Interspecific and intraspecific competitive interactions in Brook charr, *Salvelinus fontinalis*, and Brown trout, *Salmo trutta*.

Andreas Malmros

SVERIGES LANTBRUKSUNIVERSITET

SLU

Examensarbete 20p
vt – 2006
Handledare: Pär Byström

Institutionen för Vattenbruk
901 83 Umeå

Abstract.

A large-scale field enclosure experiment was conducted to examine the contradicting information about the competitive interactions between YOY brown trout and YOY brook charr. Interactions that is supposed to be based on aggression and growth capacity. Different densities of brown trout and brook charr were held together and alone in earth ponds for six weeks to evaluate choice of diet and growth rate. There were large differences between brown trout and brook charr in the their growth responses due to intra- and interspecific competition. Brook charr had the highest growth capacity of the two species. Despite that brook charr had a higher growth capacity and also a larger gap than brown trout, had brook charr only higher growth rate than brown trout when alone while brown trout not were affected by the presence of brook charr. Brown trout were less affected by interspecific competition from brook charr and were more affected by intraspecific competition. Since trout had a higher growth rate than charr in the sympatric treatments, this suggests that trout is the better competitor in environments like lakes, ponds and pools where resources are harder to monopolise through interference interactions.

Introduction.

Interspecific and intraspecific competition between individuals for resources has profound impact on individual growth rates, fecundity and survival. (Begon et al. 1996; Marchand & Boisclair 1997; Wootton 1998; Giller & Malmström 2001). In size-structured populations such as fish, body size can vary up to five orders of magnitude leading to complex competitive interactions both within and between populations and species (Byström et al. 1998; Persson et al. 1998; Byström & Garcia-Berthou 1999). For instance, competition during juvenile stages has been shown to have major effects on recruitment, overall population dynamics and species interactions (Svärdsson 1976; Persson & Greenberg 1990; Byström et al. 1998; Wootton 1998). The in many cases severe negative competitive impact by introduced, non native species on the domestic ecosystem fauna has received considerable increasing interest as intentional and unintentional introduction of exotic species have increased dramatically during the last decade (Kautsky & Kautsky 2000). A common example of introduction of non native species is salmonid fishes, which has been introduced throughout the world, generally with little attention paid to the effects on native species (Fauch 1988; Dunham et al. 2002). As a consequence, salmonids are today among the globally most wide-spread fresh water fishes (Fauch 1988; Dunham et al. 2002). As an example: brook charr (*Salvelinus fontinalis*), native to eastern North America, are now concidered to be one of the most common small-stream salmonid in the western North America and have extirpated the indigenous cutthroat trout (*Oncorhynchus clarkii spp)* in several small streams (Buys 2002). Brook charr have similary been suggested to negatively affect brown trout (*Salmo trutta*) densities in many Scandinavian waters (Kjellberg 1969). It has been suggested that YOY brook charr has an advantage over YOY brown trout due to a higher maximum growth rate and aggressiveness (Nyman 1970). In contrast, non-native brown trout has been suggested to exclude native brook charr from their prefered habitat and negatively affect brook charr densities and distribution in North America (Fauch and White 1981; DeWald and Wilzbach 1992). In order to examine potential mechanisms behind the contradicting information about the competitive interactions between YOY brown trout and YOY brook charr or brook trout (hencefourth will I refere to them as brook charr or just charr). I conducted a large scale pond experiment to in more detail analyse the competitive interaction between the two species.

Methods.

Experimental ponds and design.

I conducted an experiment to analyse the effects of intra- and interspecific competition on YOY of brook charr and brown trout. Two closely situated ponds (32m x 10,8m in size) located in Umeå, in the middle of Sweden, each divided into eight enclosures, were used for the experiment. The enclosures (4m x 10,8m, mean depth 0.9m) were separated by a reinforced dark-green plastic sheet. Each enclosure had an inflow of fresh water of 0,3 m^3/h and as each pond only had one outlet at one end of pond, each plastic sheet had an 20 cm opening reaching from the bottom to the surface made of plastic net (mesh size 3mm) to allow water to flow to the outlet. The two ponds were cleared from sub-merged vegetation (*Potamogeton spp*) one week before the introduction of fish. Freefloating green algae was removed from the ponds twice during the experiment with a large handnet and at the end of the experiment the sub-merged vegetation covered 5-10 % of the bottom surface in the one of the ponds and 35-50 % in the other pond. Herefourth I will refere to them as the vegetated pond and the pelagic pond. I used a design with four different treatments replicated four times with two replicates in each pond. 60 individuals of each species separate, single species treatment, (0,72 individuals/ m^2), a mix of 60 brook charr with 60 brown trout, high density mixed treatment, (1.44 individuals/ m^2) and a mix of 30 brook charr with 30 brown trout, low density mixed treatment, (0,72 individuals/m^2). The experiment started in early July and lasted for six weeks.

Fish.

Both YOY trout and charr were hatched and brought up in a fishfarm[1] in the middle of Sweden. After transport to Umeå, the species were held separately in two large holding tanks in the laboratory for one week prior to introduction to the enclosures. During this time, the fish were fed frozen *chironimidae* larvae. On the introduction day, (t1 on the 10/7) the fish were sorted to homogenize size distribution and thereafter released into the enclosures. At the same time a sample of 30 fish from each species were collected for initial size distribution (average for charr: 42mm/0,72g, (±1SD 2,6mm/0,13g) and trout: 44mm/1,03g (±1SD 2,45mm/0,18g)). After 14 days, (at t2, the 25/7) 10% of the fish (3 or 6 individuals of each species) were sampled from each enclosure with a seine net for later growth and stomach analysis. After 42 days (at t3 on the 22/8) the experiment was terminated and all of the fish were captured with the seine net. The net were drawn repeatedly in each enclosure until two empty drawings followed each other. All sampled fish were deep frozen until examination in the laboratory. Average survival (recapture) were between 80-100% and there were no difference between treatments in survival but the survival of brook charr differed between ponds (Two-way ANOVA: $p= 0.09$; $F= 3.86$). Escapees were found in two different enclosures: at least 14 charr from a 60 alone treatment were found in a low-mix density treatment and at least nine charr and four trout from a low-mix density treatment were found in a 60 charr alone treatment, still the eventual effect of this would be rather small and if any an increase in between replicate variation is expected and hence a decrease in the risk of making statistical type one error. In laboratory all fish were measured to the closest mm and weighed to nearest 0.01g, stomachs were sampled from 12 individuals round the average size of individuals within each enclosure. The stomachs were conserved in 96% alcohol until examination.

The prey items in all of the stomachs from t2 and 5 of the stomachs (or more if any were empty) from each species and treatment at t3 were counted and classified to suborder, family or genus. Body lengths of 10 individuals (if possible) from each taxa (and size classes within some taxa) were measured to the nearest 0.1mm. The lengths of prey were then transformed to dry weights by using weight-length relationships (Dumont et al. 1975 and Bottrell et al. 1976 for zooplankton and Persson et al. 1996 for macroinvertebrates).

---

[1] Bröderna Olssons fiskodling. Lottefors.

In order to investigate potential competitive advantages due to gape size differences species gape size were estimated by measuring the gape height to nearest 0,1mm at 90° cheek angle within the size range of 34 to 92 mm for trout (n = 137) and 32 to 80mm for charr (n = 106).

Resources.

Zooplankton fauna were sampled at the start, in the middle and at the end of the experiment with a circular (diameter 250mm, mesh size 100µm) handnet drawn 4m horizontally at a depth of 0,1m in the deepest part of the enclosures. Zooplankton were conserved with Lugol´s solution. In the laboratory, the animals were counted and classified to suborder, family or genus and the body lengths of 20 individuals, or all if fewer, of each category were measured to the nearest 0,01mm. Lengths were then transformed to biomass using regressions relating length to dry weight (Dumont et al. 1975 and Bottrell et al. 1976)

The bentic fauna were sampled at the start and at the end of the experiment with a handnet (290mm high x 190mm wide, mesh size 0,5mm). The net were drawn along the bottom at one short side of each enclosure. Captured macroinvertebrates were preserved in 96% alcohol. In the laboratory, animals were counted and classified to suborder, family or genus and the body lengths of 20 individuals, or all if fewer, of each category from each sample were measured to the closest 0,1mm. Lengths were transformed to biomass using weight-lenght relationships (Persson et al. 1996). Macroinvertebrates were categorized into three groups concisting of chironomids, predator sensitive macroinvertebrates (PSM) and others. The group PSM concists mainly of ephemeroptera but also of *Acellus*, heteroptera, trichoptera, coleoptera and odonata. The group others concists mainly of *Gyralus* but also of *Lymnea* and bivalvia.

Results.

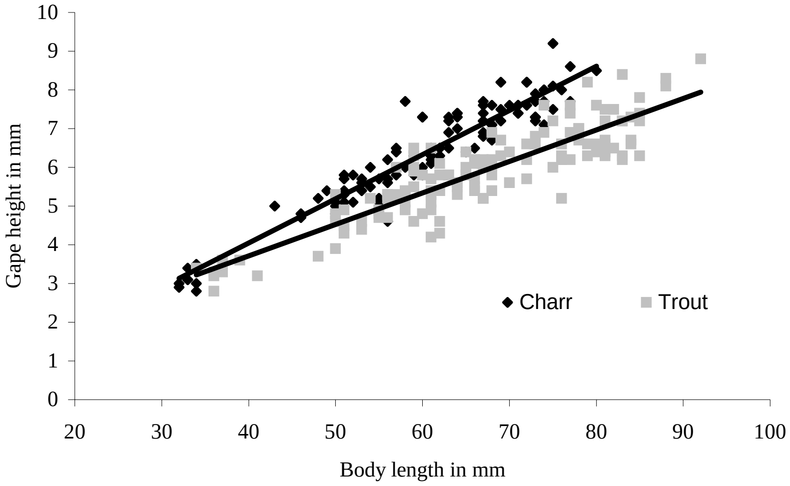


Figure 1. Gape height in relation to body length (height at 90° cheek angle) in charr and trout.

Fish.

Charr had a larger gape size in relation to body length than trout (ANCOVA: F=8.657; p=0.004) and the difference increased with fish size (figure 1)(ANCOVA: F=690.942; p=0.000). Despite their differences in gape size there was no difference in maximum prey size found in the diets between species, and if any there was a tendency for trout to include larger prey than charr (figure 2).

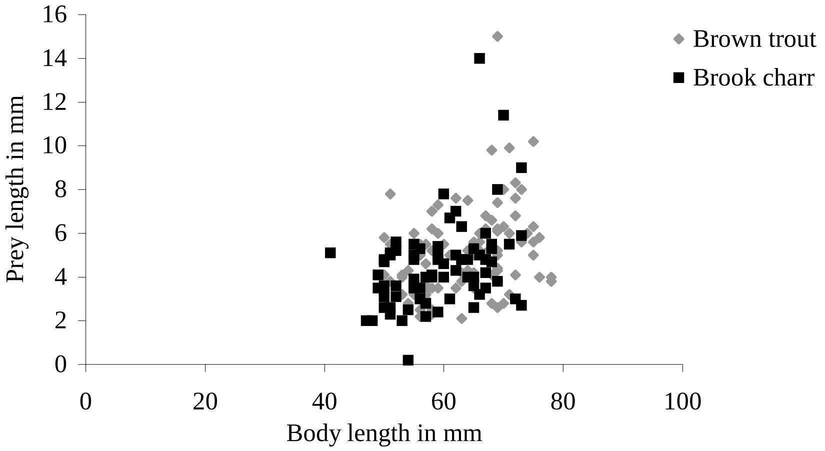
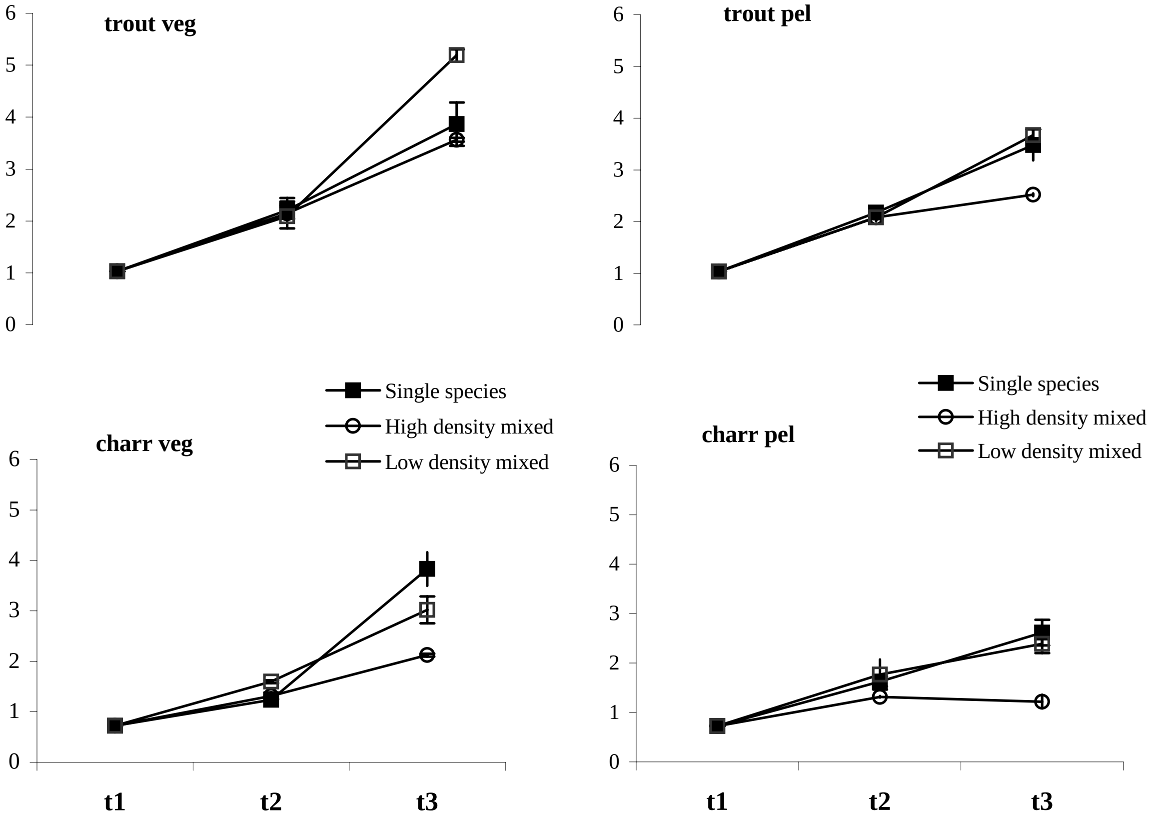


Figure 2. Largest measured prey lengths compared to body lengths in the two species.

Trout and charr differed in the their growth responses in the different treatments and between ponds (table 1 & 2 and figure 3 & 4), and both species had generally a higher growth in the vegetated pond than in the pelagic pond. Charr had the highest specific growth rate in the allopatric treatment whereas trout had the highest growth rates in the low density mixed treatment. Charr also had the highest growth potential (single species treatment in the vegetated pond) but also responded more strongly to increased competition than trout (table 1 & 2 and figure 3 & 4)



Figures 3 a-d. Increase in weight (g) over time in trout and charr in the different treatments and ponds. Vegetated pond to the left and the pelagic pond to the right.

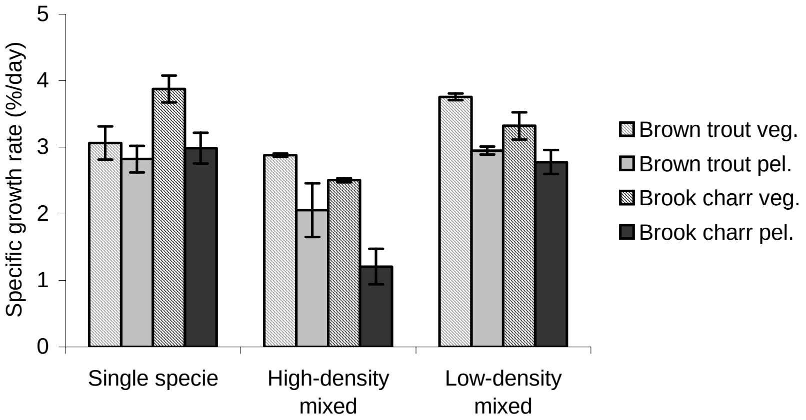


Figure 4. Specific growth rate of brown trout and brook charr in the different treatments and ponds.

Table 1. Results of Repeated-measure ANOVA's of the effects of treatments and pond over time on weight increase of charr and trout.

	weight increase				
		Charr		**Trout**	
Source of variation	**df**	**F**	**p**	**F**	**p**
treatment	2,6	30.238	**.001**	.877	.463
pond	1,6	126.103	**.000**	7.809	**.031**
treatment x pond	2,6	26.222	**.001**	5.191	**.049**
time x treatment	4,6	12.218	**.000**	2.109	.142
time x pond	2,6	52.66	**.000**	17.260	**.000**
time x treatment x pond	4,6	11.688	**.000**	18.582	**.000**

Table 2. Results of a Three-way Anova of the effects of species, treatment and pond over time on specific growth rates.

	specific growth rate		
Source of variation	**df**	**F**	**p**
species	1,12	5.460	**0.038**
treatment	2,12	51.754	**0.000**
pond	1,12	58.078	**0.000**
species x treatment	1,12	11.841	**0.001**
species x pond	2,12	4.438	0.057
treatment x pond	2,12	8.560	**0.005**
treatment x species x pond	2,12	2.649	0.111

Diet.

There were small differences in diets between the two species when they were alone (single species treatments) indicated by no significant differences between species main effects for most prey categories. The only difference found was in the group benthic cladocerans which were more represented in the trout diet (table 3 and figure 5). However, when coexisting in the mixed treatments, the diet differed between the species and charr diet constituted more of zooplankton (pelagic and benthic) whereas trout diet was more dominated by PSM (table 4 & figure 5). Overall, pelagic cladocerans were more common in the diet in the vegetated pond and in both species, chironomids decreased in dominance over time whereas, the dominance of PSM in the diet increased over time (table 3 & figure 5). The prey category others decreased in the charr diet over time and trout decreased the use of chironomids over time in the vegetated pond.

The general effects of treatment on diet of either charr or trout were otherwise small and the only difference found was that charr had more benhtic cladocerans in the diet in the mixed treatments (table 4 and figure 5).

Table 3. Results of Repeated-measure ANOVA's (*F*-values) of the effects species and pond over time on the diets of charr and trout. Diet test in mixed treatments shows results of diet in both low and high density mixed treatments.
Bold numbers indicate significant tests at the level of $p < 0.05$.
Significant level:* = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $P < 0.001$

Source of variation	***df***	***Pelagic Cladocerans***	***Benthic Cladocerans***	***Chironomids***	***PSM***	***Others***
Diet test in single species treatments						
species	1,4	2.227	**9.369***	.134	.185	2.227
pond	1,4	.814	.080	.580	1.332	.009
species x pond	1,4	3.072	3.958	5.368	.188	.584
time	1,4	.620	1.392	**27.738****	**35.645****	5.088
time x species	1,4	.046	.319	.127	.237	1.034
time x pond	1,4	1.187	2.554	.889	2.908	.062
time x species x pond	1,4	.019	.021	.386	.059	7.555
Diet test in mixed treatments						
species	1,4	**5.130***	**7.738***	.554	**12.741****	.312
pond	1,4	**6.636***	3.394	1.327	1.367	3.696
species x pond	1,4	.405	3.109	.102	1.818	.161
time	1,4	.777	1.154	**6.650***	**5.403***	.324
time x species	1,4	.799	.329	.004	.004	1.764
time x pond	1,4	.310	.828	4.226	1.461	.025
time x species x pond	1,4	.357	.159	.272	.002	.012

Table 4. Results of Repeated-measure ANOVA's (*F*-values) of the effects of treatment and pond over time on the diet of charr and trout. Bold numbers indicate significant tests at the level of $p < 0.05$.
Significant level:* = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $P < 0.001$

Source of variation	***df***	***Pelagic Cladocerans***	***Benthic Cladocerans***	***Chironomids***	***PSM***	***Others***
Charr diet						
treatment	2,6	.618	**10.997***	2.943	.493	2.771
pond	1,6	**9.844***	2.388	3.355	1.693	4.287
treatment x pond	2,6	.703	3.316	1.276	.037	.088
time	1,6	.041	.286	**8.110***	**10.393***	**20.864****
time x treatment	2,6	2.572	.085	1.387	2.802	2.258
time x pond	1,6	1.231	.199	.630	1.989	1.566
time x treatment x pond	2,6	.016	3.873	.522	2.257	**14.177***
Trout diet						
treatment	2,6	2.283	1.062	2.187	1.018	1.453
pond	1,6	.399	.933	.177	.441	.249
treatment x pond	2,6	.869	2.046	2.614	3.412	1.608
time	1,6	1.926	3.924	**22.673****	**22.221****	.042
time x treatment	2,6	.169	.166	4.930	2.718	.323
time x pond	1,6	.149	.943	**6.553***	2.768	.101
time x treatment x pond	2,6	.188	.195	.051	.077	.275

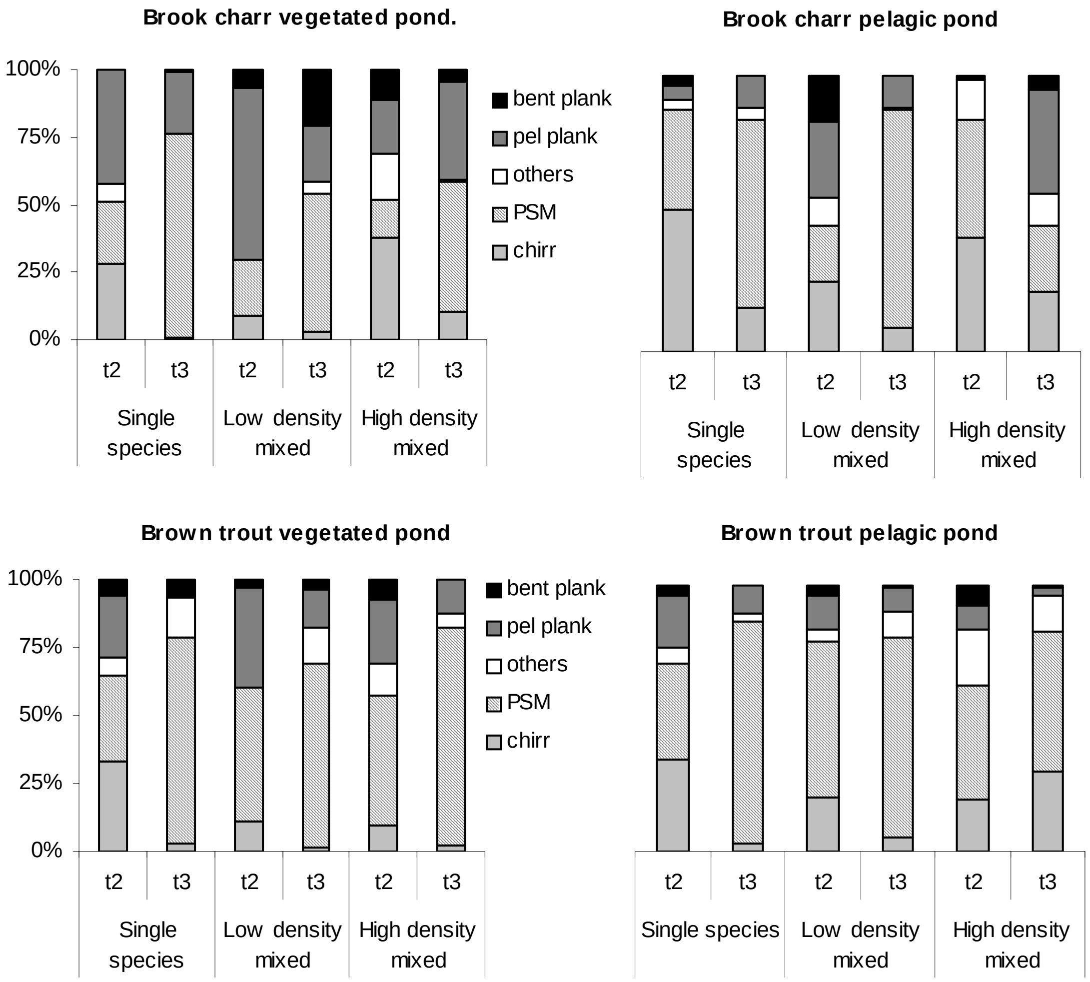
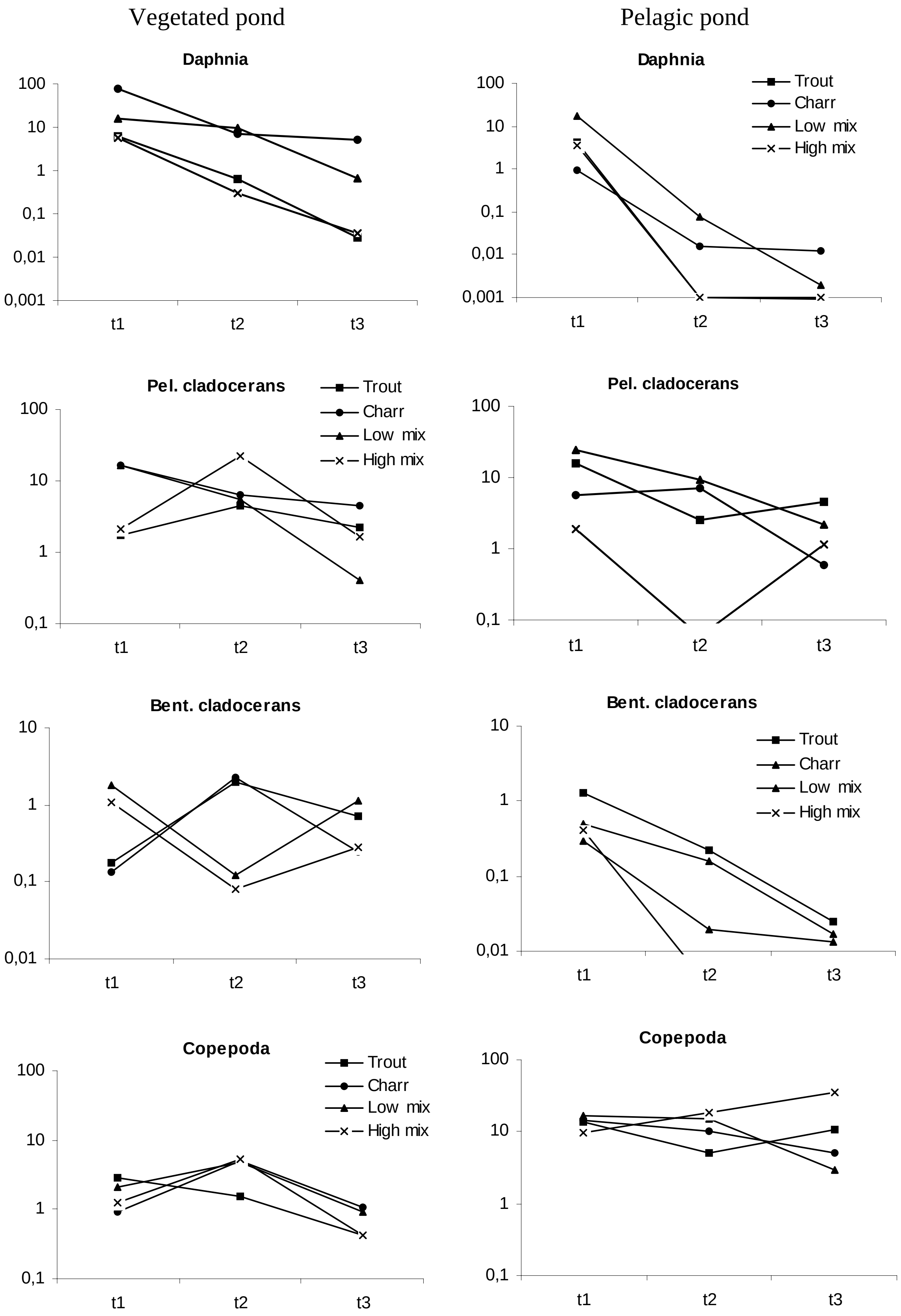


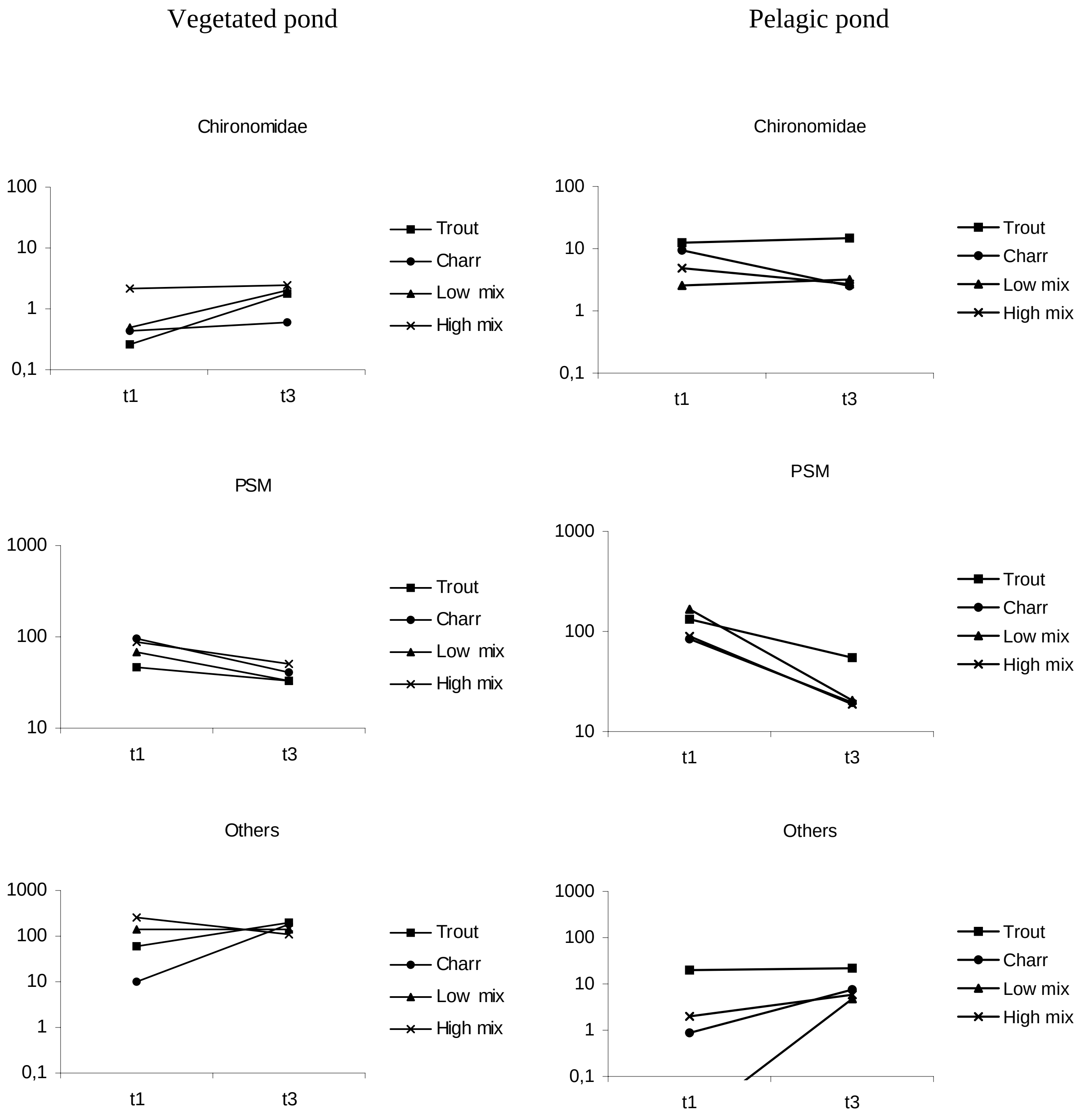
Figure 5. a-d. Diets in percent of stomach contents in the middle and at the end of the experiment of charr and trout in the different treatments and ponds.

Resources.

There were small effects of the different treatments on zooplankton resources, and only *Daphnia* showed strong effects and densities of Daphnia was more reduced in the trout alone treatments and high density mixed treatments (table 5 and figure 6). There was also differences between ponds in *Daphnia* and copepods, higher levels of *Daphnia* and lower levels of copepods were found in the vegetated pond in relation to the pelagic pond (table 5 & figure 6). Both *Daphnia* and pelagic cladocerans declined over time and *Daphnia* were found at much lower levels at t2 and t3 in the pelagic pond in relation to the vegetated pond (table 5 & figure 6).



Figures 6 a-f. Zooplankton resources levels in the different treatments and ponds over time, dry biomass in ug/l.



Figures 7 a-f. Macroinvertebrate resources levels in the different treatments and ponds over time, dry biomass in mg/l.

Table 5. Results of Repeated-measure ANOVA’s (*F*-values) of the effects of species, treatment and pond over time on zooplankton resources levels among the different treatments. Bold numbers indicate significant tests at the level of $p < 0.05$. Significant level: * = $0.01< P <0.05$, ** = $0.001< P < 0.01$, *** = $P <0.001$.

Source of variation	**df**	***Daphnia***	**Pelagic Cladocerans**	**Benthic Cladocerans**	**Copepods**
treatment	3,8	**8.803***	1.396	0.223	1.126
pond	1,8	**35.211*****	0.257	2.236	**43.538*****
treatment x pond	3,8	**10.175***	2.805	0.035	0.613
time	2,16	**23.256*****	**7.896***	1.018	2.985
time x treatment	6,16	0.546	1.351	0.681	1.192
time x pond	2,16	0.745	1.836	0.757	1.997
time x treatment x pond	6,16	0.683	1.280	0.865	0.838

No effects of treatment were found on the macroinvertebrate fauna whereas there were differences between ponds in densities of chironomids and others (table 6). Chironomids were found at higher levels in the pelagic pond whereas on the group others showed the opposite pattern (figure 7). PSM declines in both ponds but with a higher rate in the pelagic pond (table 6 & figure 7). Overall, the resource level were higher in the vegetated pond then in the pelagic pond and decreased in both ponds over time (figure 6 & 7).

Table 6. Results of Repeated-measure ANOVA's (*F*-values) of the effects of treatment and pond over time on the macroinvertebrate resource levels among the different treatments Bold numbers indicate significant tests at the level of $p < 0.05$. Significant level: * = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $P < 0.001$.

Source of variation	df	Chironomids	PSM	Others
treatment	3,8	0.881	0.201	0.765
pond	1,8	**19.266****	0.010	**8.827***
treatment x pond	3,8	0.959	2.649	0.613
time	1,8	0.022	**55.741*****	4.519
time x treatment	3,8	1.131	1.631	0.377
time x pond	1,8	3.605	**8.807***	0.087
time x treatment x pond	3,8	0.225	0.476	1.027

Discussion.

There were large differences between trout and charr in the their growth responses to the different treatments and between ponds. Charr had a higher growth potential than trout which is concistent with Nyman's (1970) and Öhlund's (2004) findings. However, charr only had higher growth rate than trout in the allopatric treatment in the vegetated pond. Trout on the other hand had their highest specific growth rates in low density mixed treatments in the vegetated pond and had a higher growth rate than charr in all of the sympatric treatments. Thus, charr seems to be more affected by the presence of trout than the presence of equal density of intraspecific competitors whereas trout were more affected by intraspecific competition than by competition from charr (compare low density mixed treatments vs. charr treatments), which is supported by DeWald and Wilzbach (1992) who found that trout had a negative effect on charr activity.

Growth for both charr and trout were higher in the vegetated pond than in the pelagic pond, which together with the lower resource levels suggests that production was lower in the pelagic pond (Byström and Andersson (2005) found similar production rates in the two different ponds). Hence, charr seemed to suffer in low productive environments as the growth in the low productive pelagic pond were strongly reduced to almost 1% of that in the high density mixed treatment. This suggest that charr in low productive waters may experience starvation in sympatry with trout, which also has been suggested by Waters (1983) and Dunbrack et al. (1996). Despite the fact that charr has a larger gape than trout there was nothing that suggests that this had any competitive advantage for charr or that charr were able to ingest larger food items as there were no difference between the species in maximum prey size consumed. There were no clear differences in diets between the species in allopatric treatments but when coexisting there were differences between the species in their diet choice suggesting that there are competitive interactions between the species which is also supported by Nyman (1970) and DeWald & Wilzbach (1992). DeWald & Wilzbach also found that both charr and trout due to loss in efficiency decreased their numbers of prey captured per time unit in sympatry in relation to allopatry and that charr were more affected than trout.

There was no strong evidence for exploitative competition as resource levels in both ponds were fairly similar between treatments. However, declining resource levels overall in both ponds during the experiment together with species specific and density dependent growth responses suggest that resources were limited, see also Byström and Andersson (2005), and Nilsson (2005) for similar growth responses between the two different ponds. *Daphnia* were strongly reduced in abundance half way through the experiment and the effect were stronger in the trout treatments and high density mixed treatments. Both species seemed to prefer pelagic plankton and *Daphnia* in particular (see also Parker et al. 2001 for charr) since despite the low resource levels of *Daphnia* at the end of the experiment, they were still present in both species diets. The variations in chironomids and predator sensitive macroinvertebrates (PSM) presence in the diet over time is not concistent with the estimated availability of resource levels over time, and might instead be dependent on increasing fish size over time, and hence, capacity to ingest larger preys and/or food preference. Hildebrand and Kershner (2004) have for example found that chironomids are not prefered food, at least not for charr, despite high abundance.

Competitive interactions within and between salmonids have been extensively studied and trout and charr is known to cause that other salmonid species change their habitat use. For example, in sympatry with trout, Artic charr (*Salvelinus alpinus*) is forced out in the pelagical while trout occupies the more productive litoral zone. This causes a change in diet for Artic charr from macroinvertebrates to more pelagic prey (Svärdsson & Nilsson 1985; Alanärä et al. 1994). Atlantic salmon (*Salmo salar*) in sympatry with trout, is found further out in the stream in relation to allopatric populations (Kennedy and Strange 1986; Heggenes and Saltveit 1990). Charr had advantages over cutthroat trout (*Oncorhynchus clarkii*) in a laboratory environment due to higher aggressiveness and feeding ability (DeStaso III and Rahel 1994). Charr also negatively affected first winter survival of wild cutthroat trout in a North American stream experiment (Gregory and Griffith 2000) however, due to species specific differences in size the authors suggests that the competition was size dependent.

Most of all above studies points to the importance of interference interactions between salmonid species. Even within species are strong interference present and according to Curry et al. (1993) charr growth is not strongly correlated with food quality but with differences in social behaviour, and Dunbrack et al. (1996) have suggested that decreasing food densities for charr are correlated with increased aggressiveness and which results in lower growth. However I can not with my experimental design and results distinguish between the effects of exploitative and interference competition between the two species. Still, since interference interaction are more likely to be dominant in lotic environments where positions in streams for access to food and shelter are important (Fauch & White 1981, 1986; Fauch 1988; Kozel & Hubert 1989; Näslund & Bergström 1994), than in lentic environment like the experimental ponds. In lakes, pools, or slow running waters, the opportunities of monopolisation of resource is less likely since resources in such environments are more or less evenly distributed. As charr is regarded to be the more aggressive of the two species in terms of feeding positions (Nyman 1970; Fauch & White 1986) the results of my experiment suggests that exploitative competition are the more important interaction between the species as trout had a stronger effect on charr growth than vice versa.

Acknowledgements.
First of all I would like to thank Pär B for all of his hard fighting with me and my statistical ignorence (much of which he is to blame). And last I wish to thank the Olsson’s for the fish!

Referenses.

Alanärä, A., Eriksson, L-O and Brännäs, E. 1994. *Röding (Salvelinus alpinus).* Laxfiskarnas biologi, Kompendium nr 9, pp. 34-39. (red. Alanärä, A) Swedish University of Agriculture Sciences. (Sw)

Begon, M., Harper, J. L. and Townsend, C. R. 1996. *Interactions.* Ecology. pp:211-482. Third edition Blackwell Sciences Ltd, London, England.

Bottrell, H. H., Duncan, A., Gliwich, Z., Grygierik, M., Herzig, E. A., Hillbrich-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419-465.

Buys, D. J. 2002 Competition between Bonneville Cutthroat trout and Brook trout in laboratory and field experiments. Master of Science Dissertation. Utha State University 2002

Byström, P. and Andersson, J. 2005 Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Artic char). Oikos 110: 523-536.

Byström, P. and Garcia-Berthou, E. 1999. Density dependent growth and size specific competitive interactions in young fish. Oikos 86: 217-232. Copenhagen, Denmark.

Byström, P., Persson, . and Wahlström, E. 1998. Competing predators and prey-juvenile bottlenecks in whole-lake experiments. Ecology 79: 2153-2167.

Curry, R. A., Allen, S., Fox, M. G. and Morgan, G. E. 1993. Growth and Food of young-of-the-year Brook Charr, Salvelinus fontinalis, in lake and creek environments.
Environmental Biology of fishes, 37 (2): 131-138.

De Staso III, J. and Rahel, F. J. 1994. Influence of water temperature on interactions between juvenile Colorado river Cutthroat trout and Brook trout in a laboratory stream. Transactions of American Fisheries Society 123:289-297.

DeWald, L. and Wilzbach, M. A. 1992. Interactions between Native Brook Charr and Hatchery Brown Trout: Effects on Habitat Use, Feeding and Growth. Transactions of the American Fisheries Society 121:287-296.

Dumont, H. J., Van de Velde, I. and Dumont, S. 1975. The dry weigth estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and bentos of continental waters. Oecologia 19: 75-97.

Dunbrack, R. L., Clarke, L. and Bassler, C. (1996). Population level differences in aggressiveness and their relationship to food density in a stream salmonid (*Salvelinus fontinalis*). J. Fish biol, 48 (4): 615-622.

Dunham, J. B., Adams, S. B., Schroeter, R. E. and Novinger, D. C. 2002. Alien invasions in aquatic ecosystems: Toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12: 373-391. (2003) Kluwer Academic Publishers. the Netherlands.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: What have we learned? Can. J. Fish. Aquat. Sci., Vol. 45: 2238-2246.

Fausch, K. D. and White, R. J. 1981. Competition between Brook trout *(Salvelinus fontinalis*) and Brown trout *(Salmo trutta*) for positions in an Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220-1227.

Giller, P. S and Malmström, B. 2001. The biology of streams and rivers. pp:187-191 Oxford University press. Oxford , England.

Gregory, J.S. and Griffith, J.S. 2000. First-winter survival of caged wild and hatchery cutthroat in allopatry and in sympatry with brook trout. Intermountain Journal of Sciences, Vol.6, No.3.

Heggenes, J. and Saltveit, S.J. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in an Norwegian river. J. Fish. Biol. 36:707-720

Hildebrand, R. H. and Kershner, J. L. 2004. Influence of Habitate Type on Food Supply, and Diet Overlap of Bonneville Cutthroat Trout and Nonnative Brook Trou in Beaver Creek, Idaho. North American Journal of Fish Management, (24): 33-40.

Kautsky, L. & Kautsky, N. 2000. *The Baltic Sea, Including Bothnian Sea and Bothnian Bay*. Seas at the Milennium: An Environmental Evaluation. (Edited by C. Sheppard). Chapter 8, pp:121-133. Elsevier Science Ltd. 2000.

Kennedy, G.J.A. and Strange, C.D. 1986. The effects of intra- and inter-specific competition on stocked juvenile Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream. J. Fish Biol. 28:479-489.

Kozel, S. J. and Hubert, W. A. 1989. Factors Influencing the Abundance of Brook Trout (*Salvelinus fontinalis*) in Forested Mountain Streams. Journal of Freshwater Ecology, Volume 5, Number 1:113-122

Kjellberg, G. 1969. Några data om bäckrödingen. Information från Sötvattenslab. Drottningholm 4: 6p (Sw).

Marchand, F. & Boisclair, D. 1997. Influence of fish density on the energy allocation pattern of juvenile brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 55: 796-805 (1998).

Nilsson, P. 2005. Effetcs of refuge availability on growth and survival of YOY Artic char (Salvelinus alpinus). Swedish Master's Level thesis. Swedish University of Agricultural Sciences, Department of Aquaculture.

Nyman, O. L. 1970. Ecological interaction of Brown trout, *Salmo trutta* L., and Brook trout, *Salvelinus fontinalis* (Mitchill), in a stream. The Canadien Field-Naturalist Vol. 84:343-350.

Näslund, I. & Bergström, P. 1994. *Öring (Salmo trutta).* Laxfiskarnas biologi, Kompendium nr 9, pp. 10-29. (red. Alanärä, A) Swedish University of Agriculture Sciences. (Sw)

Oberdorff, T., Hugueny, B., Compin, A. and Belkessam, D. 1998. Non-interactive fish communities in the coastal streams of North-western France. J. Animal. Ecol. 67: 472-484.

Parker, B. R., Schindler, D. W., Donald, D. B. and Anderson, R. S. 2001. The effects of stocking and removal of a nonnative salmonid on the plankton of an alpine lake. Ecosystems, Vol 4, pp 334-345

Persson, L. and Greenberg, L. A. 1990. Juvenile competitive bottlenecks: The Perch (Perca fluviatilis) – Roach (Rutilus rutilus) interaction. Ecology 71(1). pp. 44-56.

Persson, L., Andersson, J., Wahlström, E. and Eklöv, P. 1996. Size-specific interactions in lake systems: Predator gap limitation and prey growth rate and mortality. Ecology 77: 900-911.

Persson, L., Leonardsson, K., De Roos, A. M. et al. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. Theor. Popul. Biol. 54: 270-293.

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Report. Institute of Freshwater Research. Drottningholm 55. pp. 144-171.

Svärdsson, G. and Nilsson, N-A. 1985. Fiskebiologi. Report. Institute of Freshwater Research. Drottningholm. (Sw)

Waters, T. F. 1983. Replacement of Brook Trout by Brown Trout over 15 years in a Minnesota Stream: Produktion and Abundance. Transactions of the American Fisheries Society. Vol 112, pp 137-146.

Wootton, R. J. 1998. Ecology of teleost fishes. Kluwer Academic Publishers. Dordrecht, The Netherlands.

Öhlund, G. 2004. Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*). –Implications for distributional patterns in small lotic systems. Swedish Master's Level thesis. Swedish University of Agricultural Sciences, Department of Aquaculture.