. Larval sampling started immediately after the ice-break which occurred earliest at the end of April (in 1992 in Lake Pyhäjärvi) and latest in the middle of

June (in 1996 in Lake Kitka). Sampling lasted for 1–6 weeks and the total population size of newly hatched fish (total length<12 mm) in each lake was calculated from the samples taken during the first week after the ice-break. Also the population size of larval vendace sampled two weeks later (third week after the ice-break) was calculated and the mortality between the two sampling periods was estimated. Estimate of the subsequent recruitment of vendace was based on CPUE statistics, mainly calculated by the depletion method (Carle & Stubb 1978, Helminen et al. 1993, Auvinen and Jurvelius 1994).

TABLE 1 Number of samples of stocked brown trout captured by the local fishermen in 1991–1996 in the three study lakes according to the age and mean stocking rate (R, individuals per hectare) as well as mean length (L, cm) of brown trout at release. The dashed line crossing vertically the table show the time when last fish were released into the lake, according to age group.

Lake	Age	R*	L,	Year of capture						
			cm	1991	1992	1993	1994	1995	1996	Totals
Kylmäluoma	2-year-old	1.97	16.3	0	4	11	6	3	0	24
Ylioudonjärvi	2-year-old	1.96	16.3	1	9	6	6	8	2	32
Iso-Porontima	2-year-old	2.02	15.3	2	63	40	37	57	1	200
Kylmäluoma	3-summer-old	2.02	22.2	0	37	37	27	27	13	141
Ylioudonjärvi	3-summer-old	2.09	22.5	1	15	17	27	31	8	99
Iso-Porontima	3-summer-old	2.02	22.5	0	87	75	58	73	0	293
Kylmäluoma	3-year-old	0.97	24.8	3	12	16	22	1	0	54
Ylioudonjärvi	3-year-old	1.09	24.4	7	32	12	15	15	1	82
Iso-Porontima	3-year-old	0.97	23.2	25	51	32	24	121	0	253
Kylmäluoma	4-summer-old	1.01	30.9	13	31	83	31	59	2	219
Ylioudonjärvi	4-summer-old	1.12	30.2	1	17	12	8	10	2	50
Iso-Porontima	4-summer-old	1.01	30.9	5	31	16	23	10	0	85
			Totals	58	389	357	284	415	29	1532

* Rates were calculated only from 1991–1994 releases because in 1995 in Iso-Porontima stocking rates were increased to 3 fish per hectare for the 2-year and 3-year-old trout.

3 RESULTS AND DISCUSSION

3.1 Relations between diet, growth, visceral fat content and yield of stocked brown trout in three small lakes in northern Finland (Paper I)

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.) (IPO 1991–1993, possibly YLI 1991), ninespine stickleback (*Pungitius pungitius* L.) (IPO 1993–1995) and one-summer-old perch (*Perca fluviatilis* L.) (YLI 1995–1996) than their insectivorous conspecifics. When trout fed mainly on invertebrates (KYL 1991–1994, YLI 1992–1994), such as larvae of trichopterans and ephemeropterans, and adult hymenopterans, their growth rate was 2–3 times slower than for piscivorous trout, and the lipid content of the viscera decreased strongly during the first growing season. Storage lipids of juvenile salmonids may be used for feeding activities during the growth season, but they are usually maximised at the onset of winter (Gardiner & Geddes 1980, Cunjak 1988, Heggenes & Saltveit 1989, Bull & Metcalfe 1997, Berg & Bremset 1998). Overwinter survival of juvenile salmonids is tightly dependent on the ability of fish to regulate energy reserves prior to winter (Bull et al. 1996, see also Jokela 1997). In the present study, within-season patterns in growth and lipid content differed remarkable across lakes. In IPO the growth rate of the trout during the first growing season was highest in July and August and decreased thereafter moderately until December. This seasonal decrease in the growth rate was coincided with increasing 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 on the month of the season, but the lipid content of the viscera decreased strongly during the summer. This suggest that these trout used visceral energy reserves accumulated in the hatchery for maintenance and searching food.

Invertebrate food, low growth rate and depletion in visceral lipids were characteristics of stocked brown trout in KYL and YLI in most years. Because negative net relative yield (NRY) means decrease in fish biomass, it is reasonable to conclude that negative NRY were associated with increased natural mortality of stocked brown trout in the studied boreal lakes. Correspondingly, positive values of the NRY were obviously associated with feeding on small fish, good growth and high levels of storage lipids at the onset of winter (suggesting relatively low overwinter mortality). The first summer at the sea has been found critical for 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 visceral lipid content were at the minimum during this time.

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). Second, in YLI the trout shifted from invertebrates to feed on 1-S-O perch in 1995. As a result, the diet shift enhanced growth of the trout extremely in 1995. These findings suggest a causal relation between abundance of very small fish prey and growth of juvenile brown trout during the first year after release in boreal lakes. This is exactly the same result than O'Gorman *et al.* (1987) found between brown trout and alewife (*Alosa pseudoharengus*) in Lake Ontario.

Size at release and season of stocking were less significant factors affecting diet, growth and yield of stocked brown trout, except the largest post-smolt trout at release showed the poorest performance independently of the quality of the foraging environment. Stocking smolt-sized (100–200 g) trout into a lake where abundant and small sized (<4 g) prey fish stocks are present is recommended for management of brown trout stocks in boreal lakes.

3.2 Vendace recruitment and predator-prey interaction between brown trout and vendace (Papers II and III)

We showed that recruitment of an autumn spawning vendace is determined in the following spring due to variation in larval mortality during the first three weeks after the ice-break (Paper II). In addition, we conclude that the number or total area of nursery places do not restrict the recruitment of vendace. The recruitment was strongly and positively correlated with the larval abundance measured three weeks after ice-break but not with the larval abundance obtained immediately after ice-break. The major part of the larval and juvenile mortality occurred during the first three weeks after the ice-break (65% on average), and in most of the years (but not always) final determination of recruitment was concluded to take place at that time. Weight of vendace after the first growing season was at maximum 15–32 g in Lake Pyhäjärvi (SW) and at minimum 1–4 g in Lake Kitka. This large range was due to differences in fish density and lake productivity.

A very high recruitment estimate, and that the growth of vendace was poor (average weight of 0+ vendace was 2.7 g) in Lake Kitka (Paper II), suggested that density of vendace population in Lake Kitka was close to that observed in IPO for extreme strong year-class 1991 (Paper III). The fish of this particular year-class in IPO grew slowly; after the first summer the mean wet body mass of 2.0 g was reached, and after the third summer 6.9 g. The year-class 1991 dominated the vendace population until 1994. In 1991, the brown trout weighing on average 455 g (S.D. ± 106) fed predominately on vendace and the average wet body mass of vendace in the stomachs was 1.2 g. This was also the case in Lake Kitka as the trout weighing on average 1032 g (S.D. ± 456, n=395) fed strongly on relatively small (on average 3.0 g, S.D. ± 1.6) vendace (own unpublished data from 1991–1996). In IPO, proportion of vendace in the trout diet decreased as the mean wet body mass of vendace increased from 1992 to 1994. At the same time, the proportion of nine-spined stickleback in the diet of brown trout increased. The mean wet body mass of nine-spined stickleback in the stomachs was 0.2–0.4 g in 1991–1994. The diet shift from vendace to nine-spined stickleback was probably affected by the increase in the mean size of vendace of the year-class 1991 and by the poor recruitment of vendace in 1992–1994. There was also tendency that the 2-year-old trout shifted sooner to fed on stickleback than older trout. The growth rate of brown trout decreased in 1993 when the diet shift took place. In spite of the predation pressure by brown trout, the year-class 1991 of vendace resulted in a fairly high catch of 15 kg per hectare, predominantly in 1993. This suggest that the growth pattern of vendace population was not predator-induced, suggesting a 'bottom-up' control between the trophic levels. Trout predation on vendace was intensive only when abundance of small vendace was high (Paper I and Paper III). Consequently, I suggest that low density stocks of vendace are not under heavy predation by brown trout because high growth rate of vendace result in shortened period of predation pressure by brown trout. Also results of Paper II provide indirect evidence to this hypotheses, since variation in larval mortality determined year-class strength of vendace, i.e. other factors including trout predation were less significant. As we found that abundance of young-of-the-year vendace was dependent on larval mortality, modeling of this mortality and the following growth pattern of vendace would open new avenues in stocking management of brown trout as well as optimizing the commercial vendace fisheries.

More generally, the predator-prey interaction between brown trout and its prey fish species seems to be regulated by combined effects of population density and size-structure of both species (Olson 1996b). The interaction observed in the present study was sensitive to prey growth as earlier found between brown trout and alewife (*Alosa pseudoharengus*) (O'Gorman et a. 1987), spot (*Leiostomus xanthurus*) and flounder (*Paralichthys lethostigma*) (Rice et al. 1993), and between largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrohirus)* (Olson 1996a). There was some evidence that predation by the smallest trout was limited by mouth size. On the other hand, the finding that the trout shifted from unpreferred food items towards preferred food, and ate them thereafter disproportionately, suggest that diet selection by the trout was frequency-dependent (Hughes 1997).

3.3 Phenotypic correlation of juvenile growth rate between different consecutive foraging environments in brown trout: a field experiment (Papers IV and V)

We studied phenotypic correlation in growth rate of juvenile brown trout individuals between high and low density hatchery environments and between hatchery and natural lake environments (Paper V). If similar phenotype is favorable in two consecutive environments, the average growth rate may decrease or increase as a response to the new environment, but individuals that had a high growth rate in the old environment should also have a high growth rate in the new environment (positive phenotypic correlation in growth between the two environments). In other words, the environment may modulate the mean growth rate of the population, but the relative differences among the individuals may remain the same. In contrast, if different phenotypes are favored in the new environment than in the old, the predictability of the growth trajectory may break down (no phenotypic correlation in growth between the two environments). In this case, individuals that had high growth rate in the old environment may not have high growth rate in the new environment, and therefore the relative differences in growth among individuals between the old and new environments may change. Because growth rate is correlated with fitness, a change in the relative performance of individuals across environments implies that genotypes (individuals) that had the best phenotype in the old environment do not necessarily have the best phenotype for the new environment (for examples, see Roff 1992, Stearns 1992).

At the low density hatchery environment, we found that between-tank differences in the fish density modulated significantly the mean growth rate of the fish. In the wild, differences in the food quality caused significant between-lake differences in the mean growth rate of trout. In other words, we found environmental factors that modulated the mean growth rate of the fish population in both contrasted sets of environments.

At the individual level, a significant positive growth correlation was found between high and low density hatchery stocks, indicating that growth was determined by similar phenotypic traits at the hatchery. In majority of the cases (i.e. in 22 cases out of 24) growth correlation between hatchery and nature was poor. This was true for fish stocked in fall or they were stocked in a lake where they had to learn to forage on bottom-dwelling invertebrates. Only for two cases when the trout were released in spring to a lake with small fish as main prey (i.e. IPO in 1992 and 1994) growth rate at the hatchery was significantly correlated with growth in the wild.

Our results suggest that when the consecutive environments differ dramatically, relative performance of individuals may change. Hence, growth rate may be affected by different phenotypic traits depending on the ecological characteristics of the foraging environment. Our result emphasizes that evolutionary quality of an individual does not necessarily carry further than the environment where it is measured; genotypes that have the best phenotype in one environment do not necessarily have the best phenotype in another environment.

3.4 Is it possible to improve stocking success of brown trout by human actives?

Our knowledge on factors determining stocking success of brown trout in Finnish lakes has increased soundly in the 1990s. Vehanen (1995) detected that high yields of stocked brown trout were found in lakes with proportionally high yields of vendace and whitefish (potential food of trout) and proportionally low yields of pike and burbot (potential predators of trout). Vehanen and Aspi (1996) suggested that most Finnish lakes could be classified to the corresponding food-rich and predator-rich lakes in order to justify stocking of brown trout in relation to food reserve and the risk of predation. All the lakes used in the present study were characterized by relatively high yields of vendace and whitefish and relatively low yields of pike and burbot. Although whitefish was an important species in the yields (especially in KYL), only one trout out of 1532 actually fed on whitefish. On the other hand, fish prey < 1 g were highly preferred by the brown trout, but they were not caught by any fishing gear. The yield of vendace was highest in IPO in 1993 because the fish of the strong 1991 year-class were large enough for commercial fishery. During this particular year 1993, the stocked brown trout, however, shifted to feed on nine-spined stickleback because fish of the current vendace population were too large for the trout (Paper III). In summary, catch statistics were seriously unsuitable for independent estimates of available prey abundance, and hence the lake classification scheme proposed by Vehanen and Aspi (1996) may be an unwarranted tool in adjusting stocking rate of brown trout in a given lake and year. It may be, however, useful in a general level: stocking brown trout into a lake famous for strong stocks of pike, for example, is certainly not a very wise decision.

It would be important that managers in Finland as well as in other northern countries could understand and accept the fact that at high latitudes, interannual variation in the abundance of vendace, as well as other fish species predated by brown trout, is often considerable. Our possibilities to predict this variation are small because seasonal and environmental factors controlling for the variation are casual (Paper II). However, the stocked brown trout clearly preferred very small prey fish, and therefore any procedure that allow information on abundance of these stocks would be highly useful in adjusting stocking of brown trout. In Paper II, we suggested that if larval mortality of vendace could be modeled, it would be a useful tool in estimating abundance of prey fish stock. Because density and growth of vendace are inversely related, it would also be possible to predict the time period when the vendace are at vulnerable size for brown trout. This procedure would allow a true empirically based tool for trout management, and, what is the most important, these decisions could be made early enough. However, gathering data for such model would probably be expensive. Therefore, it is quite evident that use of this tool would be relevant only in lakes with combined interests of commercial vendace fisheries and management of brown trout.

Finally, a common 'hypotheses' proposed by many hatchery-oriented managers that fast growth rate at the hatchery is a indicator of fast growth in the wild, seems to be a untrue conclusion for brown trout according to the results of the present study. It is well known that there are between-stock differences in growth rate, and that considerable additive genetic variance occurs in the traits affecting growth rate in many cultured salmonid species (Gjerde 1986). The present results, however, suggest that very little, if anything, could be done by selection programs for growth rate at the hatchery in order to improve growth rate in the wild. The traits important for growth in the natural environment are not necessarily the traits that are selected for in the hatchery environment, suggesting that also fitness rank of an individual depends strongly on the environment. Therefore, it would be important that the conservation programs of wild stocks of brown trout would be designed so that the effect of size-dependent fecundity variation is not allowed to affect the composition of the next generation. This may be achieved by using similar numbers of eggs for each female in the breeding.

The best and probably the only extensive solution for management and conservation of the Finnish lake-run stocks of brown trout would be an essential decrease in the gillnet fishery. Rehabilitation of poor stream conditions, for instance, may exhibit worthless work without parental fishes spawning there. Ecological and sociological consequences of the fishery where gillnets are replaced by other gears are exclusively unstudied area, simply due the fact that gillnetting is a throughout exercise in the Finnish freshwaters. Such studies, however, should be done before manifesting any serious discussion on the citizens' legalization to use gillnets in Finland.

4 CONCLUSIONS

In this work I have shown that growth, fat accumulation and yield of juvenile brown trout stocked into boreal lake environment were dependent on the diet (food supply) of the trout. Growth of piscivorous trout was considerable faster than that of insectivorous trout which showed also decreasing storage lipids during the first growing season. Relative yields were highest in lakes and years when the trout fed on small fish. Large post-smolt sized trout showed poorest performance independently on the quality of the foraging environment. The recruitment of an autumn spawning vendace was determined in the following spring due to variation in larval mortality during the first three weeks after the ice-break. Predator-prey interaction between brown trout and vendace was sensitive to growth of vendace, as we found that increase in the size of vendace decreased predation by trout. At the individual level, we were able to demonstrate that growth rate in the wild (lake) was generally independent on the growth rate at the hatchery.

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YHTEENVETO

Muikun kannanvaihtelujen vaikutus järvitaimenistutusten tuloksellisuuteen

Koillismaalla vuosina 1991–1997 toteutetun tutkimushankkeen tavoitteena oli tutkia kenttäkokein, miten istutusjärvien ravintoresurssit vaikuttavat eri kokoisten ja ikäisten järvitaimenistukkaiden kasvuun ja vararavinnon määrään ja saaliiseen. Tutkimuksessa merkittiin neljän ikäisiä taimenia, joiden istutuspaino vaihteli 30 g ja 400 g välillä. Paikalliset kalastajat keräsivät vuosina 1991–1996 1532 merkittyä taimenta. Muikun keväisen poikaskuolevuuden ja seuraavana talvena rekrytoituvan kannan suhdetta tutkittiin toisella laajalla kenttäaineistolla.

Taimenistutusten tuloksellisuus oli riippuvaista siitä, kuinka suuressa määrin taimenet pystyivät syömään pienikokoista (< 4 g) kalaravintoa, kuten muikkua, kymmenpiikkiä tai kesänvanhaa ahventa. Kasvu oli silloin erinomaista: n. 40 grammaiset istukkaat olivat kahden kasvukauden jälkeen noin 1 kilon painoisia ja n. 150-grammaiset vastaavasti noin 2,4-kiloisia. Istukkaat pystyivät lisäämään myös vararavinnon määrää kasvukauden aikana, joka luultavasti paransi istukkaiden elossapysymistä talven yli, josta syystä istukkaista saatu saalis oli selvästi suurempi kuin istukkaiden paino istutushetkellä. Jos istutusjärvessä ei ollut tarjolla kalaravintoa, istukkaat söivät enimmäkseen hyönteisravintoa. Tällöin niiden kasvu oli 2–3 kertaa huonompaa kuin hyvässä tilanteessa. Tätäkin tärkeämpää oli se, että istukkaat käyttivät kaiken kalanviljelylaitoksessa kertyneen vararavinnon loppuun ensimmäisenä kasvukautenaan (jolloin kasvu oli erittäin heikkoa), joka luultavasti nosti istukkaiden talvenaikaista kuolevuutta. Huonossa ravintotilanteessa istutuksista saadun saalin paino oli pienempi kuin istukkaiden paino istutushetkellä. Istutusajalla (kevät versus syksy) tai istukkaiden iällä oli huomattavasti vähäisempi vaikutus istutustulokseen, lukuunottamatta suurimpia noin. 300-grammaisia istukkaita, joiden antama tulos oli huono ravintotilanteesta riippumatta.

Rekrytoituvan muikkuvuosiluokan vahvuus määräytyi sen mukaan, mikä oli muikunpoikasten kuolevuus kolmen ensimmäisen viikon kuluessa jäiden lähdöstä. Peto-saalis -suhde taimenen ja muikun välillä oli hyvin herkkä muikkupopulaation kasvulle: kun muikut saavuttivat yli neljän gramman koon, taimenet siirtyivät syömään muita pienikokoisia ravintokaloja kuten kymmenpiikkiä. Taimenistukkaiden yksilöllinen kasvunopeus järvissä oli riippumatonta niiden kasvunopeudesta laitosvaiheessa. Toisin sanoen nopea laitoskasvu ei ennusta nopeaa kasvua luonnonympäristössä, luultavasti siksi, että kasvua ohjaavat piirteet ovat erilaisia eri ympäristöissä.

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Responsibilities of Teuvo Niva in the articles of this thesis

Paper I. I was responsible in planning, designing, tagging and collecting all data. I analyzed the trout in the laboratory. Anita Väisänen was responsible in lipid analysis. I handled the data and wrote the article.

Paper II. Juha Karjalainen planned the study and organized the collecting of data. I collected the vendace samples and CPUE data from Lake Kitka. I took part in analyzing the data and writing the article.

Paper III. I was responsible in planning, designing, tagging and collecting all data. I analyzed the trout in the laboratory. I handled the data, except the log-linear analysis was made by Markku Julkunen, and wrote the article.

Paper IV. I was responsible in planning, designing, tagging and collecting all data. I handled the data and wrote the article.

Paper V. I was responsible in planning, designing, tagging and collecting all data. I analyzed the trout in the laboratory. We handled the data and wrote the article together with Jukka Jokela.

I

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

Teuvo Niva

Annales Zoologici Fennici 36 (in press)

http://www.annzool.net/PDF/anzf36/anzf36-103p.pdf

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II

Unpredictability of fish recruitment: interannual variation in young-of-the-year vendace (*Coregonus albula* (L.)) abundance

Submitted

Juha Karjalainen, Heikki Auvinen, Harri Helminen, Teuvo Niva, Jouko Sarvala, and Markku Viljanen

https://doi.org/10.1111/j.1095-8649.2000.tb00876.x

III

Effect of population fluctuation of vendace (*Coregonus albula*) on the diet and growth of stocked brown trout (*Salmo trutta*)

Teuvo Niva and Markku Julkunen

Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 50: 295–303.

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IV

Retention of visible implant tags by juvenile brown trout

Teuvo Niva

J. Fish Biol. 46: 997–1002.

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V

Phenotypic correlation of juvenile growth rate between different consecutive foraging environments in salmonid fish: a field experiment

Teuvo Niva and Jukka Jokela

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