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CONTENTS

Biochemical Genetic Variability and Taxonomy of a Marmorated Salmonid in River Otra, Norway

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Abstract

A salmonid species with atypic and distinct colouration, termed «marmorated trout» occurs in parts of the River Otra southern Norway. The objective of the study was to compare the biochemical genetic variability of the population to other salmonid populations and test the various explanation models for the phenomenon. All alleles detected were common brown trout alleles, and private alleles associated with the marmorated morph were not found. There were no indications of HW deviations or heterogeneity in the pooled sample containing all morphs, thus the samples are most likely drawn from a randomly mating brown trout population. There were no evidence of hybridization between brown trout and landlocked salmon (*Salmo salar* L.) or between brown trout and introduced brook charr (*Salvelinus fontinalis*). There was an unusual high frequency of the *CK-1*115* allele in all samples from River Otra. In the cluster analysis of 10 populations, the three populations from the Otra watercourse cluster together. The four sea trout populations cluster together, although located along a 650 km distance along the coast of Norway. The major branching pattern most likely reflects colonization history.

Keywords: Marmorated, brown trout, electrophoresis, taxonomy, colonization

Introduction

The variation observed in many salmonid species in phenotypic features such as colouration and spotting pattern, size, growth rate and age and size at maturation, has excited and confused biologists for more than a hundred years (Günther 1866, Ferguson 1989). Although some of the species in the family Salmonidae are among the most extensively studied fish species, potentially interesting populations have still not been studied, and populations with novel and undescribed features are still encountered (Ferguson and Mason 1981, Skaala and Jørstad 1987, Ferguson 1989, Schoeffmann 1994).

A freshwater resident salmonid population with atypic and distinct colouration, termed "marmorated trout" and "tiger trout" by local residents, is known to occur in certain parts of the River Otra in the Sætesdalen valley, southern Norway. The extraordinary large variability in the colouration of the population in the area has been recognized for over a hundred years, and the common brown trout morph is found together with the atypic morph and a number of intermediate morphs (Pottinger 1888). The frequency of the various morphs differs among localities within River Otra, as in some areas the atypical morph is completely missing, while in others it dominates. The geographical distribution of the marmorated morph is not known in detail, but according to anecdotal information, it has also been found scattered in upper areas of the watercourse. The atypical colouration of this population has not been reported to occur in Norwegian Salmonid populations outside River Otra.

The marmorated population in River Otra has not been described previously, and there is no

scientific information about this apparently local morph. Several hypothesies have been put forward to explain its occurrence. Two hypotheses explain the marmorated Salmonid as a species hybrid, the first of which as a hybrid between common brown trout (*Salmo trutta*) and introduced brook charr (*Salvelinus fontinalis*), the second as a hybrid between brown trout and landlocked salmon (*Salmo salar*) (Dahl 1927). According to Dahl (1927), a number of morphological features of a suspected hybrid were not those of trout, nor those of salmon, and accordingly Dahl was convinced that this was a hybrid between brown trout and the landlocked salmon. Until now, the phenomenon has not been studied, and thus it was not known if the marmorated morph is a species hybrid, or if the atypical marmorated and common morphs in the area represent two different taxonomic units, or if there is a local polymorphism in one or more loci regulating the expression of colouration in brown trout.

However, with biochemical genetic methods, species hybrids can easily and reliably be detected (Campton 1987, Verspoor and Hammar 1991). The objective of the study was to investigate the biochemical genetic variability of the marmorated salmonid population in the area to test the various explanation models for the phenomenon and to determine its taxonomic position.

Materials and methods

River Otra is a large river with a water discharge ranging from 15 to 400 $m^3 s^{-1}$. It runs from the upper part of the Sætesdalen valley and some 150 km before it discharges into the sea at Kristiansand on the southern coast of Norway (Fig. 1). The area was glaciated until 10,000 B.P. (Jacob Møller, University of Tromsø, pers. comm.), when a change in climate and a corresponding rise in temperature resulted in deglaciation and a land uplift. Thus, at present there is a barrier to ascending fish at the Vigelandsfossen waterfall, and the trout sampled from the watercourse represent freshwater resident populations. Two other salmonid fish species are found in the area, a landlocked population of Atlantic salmon, *Salmo salar* L., termed blege, and introduced brook charr, *Salvelinus fontinalis*. Thus, the marmorated morph could potentially be a species hybrid between two of the present species. The geographical distribution of the landlocked salmon is at present somewhat contracted compared to its original distribution, probably due to man made habitat disturbances. Its southern border is now Evje and its northern limit Ose in the northern part of Lake Byglandsfjord.

In June 1993 samples of trout were obtained from a local fishery in the Evje area, Sætesdalen
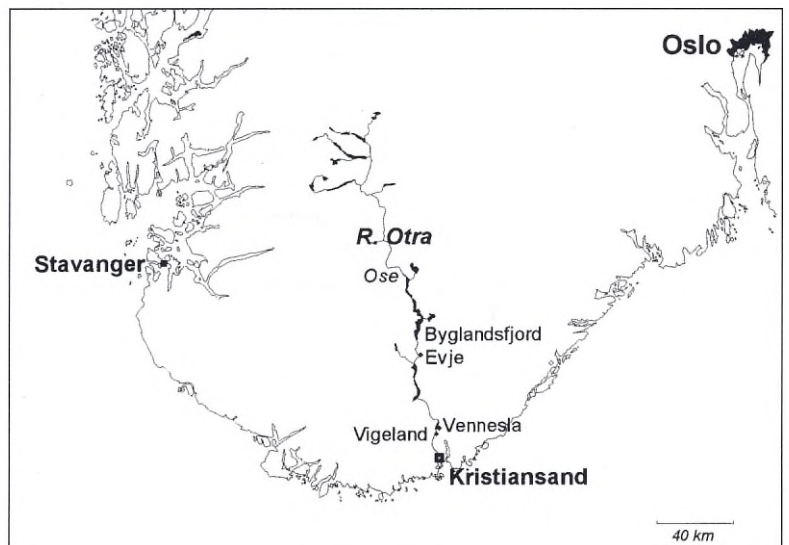
Fig. 1. Map of southern Norway with River Otra.

valley, southern Norway (Fig. 1). Five localities within a 13 km stretch of the River Otra were sampled by gillnetting. The distance between Evje and the sea is 60 km. Another sample was collected in 1994, in Lake Vennesla about 40 km downstream from Evje for comparison of genetic and phenotypic characters. Further downstream a sufficient number of trout samples could not be obtained due to low abundance. Individual trout were packed in dry ice and transported to the Institute of Marine Research, Bergen where they were kept at -80 °C until starch gel electrophoretic analyses. Prior to electrophoretic analyses, all individuals were classified phenotypically in three categories; common, intermediate and marmorated. Length, weight and sex were recorded (Table 1). In one of the localities the individuals had been gutted, and thus weight and sex could not be recorded. Furthermore, these individuals could not be analysed electrophoretically for loci expressed in liver, such as *MDH-2**, which is highly polymorphic in brown trout.

Apart from the three samples from River Otra (River Otra at Evje, Lake Byglandsfjord and Lake Vennesla), 7 more populations (Skaala 1992) representing both freshwater resident and anadromous trout were included. The four anadromous populations are distributed along a 650 km distance from River Aurlandselv in the Sognefjord to River Årungselv in the Oslofjord. Lake Bjornes and Tunhovd are resident populations from River Numedalslågen, while River Brumunda is a resident population from Lake Mjøsa in eastern Norway. A known species hybrid between brown trout and brook char was included as a reference in the material.

Table 1. Mean length in cm ±SD, length range and sex ratio of the trout morphs in the pooled material from River Otra at Evje.

Morph	*N*	Length	Range	Sexratio
Common	68	19.9±3.3	13.6-27.4	0.7
Intermediate	33	19.9±3.0	12.2-24.8	1.0
Marmorated	25	22.4±2.0	18.4-25.3	0.9

After punching, the pooled sample from Evje was split according to morph into common, intermediate and marmorated morphs for calculation of genotypic distributions and genetic variability at polymorphic loci. The observed distributions were tested for conformance to Hardy Weinberg equilibrium at *AAT-4**, *CK-1**, *G3PDH-2**, *LDH-5** and *MDH-2**. At *MDH-3,4** only two genotypes can be distinguished and thus testing was not possible. For this comparison monomorphic loci were left out, as was also *GPI-2** where only one individual (intermediate morph) was heterozygous for the *130* allele.

Two buffer systems were used: (A) tris-citrate-borate gel buffer: 0.015M Tris, 0.001M citric acid, 0.003M boric acid, and 0.001M LiOH; electrode buffer: 0.3M boric acid and 0.1M LiOH; both buffers were adjusted to pH 8.6. (B) citrate gel buffer: 0.002M citric acid; electrode buffer: 0.04M citric acid; both buffers were adjusted to pH 6.1 with N-(3-aminopropyl)morpholine. The following enzymes were typed electrophoretically: AAT (E.C. 2.6.1.1), ADH (1.1.1.1), CK (2.7.3.2), G3PDH (1.1.1.8), GPI (5.3.1.9), LDH (1.1.1.27), MDH (1.1.1.37), MEP (1.1.1.40), and PGM (5.4.2.2), putatively encoded by 26 loci. More details about combination of buffers and tissues, and about electrophoretic key parameters are given in Skaala et al. (1996). The genetic data were processed by the BIOSYS-1 PC program package of Swofford and Selander (1989). Genotypic distributions were tested by using a G-test (Sokal and Rohlf 1969).

When two taxa are fixed for different and detectable alleles at a locus, F1 hybrids are heterozygous for the different parental alleles. Thus, one locus is sufficient to detect all F1 hybrids. On the other hand, using a single diagnostic locus will only allow for detection of a portion of post-F1 hybrids, and F1 and post-F1 hybrids cannot be distinguished. However, by studying six or more independent diagnostic loci the discrimination of F1 and post-F1 hybrids will approach 100% (Avise and Van den Avyle 1984, Campton 1990, Verspoor and Hammar 1991). Even in the absence of fixed allelic differences recent hybridization can be detected. This requires that the common alleles in the two taxa differ at two or more

loci. In such cases hybridization results in non-random association of alleles and an excess of individuals heterozygous at multiple loci compared to that expected in the absence of interbreeding (Campton 1987, 1990).

Results

The colouration of the marmorated morph differs from that of common brown trout in that black and red dots are replaced by a marmoration pattern that consists of black, brown/red, green and light brown colours. Some individuals have a red brownish background colour on the body sides while the gillcovers and the top of the head and back are marmorated (Fig 2a). In other individuals the dorsal side has a black and greenish marmorated pattern that brings the colouration of mackerel to ones mind (Fig 2b). Individuals with intermediate colouration, ranging from almost common brown trout type to almost typical marmorated type are commonly caught in this area.

Fig 2a. Marmorated morph (upper) and common morph (lower) from River Otra.

Fig. 2b. Marmorated morph from River Otra.

The frequency of the common, intermediate and marmorated morphs in the pooled sample consisting of all three phenotypic categories from Evje was 54, 26 and 20%, respectively. In the sample from Lake Vennesla only one out of 41 individuals had the intermediate colouration, and none were typically marmorated. There is a numerical difference in mean lengths between the marmorated morph and the two other morphs, the marmorated individuals on average being bigger.

The following polymorphic loci and variant alleles were found in the Otra watercourse: *AAT-4*74, G3PDH-2*50, CK-1*115, LDH-5*90* (previously denoted **100), MDH-2*152, MDH-3/4*85* and *GPI-2*130*. Only previously reported and typical brown trout alleles were detected. There was an unusual high frequency of the *CK-1*115* allele (Table 2) in the sample from the Evje area, and also in the samples from Lake Byglandsfjord further upstream, and in Lake Vennesla further downstream in the watercourse.

Table 2. Allelic frequencies at nine polymorphic loci in common, intermediate and marmorated trout morphs, pooled sample from Evje and other Norwegian reference trout populations.

Locus	Evje				Other reference trout populations								
	Comm	Inte	Marm	Pool	Bjor	Brum	Bygl	Tunh	Venn	Aurl	Lang	Oyre	Arun
AAT-4*													
(N)	53	28	16	97	52	71	96	32	41	47	55	103	20
*100	.991	.982	.969	.985	.750	.979	1.000	.813	.963	.777	.927	.646	.900
*74	.009	.018	.031	.015	.250	.021	.000	.188	.037	.223	.073	.354	.100
CK-1*													
(N)	68	33	25	126	70	96	96	49	42	104	61	102	20
*100	.125	.152	.120	.131	.743	.224	.229	.837	.488	.962	.869	.848	1.000
*115	.875	.848	.880	.869	.257	.776	.771	.163	.512	.038	.131	.152	.000
G3PDH-2*													
(N)	68	33	25	126	81	95	96	50	41	104	61	102	20
*100	.699	.742	.820	.734	.914	1.000	.688	.830	.756	.990	.861	.907	.800
*50	.301	.258	.180	.266	.086	.000	.313	.170	.244	.010	.139	.093	.200
LDH-5*													
(N)	68	33	25	126	81	95	94	31	41	104	60	102	18
*100	.081	.061	.080	.075	.519	.000	.005	.210	.171	.038	.167	.034	.083
*90	.919	.939	.920	.925	.481	1.000	.995	.790	.829	.962	.833	.966	.917
MDH-2*													
(N)	68	33	25	126	78	95	96	43	41	104	61	103	20
*100	.691	.667	.700	.687	.506	.921	.630	.523	.671	.615	.803	.728	.725
*152	.309	.333	.300	.313	.494	.079	.370	.477	.329	.385	.197	.272	.275
MDH-3/4*													
(N)	68	33	25	126	81	49	96	51	41	57	61	103	20
*100	.706	.652	.680	.679	.852	.929	.693	.922	.573	.772	.721	.689	.825
*85	.294	.348	.320	.321	.148	.071	.307	.078	.427	.228	.279	.311	.175
MEP-2*													
(N)	68	33	25	126	81	95	96	51	41	62	61	103	20
*100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.968	1.000	1.000	1.000
*60	.000	.000	.000	.000	.000	.000	.000	.000	.000	.032	.000	.000	.000
GPI-2*													
(N)	68	33	25	126	81	95	96	51	41	104	61	103	20
*100	1.000	.985	1.000	.996	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
*130	.000	.015	.000	.004	.000	.000	.000	.000	.000	.000	.000	.000	.000
GPI-3*													
(N)	68	33	25	126	81	95	96	51	41	104	61	103	20
*100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.937	1.000
*110	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.000

Table 3. Genetic variability (SE) at 9 loci in all populations.

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
				Direct-count	HdyWbg expected**
1.Otra at Evje	122.8 (3.2)	1.8 (.1)	88.9	.208 (.077)	.185 (.064)
2.Bjornes	76.2 (3.3)	1.7 (.2)	66.7	.190 (.052)	.242 (.070)
3.Brummunda	87.3 (5.5)	1.4 (.2)	55.6	.076 (.040)	.075 (.040)
4.Otra at Bygland	95.8 (.2)	1.6 (.2)	55.6	.203 (.087)	.188 (.074)
5.Tunhovd	45.4 (2.8)	1.7 (.2)	66.7	.191 (.054)	.206 (.060)
6.Otra at Vennesla	41.1 (.1)	1.7 (.2)	66.7	.291 (.100)	.242 (.075)
7.Aurland sea trout	87.8 (8.2)	1.8 (.1)	77.8	.177 (.078)	.157 (.061)
8.Langang sea trout	60.2 (.7)	1.7 (.2)	66.7	.193 (.061)	.179 (.051)
9.Oyre sea trout	102.7 (.2)	1.8 (.1)	77.8	.239 (.076)	.211 (.061)
10.Årung sea trout	19.8 (.2)	1.6 (.2)	55.6	.185 (.069)	.153 (.054)

*   A locus is considered polymorphic if more than one allele was detected.
** Unbiased estimate (Nei 1978).

The percentage of polymorphic loci was higher in the Evje sample than in any of the other samples included, and the mean number of alleles per locus was in the upper part of the range for the populations compared, and similar to the values found for the anadromous populations (Table 3). The mean heterozygosity (observed) was also high compared to the other populations included, as only two populations (sea trout from River Øyre and resident trout from Lake Vennesla) were more heterozygous. In the total material there is a significant heterogeneity at all loci apart from GPI-2*, most strongly pronounced at CK-1* (χ=697.9, P<0.0001), LDH-5* (χ=353.4, P<0.0001), AAT-4* (χ=196.7, P<0.0001) and GPDH-2* (χ=153.6, P<0.0001). There were no indications of deviations from the expected HW distributions at any loci in the pooled sample from Evje with all three morphs.

In the cluster analysis based on 9 polymorphic loci of 10 populations, including seatrout and freshwater resident trout, the three populations from the Otra watercourse cluster together (Fig. 3). There is a major branching point with a large genetic distance (D=0.077) between the populations from the Otra watercourse and River Brummunda, and the other 6 populations. The four sea trout populations included cluster together, although located along a 650 km distance along the coast of Norway.

No private alleles were found in any of the morphs at any of the investigated loci, and there were no significant differences in allelic frequencies between morphs. Mean number of alleles was 2.0 for all three morphs, but mean heterozygosity was slightly higher for the intermediate morph (0.329±0.1) than for the common (0.300±0.08) and the marmorated (0.303±0.09) morph. At AAT-4*
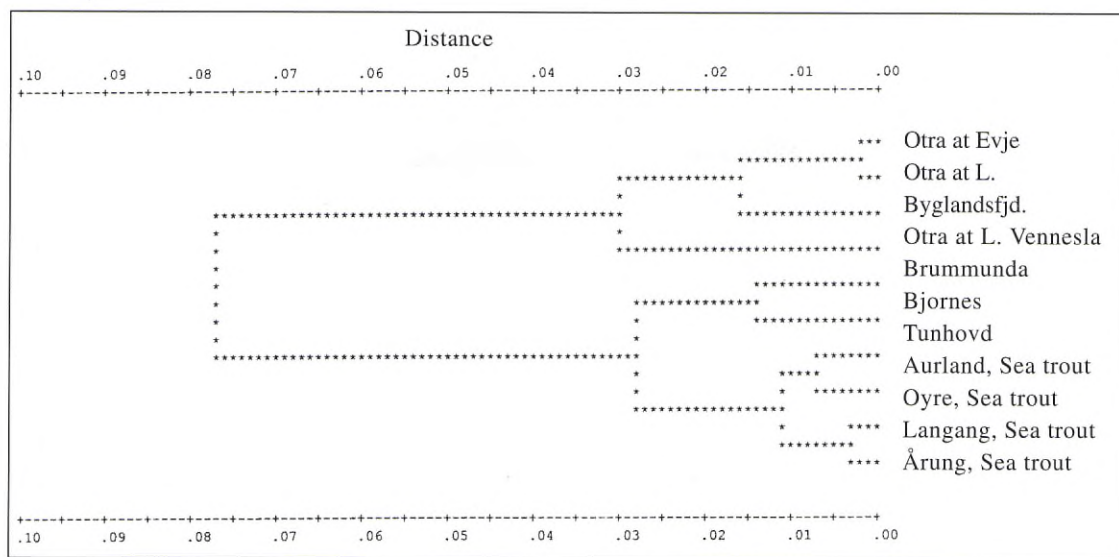
Fig. 3. Cluster dendrogram with genetic distances between ten Norwegian brown trout populations, including the sample from River Otra at Evje with the marmorated morph.

there was a significant heterogeneity (*P*<0.001) among morphs, probably due to small numbers. There was no genetic heterogeneity at any of the other loci or in the pooled sample over all tested loci. None of the comparisons of genotypic distributions in the three morphs at the studied loci came out with significant differences between the various morphs, when using the G-test.

Discussion

All alleles detected have previously been described for brown trout, thus there were no "new" alleles in the populations from River Otra, neither did we find any private alleles at the studied loci associated with the marmorated phenotype. Thus there are no indications of a large genetic difference between the common and the marmorated morph in the area, as would be expected if they were separate species.

The genetic variability in the trout from River Otra, calculated as mean number of alleles per locus and the percentage of polymorphic loci, lies in the upper part of the range for the populations included in this study. Also, the mean heterozygosity lies within the range for the included populations. This indicates a colonization by a

genetically very diverse population, or by two or more separate lines.

The absence of deviations from expected Hardy-Weinberg distributions of genotypes at any loci in the pooled sample from Evje with all morphs included, further point towards a panmixis in the trout population in the Evje area, and that these samples are drawn from a randomly mating population.

The frequency of the *CK-1*115* allele is usually low in Norwegian populations, apart from some populations from the Lake Mjøsa (e.a. River Brummunda) district. In a previous study (Skaala 1992), the mean frequency of this allele in 13 seatrout populations was 0.062±0.058, and in 17 freshwater resident populations 0.155±0.215, while it is 0.869 in the pooled sample from Otra at Evje. Also in the two other populations from Otra, Lake Byglandsfjord and Lake Vennesla, the frequency of *CK-1*115* is much higher than it is in other Norwegian trout populations. Only in the Lake Mjøsa area populations with a similar genotypic distribution at this locus have been found (Skaala 1992). This allele is often found in higher frequencies in the Baltic region (Ryman 1983), and in particularly in the Lake Vänern area, than in Norwegian sea trout stocks. Thus, the dicho-

tomy in the UPGMA dendrogram may reflect common incidents in colonization history. In an extensive brown trout study in Lake Melvin, Ireland, the fast allele at this locus was found in relatively high frequencies only in the sonaghen type, recently proposed as one of three subspecies in the lake (Ferguson and Taggart 1991, McVeigh et al. 1995). A further study on mitochondrial DNA is required to resolve further and in more detail the phylogeny of the trout in River Otra.

Through the development of biochemical genetic methods, there has been an improved opportunity to detect species hybrids during the last 25 years. Thus, it is now recognized that in some organisms the propensity of taxonomically distinct units to interbreed is more pronounced than previously known (Jansson et al. 1991, Verspoor and Hammar 1991). The reason that hybridization is more common in some fishes than in other vertebrates, may be found in their external fertilization, competition for spawning habitat, susceptibility to secondary contact between previously isolated populations and widespread stocking of hatchery reared individuals. The known trout-charr species hybrid included as a control, demonstrated a combination of electrophoretic banding patterns expected from a species hybrid between brown trout and brook charr, but none of the individuals from River Otra revealed this electrophoretic banding pattern. The electrophoretic investigation did not detect any brook charr alleles in any of the trout morphs studied, thus the trout-charr hybrid hypothesis is rejected. This is also in agreement with historical information about the occurrence of brook charr and marmorated trout in the watercourse, as the marmorated morph was known long before the introduction of brook charr took place just before 1980.

Dahl (1927) who studied the landlocked salmon, captured one specimen with a mottled or tigred colour pattern. The photograph of the specimen presented by Dahl (1927), clearly shows an individual with a marmorated pattern, similar to one of the patterns we have observed. According to Dahl a number of morphological features, such as the head, position of eye and

the length of the upper maxillary is not that of the trout, nor that of salmon. Furthermore, Dahl found the tail to be slender and the anal fin comparatively large. Thus, Dahl was convinced that this was a hybrid between brown trout and the landlocked salmon. However, all isozyme loci studied showed electrophoretic banding patterns typical for brown trout, and hybrids between trout and salmon were not detected. In fact, in the River Otra samples, not a single hybrid was detected although samples were drawn from an area where all three species are overlapping and fairly abundant. Furthermore, none of the hybrids we have detected previously, either in natural habitats or in hatcheries, have exhibited a marmorated colour pattern like the trout from River Otra, and to our knowledge, there are no references in the litterature on hybrids between Atlantic salmon and brown trout that indicate that hybrids are marmorated. Thus, the explanation by Dahl (1927) that the marmorated trout is a result of hybridization between brown trout and the landlocked salmon, locally known as "blege", is also rejected.

Although the geographic distribution of the marmorated morph is not known in detail, its present distribution overlap to some extent with that of the landlocked salmon. However, from the ongoing sampling of trout and salmon spawners, it is known that spawning areas are separated, although landlocked salmon is occasionally caught in the spawning areas of the trout and vice versa. Also, the time of spawning is different between the landlocked salmon and the trout, as the peak in salmon spawning occurs about four weeks later than the peak in trout spawning. Thus, the barrier to gene flow between these species populations must be fairly strong in this area.

The rejection of the species hybrid hypotheses leaves us with two possible explanations for the observed phenomenon: either there is a polymorphism within a single trout population, or there are two different populations with similar genotypic distributions at the examined loci, but different in other parts of the genome. In Lake Melvin, the three different trout morphs have been proven to represent different sympatric popu-

lations, also referred to as subspecies (Ferguson and Taggart 1991). In northern parts of Italy, in Albania, Austria and in parts of former Yugoslavia a marbled trout, sometimes recognized as a subspecies, *Salmo trutta marmoratus*, or a separate species, *S. marmoratus* Cuvier, is found. The taxonomic position and the management of this trout has been discussed for a number of years (Forneris et al. 1987, Budihna and Ocvirk 1990, Povz et al. 1990, Schoeffmann 1994), but a recent study including mitochondrial DNA demonstrated that all included marmoratus populations are monophyletic in origin and represent a distinct evolutionary lineage among brown trout populations (Giuffra et al. 1994, 1996).

It is now recognized that the post-glacial colonization of brown trout in north-west Europe has been more complex than previously known, and that a number of genetic differentiated populations or types colonized watercourses after the retreat of the last glaciation (McVeigh et al. 1995, Hynes et al. 1996). These findings explain why the observed diversity in brown trout is often far greater than would be expected in relatively young ecosystems.

Thus, a closer investigation including mitochondrial DNA and a test mating including the major morphs, will be required to fill in genetic and biological information neccessary to decide the phylogeny of the marmorated trout in River Otra and to decide which measures that are needed for the future management of this biological diversity.

Acknowledgement

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A Profundal, Winter-Spawning Morph of Arctic Charr
Salvelinus alpinus (L.) in Lake Fjellfrøsvatn, Northern Norway

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Abstract

A dwarf charr that is remarkably distinct from the normal charr morph was recently discovered
in the subarctic lake Fjellfrøsvatn, in northern Norway. It spends its entire life cycle in deep
water and spawns under a thick cover of snow and ice. There is no size overlap between sexu-
ally mature fish of the two morphs (8-13 cm FL versus >16 cm), and their morphologies and
coloration are different. Their ecological niches are very distinct. The normal charr spawns in
September, and the dwarf charr spawns four months later, in February. Their spawning areas
are widely separated horizontally, and the dwarf charr spawns at a depth of 30 m, while the
normal charr spawns above a depth of 5 m. Their general habitats are also well segregated
because the normal morph is chiefly littoral and epipelagic while the dwarf charr never seems
to leave the deep benthic areas. A slight overlap in their habitats occurs in summer and early
autumn, when a few normal charr were found in the profundal. The allele frequencies at the
EST-2 and *MDH-4,5* loci did not differ between morphs. We tentatively conclude that this is a
case of sympatric splitting. Only normal charr were probably transferred to the nearby Lake
Takvatn in the 1930s.

Keywords: Arctic charr, sympatric morphs, niche segregation, winter spawning

Introduction

Lake resident, sympatric morphs of Arctic charr
Salvelinus alpinus (L.) are known from Siberia
(Savvaitova 1980a, Savvaitova et al. 1980),
Svalbard (Klemetsen et al. 1985, Svenning and
Borgstrøm 1995), Scandinavia (Nyman 1972,
Klemetsen and Grotnes 1975, 1980, Lindström
and Andersson 1981, Nyman et al. 1981, Hindar
and Jonsson 1982, Hammar 1984, Hesthagen et
al. 1995), Iceland (Sandlund et al. 1992), the
British Isles (Frost 1965, Walker et al. 1988, Mills
1989, Elliott and Baroudy 1995), continental
Europe (Dörfel 1974, Brenner 1980), Greenland
(Sparholt 1985, Riget et al. 1986) and Canada
(Ellesmere Island: Parker and Johnson 1991,
Reist et al. 1995). In some cases, genetic differ-
ences indicating that the morphs represent sepa-

rate populations are found by allozyme analysis
(Nyman 1972, Lindström and Andersson 1981,
Hammar 1984, Klemetsen and Grotnes 1980,
Hindar et al. 1986, Magnusson and Ferguson
1987 (small benthic morph versus the other three
combined), Partington and Mills 1988, Osinov
et al. 1996) or by mt-DNA analysis (Hartley et
al. 1992). In other cases, genetic differences have
not been demonstrated despite clear morphologi-
cal and ecological segregation (Klemetsen et al.
1985, Hindar et al. 1986, Magnusson and
Ferguson 1987, Danzmann et al. 1991).

The most advanced cases of sympatric morph
segregation are found in lacustrine charr. A par-
ticularly spectacular case with four sympatric
morphs is found in Thingvallavatn, Iceland
(Sandlund et al. 1992, Skulason and Smith 1995).
Open systems with anadromous charr usually

have resident charr as well, but genetic separation has never been clearly demonstrated, and they are generally believed to belong to the same population (Nordeng 1983, Klemetsen 1984, Svenning et al. 1992, Kristoffersen 1994).

In this contribution we report the recent discovery of a sympatric dwarf charr morph from the subarctic lake Fjellfrøsvatn, in northern Norway. The lake has been regularly harvested for charr and trout *(Salmo trutta)* by ice fishing, angling and household netting for generations, but the dwarf charr morph had never been reported. We will argue that this represents an extreme case of morphological and ecological segregation between sympatric charr morphs. The nearby Takvatn charr was introduced from Fjellfrøsvatn in 1930 (Svenning and Grotnes 1991) and has been studied extensively since 1980 (Klemetsen et al. 1989, Amundsen et al. 1993). It is of considerable theoretical and practical interest if the dwarf morph was transferred to Takvatn, and this question is discussed briefly.

Materials and methods

The Lake Fjellfrøsvatn is an oligotrophic and dimictic lake, 6.5 km^2 in area and 88 m deep, situated at 125 m a.s.l. and 69° N in a tributary of the Målselv river system, county of Troms, in northern Norway (Fig.1). The catchment area is about 90 km^2 and consists of woodland, predominately birch *(Betula pubescens)*, and treeless mountains. There are a few small farms and some cabins on the western side. Brown trout and Arctic charr are the only fish species. The lake is of a regular shape and has one main basin. The shore regions are mostly sandy or stony with little emergent vegetation. The lake is normally icebound from November to May/June. In 1992, the temperatures at 30 m depth varied from 8.0 to 4.2 °C between July and November. During winter stagnation, from December 1992 to May 1993, the temperatures were 0.7 °C under the ice, 2.3 °C at 5 m depth, 2.5 °C at 10 m and 3.1 °C at 30 m depth.

During the ice-free season of 1992, monthly fish sampling was done in littoral, profundal and pelagic habitats. We used survey gillnets meas-
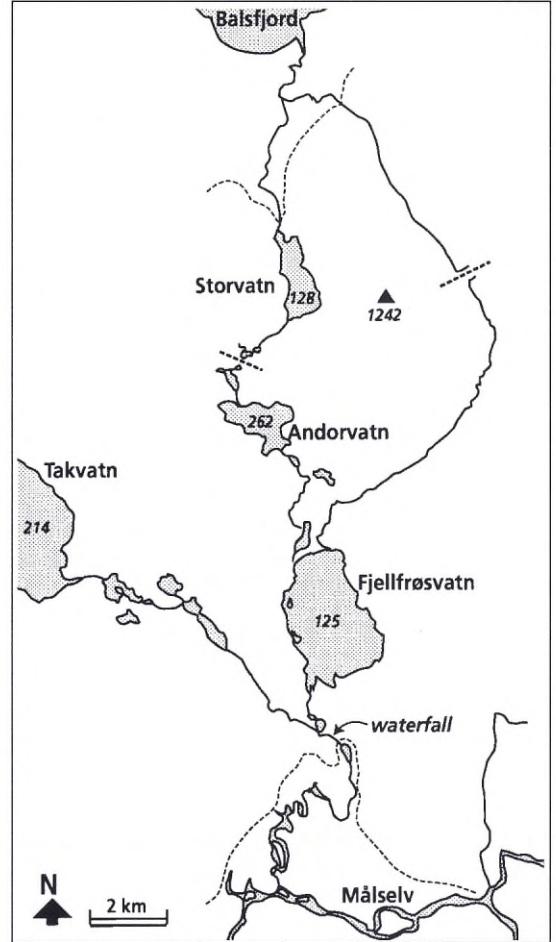
Fig. 1. The geographical setting of Lake Fjellfrøsvatn. The River Målselv drains into the sea in Malangen, a fjord to the south of Balsfjord. The maximum postglacial marine limit, at about 85 m above the present sea level, is marked by thin, stippled lines. A steep waterfall downstream from Fjellfrøsvatn, at 75-100 m elevation, is marked by an arrow. Two water divides upstream from Fjellfrøsvatn are marked by thick, stippled lines.

uring 1.5 x 40 m and made up of eight panels, each 5 m long and with bar mesh sizes 10, 12.5, 15, 18, 22, 26, 35 and 45 mm. In addition to these nets, regular nets measuring 1.5 x 30 m with bar mesh sizes of 8, 10 and 12.5 mm were used in the bottom habitats. Survey nets measuring 6 x 40 m and with the same mesh sizes as the bottom

survey nets were placed at the lake surface in the pelagic habitat. The littoral nets were set down to depths of 15 m, and the profundal nets were set at depths of 25 to 40 m. The fish were weighed (g) and measured (mm fork length). Gonad maturation was scored according to a seven-stage scale (Sømme 1941). Aging was done by surface reading of otoliths in glycerol.

Sampling under the ice was done in the littoral and profundal habitats in December 1992 and in March and May 1993. We used the same nets we used in the ice-free season. The ice thickness was about 30 cm in December, 80 cm in March and 60 cm in May. There was clear ice and practically no snow in December, about half a meter of snow on top of the ice in March and opaque ice and little snow in May. At this latitude, the polar night occurs during December. The sun returns in late January, and the midnight sun begins in late May.

Results

The range of sizes in the fish sample from Fjellfrøsvatn included charr with fork lengths of 7 to 51 cm, but few fish were above 30 cm in length (Fig. 2). The charr in the profundal catches were predominately shorter than 17 cm, (upper panel), those in the pelagic catches were between 18 and 24 cm in length (middle panel) and those in the littoral catches were between 9 to 25 cm in length (lower panel).

The length distribution of sexually mature fish had a distinct bimodality, with a lower mode of fish from 8 to 13 cm and an upper mode of fish larger than 16 cm (Fig. 2). The mature fish from the lower size mode were always caught in the profundal zone, while fish from the upper size mode were predominantly caught in the littoral and pelagic zones.

The colours of fish from the two modes were very different. Mature fish from the upper mode had typical charr spawning colours, with red to orange bellies (Skarstein and Folstad 1996) and whitish edges on the paired fins. The basic body hue was silver, and immature fish usually had parr marks on their flanks. Adult fish of the smaller mode had no spawning colours at all. Their basic
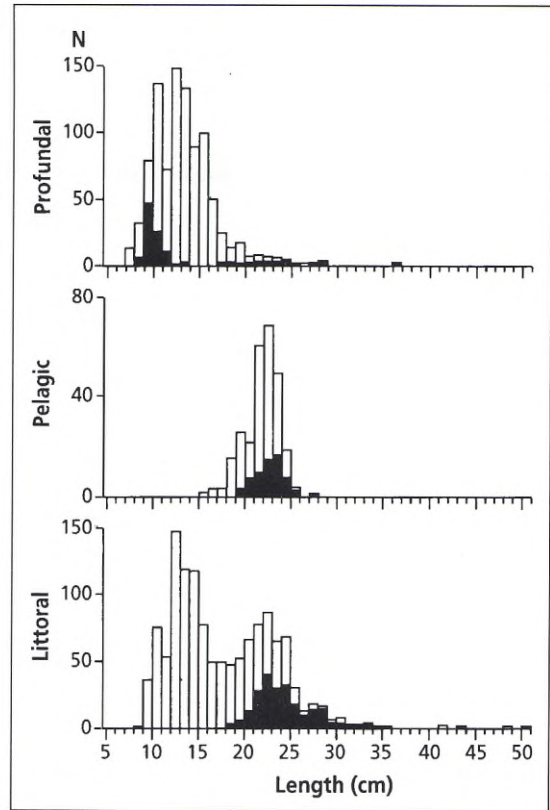
Fig. 2. Length distributions of Arctic charr samples from profundal, pelagic and littoral zones of Lake Fjellfrøsvatn 1992-93. Black bars mark spawners of the year.

body colour was pale yellow with a touch of brass rather than silver. None had any trace of parr marks. Immature fish were similar to the adults, with the same pale brass color and no parr marks. Adults of the two morphs were easily sorted in the field.

An analysis of length-at-age from pooled October, November and December samples, demonstrated a strong dimorphism in individual growth (Fig. 3). At this time, all upper mode fish had spawned and all lower mode fish were still unspent (Fig. 4). The unspent fish of the lower maturation mode had a very slow growth rate, with no yearclass exceeding 11 cm in average length. All other fish, including those from the upper maturation mode, had a much faster growth rate.
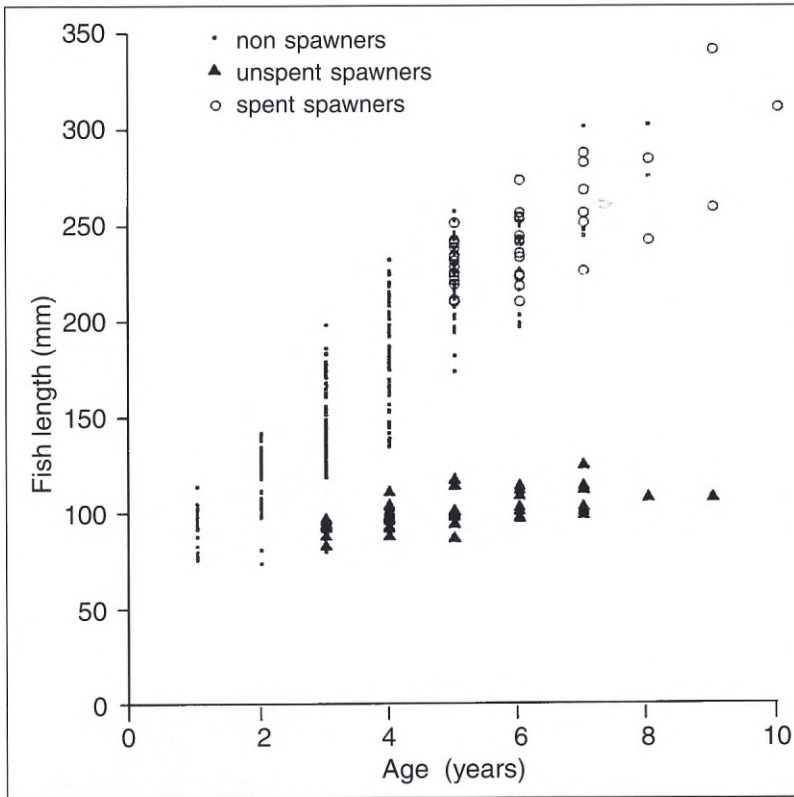
Fig. 3. Length-at-age comparisons of Arctic charr from Lake Fjellfrøsvatn, October to December 1992.

Because of their slow growth rate, fish from the lower mode are hereafter referred to as dwarf charr, and fish associated with the upper growth mode are referred to as normal charr. From age 3, the two morphs could easily be identified by length-at-age comparisons (Fig. 3). Separation of younger fish was difficult, but differences in growth rates could already be seen in two-year-old fish. Both sexes of the dwarf charr started to mature at 3 years of age, whereas the normal charr began maturing two years later at 5 years of age.

The normal charr spawned in September. No ripe fish were found after that month, and from October to May, this group was represented only by spent spawners or unripe fish (Fig. 4). Mature dwarf charr were fully ripe but still unspent all through October, November and December. The first newly spent dwarf charr were recorded in March. At that time, most of them had spawned, but one fully ripe female was still unspent. This indicates that the main spawning had taken place just prior to that sampling, presumably in February. All dwarf charr had spawned by May.

A preliminary allozyme analysis by starch gel electrophoresis of the *EST-2* locus failed to demonstrate any differences between the two morphs. We compared a sample of normal charr from August 1988 (N=29) with a pooled sample of dwarf charr from the winter of 1992-93 (December, March and May; N=22). The frequencies of the *EST-2* (100) allele were, respectively, 0.982 and 0.977.

Discussion

Adult body size is an essential character in morphological comparisons. In the present case, the size ranges of sexually mature fish of the sympatric morphs were completely separate. In accordance with the size difference, their growth patterns showed very divergent trajectories by age 3; indications of this split were already visible
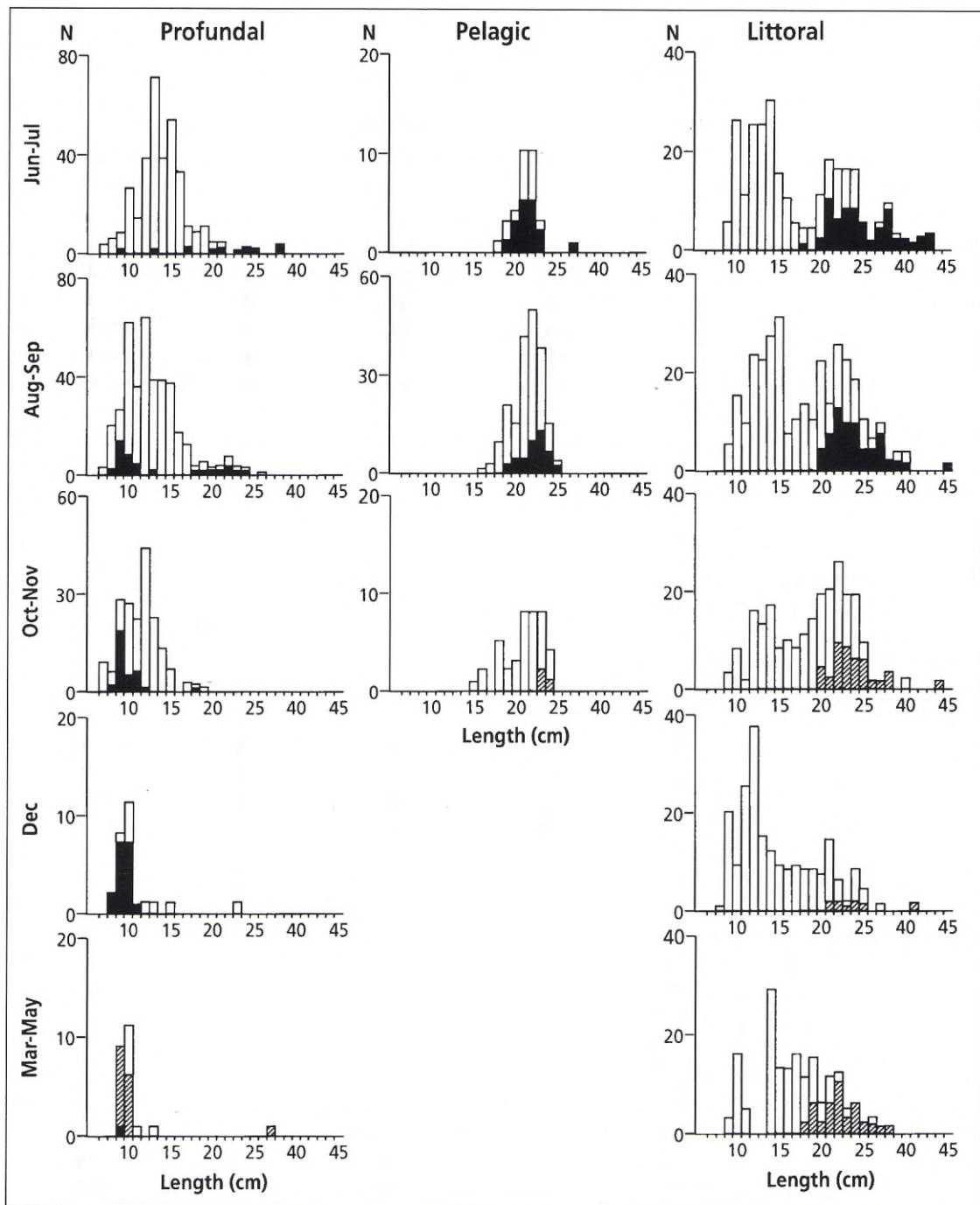
Fig. 4. Length distributions of Arctic charr samples from Lake Fjellfrøsvatn 1992-93, split on habitat and seasonal time. Black bars mark unspent spawners; shaded bars mark spent spawners.

by age 2 (Fig. 3). Their body colours were also different. Morphology and colour were, therefore, good diagnostic criteria to distinguish the two morphs. Their age spans were not different, but the dwarf charr became sexually mature two years before the normal charr did. This is an important difference in their life histories.

When comparing the three niche dimensions, place of spawning, time of spawning and spatial habitat for the two morphs, we found that a well-defined ecological niche, clearly separate from that of the normal charr, could be assigned to the dwarf charr of Fjellfrøsvatn. It spawns in a confined deep water area in the middle of the winter and seems to spend its entire life cycle in the cool and dark profundal zone of the lake.

Two niche dimensions (time of spawning and place of spawning) were completely discrete between morphs, and the third dimension (spatial habitat) was partly separate. Our observations indicate that the dwarf charr spawns in February, whereas the normal charr spawns in September. Their spawning times were, therefore, four to five months apart. Dwarf charr were invariably caught in the profundal zone, and this included ripening, running and newly spent fish. The dwarf charr therefore spawns offshore in deep water, while the normal charr spawns in shallow water at the lake shore, and their spawning sites are completely discrete. We have indications that there is a relatively restricted spawning site at a profundal sampling location along the western shore, perhaps marked by course outwash from the inlet stream, but this needs confirmation.

The habitat segregation between the morphs was extensive because dwarf charr never were caught outside the profundal zone and most normal charr were caught in littoral or epipelagic areas. The overlap in the habitat dimension occurred because some normal charr were taken in deep water along with dwarf charr during summer and early autumn (Fig. 2). Only few normal charr were caught in the profundal later in the season, and there was no overlap with mature fish on the spawning grounds.

This is not the first time different ecological niches for sympatric charr morphs have been described, but there is usually more overlap between the niches than was found here. In the following, we compare the present results with the literature to discuss the notion that the present case is an example of extreme niche differentiation. We compare our results with those from Lake H, Ellesmere Island, Canada (Parker and Johnson 1991), Iterlaa Lakes, Greenland (Sparholt 1985), Tasersuaq, Greenland (Riget et al. 1986), Arresjøen, Svalbard (Svenning and Borgstrøm 1995), Ellasjøen, Bear Island (Klemetsen et al. 1985) (all high arctic), Thingvallavatn, Iceland (Sandlund et al. 1992, Snorrasson et al. 1994) (subarctic), Skjomen Lakes, Norway (Klemetsen and Grotnes 1975, 1980), Övre Björkvattnet, Sweden (Nilsson and Filipsson 1971), Stora Rösjön, Sweden (Lindström and Anderson 1981, Svedäng 1990) (all alpine), Vangsvatn, Norway (Hindar and Jonsson 1982, Jonsson and Hindar 1982), Sirdalsvatn, Norway (Hesthagen et al. 1995), Loch Rannoch, Scotland (Walker et al. 1988), Windermere, England (Frost 1965, Mills 1989, Elliott and Baroudy 1995) and Attersee, Austria (Brenner 1980) (all temperate). Together, these cases cover a large part of the environmental and geographic variation of charr lakes with sympatric morphs, most of which are of similar ages because they came into being during the Weichselian glaciation.

Extensive size overlap between mature fish of the sympatric morphotypes occurs in Rannoch and Windermere. In most other cases, the size overlap between morphs is small (Iterlaa, Tasersuaq, Thingvallavatn (small benthic and pelagic charr), Skjomen, Övre Björkvatnet, Vangsvatn, Sirdalsvatn, Attersee) or none (Lake H, Arresjøen, Ellasjøen, Stora Rösjön). The combination of very small adult size and very narrow size range of the Fjellfrøsvatn dwarf (8-13 cm, both sexes) has not been described for any other lake with sympatric morphs, but Nyman (1987) reported allopatric charr of similar small sizes from very small, spring-fed bodies of water in Sweden. Tasersuaq, Ellasjøen and Thingvallavatn (small benthic) had mature fish below 10 cm, like those from Fjellfrøsvatn, but in these lakes, the upper end of the range extends 20 cm or more. About 8 cm in body length is probably close to the lowest possible limit for maturation in female

salmonids and indicates a fecundity of about 30 eggs, or even fewer.

Habitat segregation is usually found between sympatric charr morphs. When segregated, normal charr tend to prefer epipelagic and littoral areas. Dwarf charr morphs tend to prefer bottom areas, but the depth of the dwarf charr habitat varies between lakes. In some cases, there is a clear preference for littoral areas (Thingvallavatn (small benthic morph), Skjomen). In other cases, dwarf charr are found in profundal areas (Sirdalsvatn, Attersee, Fjellfrøsvatn). The degree of segregation varies with lakes and with seasons, and there is almost always some habitat overlap. The overlap is extensive in some lakes, as in Windermere and Rannoch. Most commonly, the normal charr habitat overlaps the dwarf charr habitat along the bottom profile; the reverse is rarely found. In many lakes, the spawning sites for both morphs are not described or not well known. In some cases, such as for Thingvallavatn (except for the large benthic morph) and Vangsvatn, the sympatric morphs have overlapping spawning grounds. In other cases, there are good indications that they are spatially separated (Skjomen, Rannoch), and in Windermere, Sirdalsvatn, Attersee and Fjellfrøsvatn, the spawning sites of the sympatric morphs are definitely discrete.

The spawning times are not known or not described for some lakes. In other cases, the spawning times are known to overlap (Thingvallavatn (except the large benthic morph), Vangsvatn, Rannoch) or are believed to do so (Tasersuaq, Övre Björkvatn, Stora Rösjön, Arresjøen). In Thingvallavatn, the large benthic morph spawns earlier in the autumn than the other morphs do. The same is true in Skjomen, where the dwarf charr spawn earlier than the normal charr do. In addition to Fjellfrøsvatn, the most extreme cases of time separation are found in Sirdalsvatn and in Attersee and in the well-documented case of Windermere, where autumn spawning and spring spawning charr have been known for more than 300 years (Elliott and Baroudy 1995).

When compared to this set of well-studied cases from a wide geographic range, we find that Fjellfrøsvatn, as schematically illustrated in Fig. 5, does provide an extreme example of niche segregation among sympatric lacustrine charr morphs. Most other cases display extensive overlap in size and along several niche dimensions. The pronounced niche segregation of the present charr morphs is strengthened by the recent finding that their parasite communities are also distinctly different (Knudsen et al. 1997).

The profundal morphs of Attersee and Sirdalsvatn, as well as the small benthic morph of Thing-
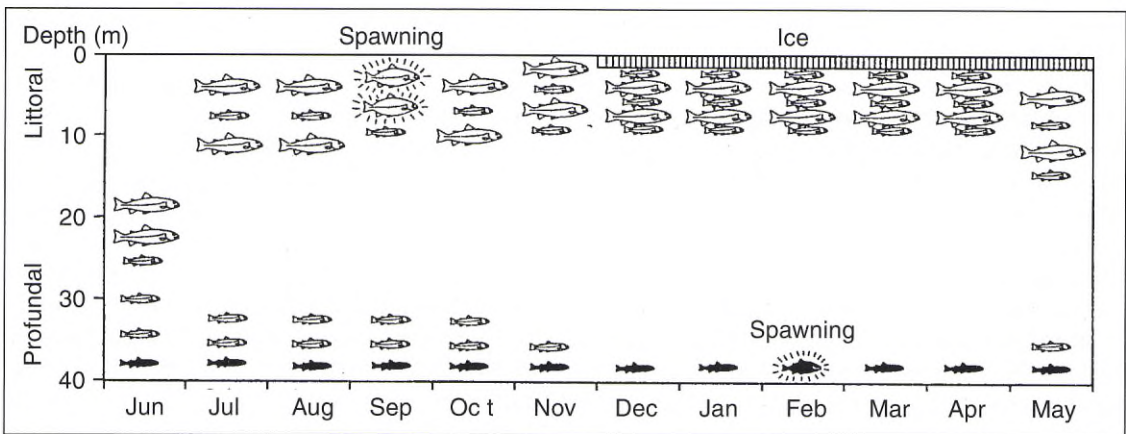

Fig. 5. Schematic sketch of the habitat distribution of normal charr (white) and dwarf charr (black) during an annual cycle in Lake Fjellfrøsvatn.

vallavatn, are also extreme cases of niche segregation of sympatric charr morphs. Thingvallavatn is unusual because here there are four sympatric morphs and because the small benthic morph is confined to littoral, interstitial crevices of lava blocks. This special habitat provides good shelter and feeding (*Lymnaea* spp., snails) and is not found in many other lakes. Sirdalsvatn is particularly interesting in comparison to Fjellfrøsvatn because both lakes have profundal dwarfs that are entirely segregated from the normal charr in their times and places of spawning. The striking difference is, however, that the Sirdalsvatn dwarf charr spawns in the summer (July to September, Hesthagen et al. 1995), while the Fjellfrøsvatn dwarf spawns in the winter. The spawning times of these profundal populations are both extreme cases. To our knowledge, similar spawning times for charr are not reported elsewhere in Scandinavia. Interestingly, Hesthagen et al. (1995) found ripe dwarfs at all times of the year, although the peak spawning took place in the summer. In Attersee, Austria, Brenner (1980) found the permanently profundal charr to be ripe and running at all months of the year, but with the main spawning period from July to November. Together, these three cases may be taken to indicate that deep-living, sympatric charr populations tend to develop spawning seasons that are different from their sympatric morphs but that the exact time of the year may be of secondary importance in the profundal environment, which has less seasonal variation in light and temperature than the other lake habitats have.

In ice-covered lakes, the winter stagnation provides higher temperatures in deep water than in shallow water. The actual temperatures differ between years because the weather conditions, especially wind, in late autumn determine the duration of the autumn circulation and thereby the temperature at freeze-over. In the winter of 1992, the temperature at 30 m depth in Fjellfrøsvatn was 3.1 °C, and it was 2.3 °C at 5 m and 0.7 °C under the ice. We have located two littoral spawning sites in the lake, one inshore of an islet on the western shore and one to the east of the outlet. Our observations so far indicate that the spawning of the normal charr in these sites

takes place in very shallow water, probably at a depth of 2 to 3 m. In 1992, this meant that development temperatures for the eggs were 2 °C or lower, and probably around 1.5 °C, during the winter. In comparison, the winter-spawned eggs of the dwarf charr were deposited in the profundal, where the temperature was 3.1 °C, which gives a temperature difference of about 1.5 °C between the two depths. This means that the eggs of the dwarf charr develop faster than the littoral eggs of the normal charr do and that this difference compensates for at least some of the time lag in spawning times.

In an outspoken discussion of the charr problem, Behnke (1989) reviews several recent European publications. He refutes the hypothesis of three sibling species (Nyman et al. 1981) and concludes, as have many authors in recent years, that all charr morphs of Scandinavia, Great Britain and Iceland are derived from one common ancestor from postglacial times. He does, however, assume that slight genetic differentiation may have taken place in several refugia during the last glaciation. He agrees that sympatric populations may be the result of incipient sympatric speciation but maintains that different selection pressures in postglacial allopatry would precondition reproductive isolation and rapid divergence in later sympatry. Behnke's review and discussion is challenging because he, unlike many recent authors, leaves the door open to the possibility that different speciation processes have been involved, as did Klemetsen (1984), who argued that both allopatric and sympatric processes may have contributed to the diversity in charr we see today.

The modern discussion of sympatric speciation in charr started with the contributions of Savvaitova (1980 a,b) and Balon (1980). Explicit statements about incipient sympatric speciation appeared in case studies of Bear Island (Klemetsen et al. 1985), Greenland (Riget et al. 1986), Iceland (Sandlund et al. 1992) and southern Norway (Hesthagen et al. 1995). Recent general discussions were contributed by Griffiths (1994), who reviewed the literature and discussed mechanisms for bimodal size structures, and by Skulason and Smith (1995), who discussed

trophic polymorphism as a sympatric process in vertebrates based on the four charr morphs of Thingvallavatn.

The extreme ecological and morphological segregation of the Fjellfrøsvatn dwarf charr may suggest that this is an allopatrically derived form with a different immigration history from that of the normal charr. If so, the evolution may have started either in a separate glacial refuge or in another local lake in postglacial times (Behnke 1989). Our tentative conclusion is, nevertheless, that this is a case of incipient sympatric speciation.

Fjellfrøsvatn is situated in a tributary of the Bardu-Målselv river system, which is the largest river system in the county of Troms and stretches from the sea and across the Swedish border to the main water divide of Scandinavia. The maximum postglacial marine transgression in the Målselv valley was about 85 m above the present sea level (Jacob J. Møller, Tromsø Museum, pers. comm.). This took place over a short period between 9500 and 9000 years B.P. Målselv has anadromous charr, trout and salmon *(Salmo salar)* today. The charr most certainly was the first immigrant, and the species has probably been in the Målselv system since early postglacial times. The upper reaches of the Fjellfrøselv tributary have probably always been inaccessible to ascending fish because of a steep waterfall about 1.5 km downstream from Fjellfrøsvatn (Fig. 1). Today, the waterfall drops from a height of about 100 to 75 m. The maximum sea level did not extend above 90 m (J.J. Møller, pers.comm.). Therefore, the upper part of the waterfall was probably a migration barrier for fish even at the time of maximum sea level. We believe that the Fjellfrøsvatn charr is a landlocked form with an anadromous ancestor. It was probably helped by man past the waterfall (Klemetsen et al. 1989). A recent find of a single shell from an oyster *(Ostrea edulis)* on the beach of the lake is believed to have been brought up by man for food or bait (J.J. Møller pers. comm.). Oysters were abundant in northern Norway 6000 years B.P. but not today (Møller 1984). This indicates that man visited the lake in early postglacial times and therefore could have carried charr past the waterfall.

Fjellfrøselv branches off Målselv towards the north, away from the Scandinavian water divide. This makes natural immigration by the dwarf morph from the east less likely. Immigration via an upstream lake is possible in theory because one sizable lake (Andorvatn, 262 m a.s.l.) is found in one of the tributaries of Fjellfrøsvatn (see map, Fig. 1). The water divide is located at about 300 m elevation just north of that lake. The stream on the other side runs via Storvatn (128 m a.s.l.) into Balsfjord. There is another inlet stream from the north that runs through a long, narrow valley with no lakes. The water divide is at about 400 m elevation. The stream on the other side joins the stream from Storvatn close to the sea.

The only possibility for a stepwise immigration of the dwarf charr, either upstream past the waterfall or downstream over the water divide towards Balsfjord (Fig. 1), is that man moved it, as he probably did with the normal charr, which was then an attractive sea-run fish. We find this unlikely because man would probably not bother to move a miniature charr that was of no interest as a source of food or, in modern times, as a sports fish. Stepwise immigration with man's help is a possible but rather farfetched explanation in this case, and we tentatively conclude that the double morph situation in Fjellfrøsvatn is a result of sympatric splitting.

We found no differences in the *EST-2* allele frequencies between the morphs. Neither did Osinov et al. (1996), but they found indications of a difference at the s*MDH-3,4* loci (their notation), which was not statistically significant, presumably because of a low sample size. They screened 34 loci but found no other polymorphisms. Their allozyme analysis indicates that the genetic differentiation between the morphs is small, but if the difference at the *MDH* loci turns out to be significant, the situation at Fjellfrøsvatn will be similar to that in the southern Norwegian lakes of Selura and Sirdalsvatn, where sympatric morphs differed at the *MDH* loci (Hindar et al. 1986). As both Klemetsen and Grotnes (1980) and Hindar et al. (1986) observed, sympatric allozyme differences indicate that the morphs represent discrete populations with restricted gene flow.

Svenning (1985, 1989) has traced the history of the introduction of charr from Fjellfrøsvatn to Takvatn in 1930. It appears that about 40 fish that were ready to spawn were put out into Takvatn in October of that year. There is reason to believe that these were normal charr. At that time of the year, only normal charr would be ready to spawn. Also, in 1930, nobody knew about the deep-living dwarf morph. All major habitats have been frequently sampled in Takvatn since 1985. Small fish are regularly caught in the profundal zone, but these are always young charr, which occupy the profundal as part of an ontogenetic habitat shift pattern (Klemetsen et al. 1989, 1992). Small and sexually mature charr have never been found. We conclude that the dwarf charr morph of Fjellfrøsvatn has not been introduced into Takvatn.

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Length Conversions for Lacustrine Populations of Arctic Charr, *Salvelinus alpinus*

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Abstract

Scientists measure and report fish length as standard length (SL), fork length (FL), natural total length (TL) and maximum total length (MTL) (Anderson & Gutreuter 1983). Arctic charr (*Salvelinus alpinus*) is a holarctic species and biologists from countries within its range report fish lengths differently. We developed formulae for converting among standard length, fork length, total length and maximum total length for lacustrine populations of Arctic charr based on data from 322 specimens (38-432 mm MTL) from six lakes in the United States, two lakes in Norway, and two lakes in Scotland. Conversion errors experienced when using these formulae are within the range of measurement errors.

Keywords: Arctic charr, lacustrine populations, length conversions.

Introduction

Arctic charr (*Salvelinus alpinus*) length measurements (Fig. 1) are reported in different ways in fisheries literature. Fork length (FL), total length (TL), and maximum total length (MTL) have been used to measure charr in Maine, USA (Waters 1959, Kircheis 1976, 1980) and Canada (Hammar et al. 1989); standard length (SL) and TL have been used in Austria (Balon and Penczak 1980); TL and FL in Iceland (Gydemo 1984, Sandlund et al. 1992) and Germany (Brenner 1984); and FL in Japan (Maekawa 1984) and Norway (Amundsen et al. 1993). Unfortunately, some publications have even reported fish "length" or "mean length", and have not identified which length was measured (Kipling and LeCren 1984, Svedäng 1990). Tradition and local convention account for which length measurement is most commonly used. TL is often used in much of Europe, while in the U.S. MTL is more common. In Maine, MTL is used because sport fishing regu-

lations are based on that measure of length. Without conversion formulae, biological data from many studies can be difficult to compare. Although, conversion formulae for charr are reported in Carlander (1969), they were based on only seven fish from North America. He also incorrectly stated that for charr "[t]he caudal fin is usually lacking in a fork and thus FL = TL." Charr actually have a distinctly forked caudal fin. The objective of this study was to provide a minimum number of conversion formulae among the different length measurements reported for charr that would be applicable to lacustrine populations in Europe and North America.

Methods

Arctic charr were collected with gill nets or trap nets from six lakes in Maine, two lakes in Norway, and two lakes in Scotland (Table 1). Standard length, fork length, total length, and maximum total length were measured, to the nearest
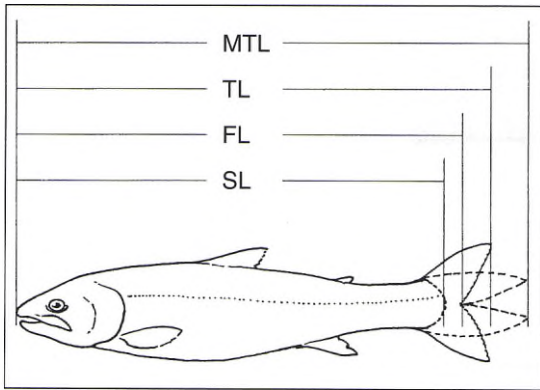
Fig. 1. Measurement location for standard length (SL), fork length (FL), total length (TL), and maximum total length (MTL).

Table 1. Collection sites for lacustrine Arctic charr samples.

Lake name	Location		Sample size
Maine			
Bald Mountain Pond	45°12'N	69°43'W	18
Big Black Pond	46°58'N	68°50'W	24
Floods Pond	44°43'N	68°28'W	71
Long Pond	44°51'N	70°40'W	31
Penobscot Lake	45°56'N	70°13'W	30
Wassataquoik Lake	46°01'N	68°57'W	22
Norway			
Møkkelandsvatn	69°49'N	16°25'E	22
Takvatn	69°07'N	19°05'E	31
Scotland			
Loch Lee	56°52'N	03°57'W	30
Loch Rannoch	56°39'N	04°17'W	42
Total			322

millimeter (mm), for 322 fish. Conversion formulae were calculated using the GLM procedure in SAS (1996) software. Using the SL to TL conversion as a test, an analysis of covariance was used to determine if lake specific regressions were indicated (Snedecor and Cochran 1967). An apriori significance level of 0.05 was used.

Table 2. Formulae for converting among four methods for measuring length on lacustrine Arctic charr ($y=a+bx$). All regressions were significant ($P=0.0001$) and all had an R^2 of 0.99.

Y	X	a	$P(a=0)$	b	$P(b=0)$
SL	FL	-2.07	0.0001	0.95	0.0001
	TL	-4.06	0.0001	0.91	0.0001
	MTL	-2.93	0.0001	0.88	0.0001
FL	SL	2.53	0.0001	1.06	0.0001
	TL	-1.89	0.0096	0.96	0.0001
	MTL	-0.84	0.0867	0.93	0.0001
TL	SL	5.13	0.0001	1.09	0.0001
	FL	2.72	0.0003	1.04	0.0001
	MTL	1.58	0.0141	0.96	0.0001
MTL	SL	3.89	0.0001	1.14	0.0001
	FL	1.25	0.0167	1.08	0.0001
	TL	-1.07	0.1102	1.03	0.0001

Results and Discussion

Samples of lacustrine charr from the ten lakes ranged from 38 to 423 mm (MTL) (Table 1 and Fig. 2). Clear linear relationships existed among the length measures (Fig. 3), and conversion regressions were calculated using data from all lakes (Table 2).

The appropriateness of these lines was then examined using the relationship between SL and TL for each of the ten lakes (Table 3). Although differences among intercepts ($P<0.00001$) for individual lake conversion regressions were detected by the analysis of covariance, all but three were not significantly different from zero (Table 3). Some of the slopes were significantly different from each other ($P<0.00001$) and all were different from zero, ranging from 1.06 to 1.14. To evaluate the effect of these statistical differences on predicted values, TL was calculated at SL = 150 mm for each lake and for the common regression line (Table 3). The differences between the predicted length from the common regression (169 mm) and the lake specific regressions ranged from +4 mm to -1 mm. This was within the expected range of error associated with measuring an individual live fish. W. MacCallum, Ontario
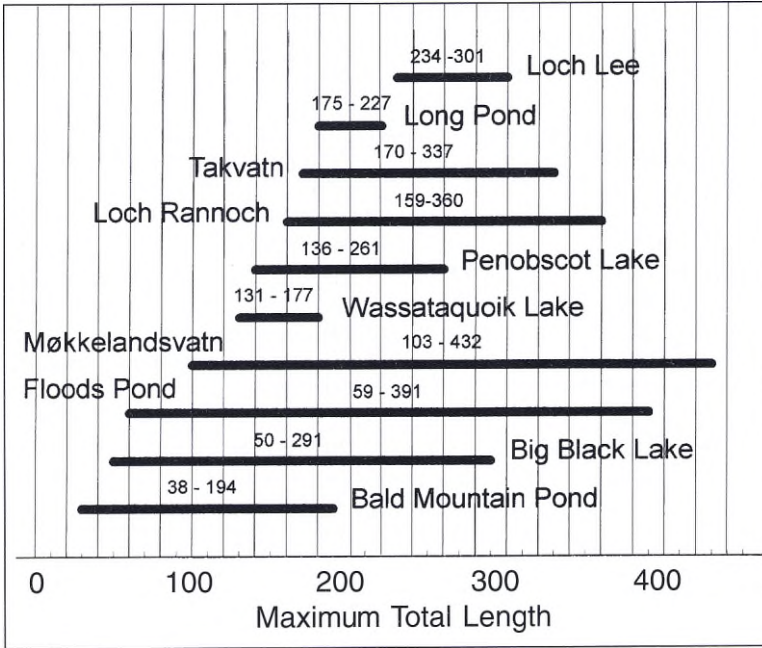
Fig. 2. Size range (MTL) of charr used to establish length conversion formulae.

Ministry of Natural Resources, Thunder Bay, Ontario (unpublished data) measured the FL of 75 charr from Char Lake in Canada's Northwest Territories to the nearest millimeter. All fish were

measured twice, on consecutive days. More than half of the fish (54.7%) were not measured to the same length. Although most of the errors were ± 1 mm; errors of ± 2 mm, and -4 mm also occurred. Thus, conversions based on the common formula introduced no more error than measuring charr in the field. Based on this test, we believe that the conversion formulae in Table 2 are appropriate for charr populations in North America and Europe.
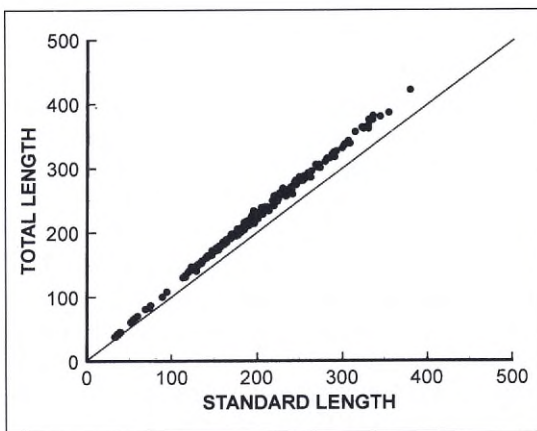
Acknowledgments

Fig. 3. Relationship between standard length (SL) and maximum total length (MTL) for charr from 6 lakes in North America and 4 lakes in Europe.

Table 3. Lake specific regressions (a=intercept, b=slope) for converting standard length to total length, with the probability (*P*) for parameter estimates equaling zero and predicted (Y) total length for standard length=150 mm.

Lake name	a	P(a=0)	b	P(b=0)	Y
Maine					
Bald Mtn. Pond	-0.61	0.1182	1.44	0.0001	170
Big Black Lake	-2.32	0.5756	1.14	0.0001	169
Floods Pond	5.16	0.0001	1.10	0.0001	170
Long Pond	1.34	0.8014	1.13	0.0001	171
Penobscot Lake	4.30	0.2881	1.12	0.0001	172
Wassataquoik Lake	5.11	0.4282	1.11	0.0001	172
Norway					
Møkkelandsvatn	5.90	0.1224	1.08	0.0001	168
Takvatn	13.84	0.0032	1.06	0.0001	173
Scotland					
Loch Lee	8.38	0.4251	1.07	0.0001	169
Loch Rannoch	16.33	0.0311	1.04	0.0001	172
All	5.13	0.0001	1.09	0.0001	169

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Significance and Temporal Persistence of Individual Specialization in Cannibalistic Arctic char, *Salvelinus alpinus*

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Abstract

A strong individual specialization observed in cannibalistic Arctic char was examined with respect to i) impacts of social interactions on the feeding patterns, and ii) temporal persistence of the individual specialization. Two experiments were carried out using a radiographic technique to study the cannibalistic response. The first experiment revealed that when restocked in separate tanks, pre-classified cannibals continued to feed on conspecific prey, whereas the majority of pre-classified non-cannibals did not become cannibalistic. This indicates that individual specialization is not a result of social interactions and dominance hierarchies within the experimental tanks. In the second experiment, it was demonstrated that pre-classified cannibals resumed cannibalistic feeding even after three months with no access to conspecific prey. Thus, individual specialization for cannibalism in char may be persistent for a long time.

Keywords: Cannibalism, Arctic char, experimental studies, feeding specialization.

Introduction

Cannibalism is widespread in the animal kingdom (Fox 1975), and occurs commonly among teleost fishes (Smith and Reay 1991). Traditionally, the killing and consumption of conspecifics has been regarded as abnormal behaviour, and has received little theoretical interest. During the last decades, however, cannibalism has been given increased attention both in relation to evolutionary, ecological and behavioural implications, and is now recognized as an important biological factor (Fox 1975, Polis 1981, Smith and Reay 1991, Elgar and Crespi 1992).

The Arctic char, *Salvelinus alpinus* (L.) is a generalist and opportunistic feeder with a broad dietary niche width including the consumption of conspecifics (Johnson 1980), and cannibalism has been reported in many natural char populations (e.g. Nilsson 1955, Skreslet 1973, Sparholt 1985, Riget et al. 1986, Amundsen 1994). In an experimental study of cannibalism in Arctic char (hereafter denoted char), Amundsen et al. (1995) revealed a strong individual specialization of the cannibalistic fish. When groups of char were given the opportunity to feed on smaller conspecifics in several consecutive trials, the same individuals were cannibalistic throughout all trials. Further, when presented with alternate weekly cycles of different food types consisting of dry pellets and small conspecific prey, some of the individuals consistently were cannibalistic, whereas others did not feed on conspecifics at all (Amundsen et al. 1995). Social interactions may lead to modifications of feeding behaviour in char and other salmonids (McCarthy et al. 1992, Thorpe et al. 1992, Jobling and Baardvik 1994), and it could be argued that the observed feeding pattern may have been the result of dominance hierarchies within the experimental tanks. Dominant individuals may have controlled the access to fish prey, leaving the subordinates to feed on other food types or not feed at all. Further, it is uncertain whether cannibalistic char would

retain this individual specialization over long time periods without having continuos access to char prey.

The present study further investigated the individual specialization of cannibalistic char. Two experiments have been accomplished using a radiographic technique to study the cannibalistic response of the predatory fish. The objectives were, firstly, to examine the possible role of social interactions on the apparent individual feeding specialization of the cannibalistic char, and, secondly, to test whether the individual cannibalistic responses would be persistent over a long time period without access to conspecific prey.

Material and methods

Predators and prey

Arctic char of the domesticated Takvatn strain were used as predators (mean total length 37.0 cm, range 34-41 cm, and mean weight 672 g, range 508-1,096 g). The fish had been hatchery-reared prior to the start of the experiments and had been fed dry pellets since first feeding. All fish used as predators were individually tagged with juvenile tags (Floy Tag: FT69). The predators were adapted to test conditions for four weeks before the start of the experiments, which were conducted in the period from October 1992 to April 1993. All experiments were conducted at a water temperature of 10-12 °C and under continuos light. Between the experimental trials, the fish were fed dry pellets. Prior to each trial, the fish were not fed for 24 h.

1+ Arctic char (5-7 cm) of the domesticated Hammerfest strain were used as prey in the experiments. The same prey fish were never used in more than one trial, and replicates were restricted to reduce the number of prey required. The experimental procedure has been licensed by the Norwegian veterinary authorities.

Identification of prey in the stomachs of the predators using X-ray

The feeding of the predatory Arctic char was examined using radiography (Nandor 2 machine,

4 s exposure, 50 kV, 80 mAs, AGFA Structurix D7 film). Preliminary studies showed that fish prey in the stomachs of predators were not visible on X-ray photos. Therefore, prior to the start of each trial, the char prey were anaesthetised using benzocaine (70 ppm) and force fed with lead shot (2.0 mm in diameter; one lead shot per fish), which acted as an X-ray dense marker. A method test revealed that the prey did not regurgitate the shot. At the end of each trial, the predators were anaesthetised with benzocaine and X-ray photographed. The presence of shot markers in the guts of the predators were used to identify which char were cannibalistic, and the number of shots correspond to the number of fish consumed by each predator.

Pre-experimental classification of the cannibalistic response of predatory fish

Prior to both experiments, the individual cannibalistic response of the predatory char was examined. Five groups of 10 individually tagged large char were placed together in 300 l circular tanks. On four consecutive trials with one week intervals, 30 small conspecifics were introduced into each tank for a 24 h period. The small char were marked with an X-ray dense lead shot in their stomach. At the end of each trial, the large char were anaesthetised and X-ray photographed to identify any prey fish consumed. The remaining prey fish in the tanks were counted to give an additional check on the number of fish that had been eaten. Predators that were recorded to have eaten fish prey during the trials, were operationally classified as cannibals. Fish that had not eaten small conspecifics on any of the four trials, were referred to as non-cannibalistic. In total, 11 of the 50 predatory fish (22%) were classified as cannibals. The number of cannibals within each tank varied from 1 to 3 (mean 2.2).

Experiment A: Impact of social interactions in the experimental tanks

Twenty Arctic char were sorted out according to the pre-experimental classification and restocked in two separate 300 l tanks; ten fish in each, giv-

ing one tank with 10 cannibals and the other with 10 non-cannibals. The fish were given an acclimation period of two weeks before the experiment was initiated. During two repeated trials separated by a week interval, 30 prey fish were introduced in each tank for a 24 h period, after which the remaining prey fish were counted and removed. The predators were aneasthetised and X-ray photographed to identify any prey fish in their stomachs, and the cannibalistic response of the fishes in the two tanks was compared.

Experiment B: Persistence of the cannibalistic response

Arctic char that had been classified as either cannibals or non-cannibals, were placed together in a 600 l holding tank, and kept for 3 months without any access to smaller conspecific prey fish. During the first part of this period (December 17 to March 2) the fish were kept at ambient water temperature (0.2-1 °C) and fed dry pellets. A total of 21 fish died while kept in the holding tank. After this period the remaining fish were randomly restocked into two 500 l circular experimental tanks, 14 and 15 fish in each, and given an acclimation period of three weeks, still without any access to fish prey. During two repeated trials separated by a one week interval, 50 conspecific prey fish were introduced in each tank for a 24 h period, after which the remaining prey fish were counted and removed. The predators were anaesthetised and X-ray photographed to identify any prey fish in their stomachs, and the cannibalistic response of the pre-classified cannibals (N=7) and non-cannibals (N=22) were compared.

Statistical tests

For comparison of the proportions of fish with cannibalistic response, the *G*-test with Yates' correction has been used (Sokal and Rohlf 1981), whereas Student's *t*-test was used for comparison of mean lengths and weights of cannibalistic and non-cannibalistic fish.

Results

Experiment A: Impacts of social interactions in the experimental tanks

In the experimental tank with the cannibals, nine out of ten fish (90%) consumed conspecific fish prey during both trials (Fig. 1). One individual did not eat fish prey in either of the two trials. During the first trial, 29 out of the 30 prey fish were eaten (mean 3.2 prey per predator). At the second trial, 50 prey fish were introduced into the tank, and a total of 46 were consumed (mean 5.1 prey per predator). Of the non-cannibals, one individual out of ten fish (10%) consumed fish prey in both experimental trials (1 and 4 prey, respectively), whereas the others did not consume conspecifics at all. The differences in proportions of fish that exhibited cannibalistic responses in the cannibal and non-cannibal tanks were statistically significant ($G_{adj.}$=9.80 and P<0.005 for both Trial 1 and Trial 2). There were no significant differences in mean length or weight between the cannibals and the non-cannibals (Table 1).
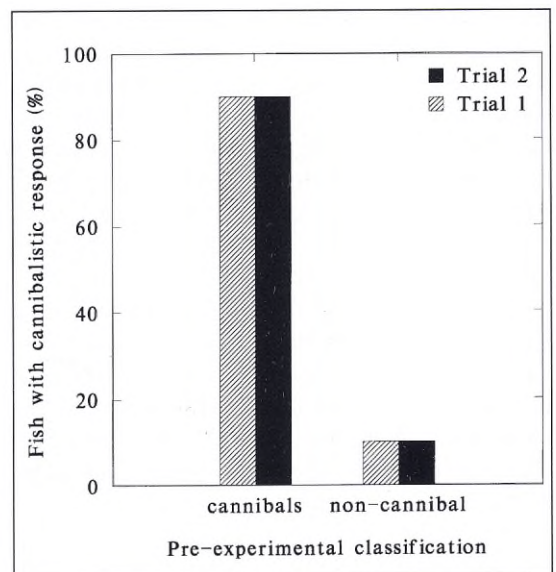
Fig. 1. Cannibalistic response of pre-classified cannibalistic (N=10) and non-cannibalistic (N=10) Arctic char after restocking the two fish groups into separate experimental tanks.

Table 1. Mean lengths and weighs of cannibals and non-cannibals at the initiation of the experiments.

	Cannibals			Non-cannibals			*t*-test
	Mean	SE	*N*	Mean	SE	*N*	*P*-values
Experiment A:							
Length (cm)	36.8	0.438	10	37.3	0.553	10	0.49 NS
Weight (g)	651	21.31	10	666	48.01	10	0.77 NS
Experiment B:							
Length (cm)	36.7	0.530	7	37.2	0.335	22	0.47 NS
Weight (g)	643	31.80	7	677	17.31	22	0.29 NS

Experiment B: Long time persistence of cannibalistic response

After three months without access to prey fish, all the pre-classified cannibals consumed conspecific prey fish during the two experimental trials (100%, $N=7$), whereas in total only 18% ($N=22$) of the pre-classified non-cannibals exhibited cannibalistic responses (Fig. 2). Of the cannibals, 86% ate fish during the first trial, whereas all consumed fish prey during the second trial.

Fig. 2. Cannibalistic response of pre-classified cannibalistic ($N=7$) and non-cannibalistic ($N=22$) Arctic char after 3 months without access to conspecific prey.

Among the non-cannibals, only 9% consumed fish during the first trial, and 18% during the second. The differences in proportions of fish with cannibalistic responses between the two groups of fish, were statistically significant (Trial 1: $G_{adj.}=12.0, P<0.005$; Trial 2: $G_{adj.}=11.8, P<0.005$). For the pre-classified cannibals, the mean numbers of prey eaten per feeding predator during the two trials were 4.2 and 6.3, respectively. For the pre-classified non-cannibals that attended cannibalistic feeding during the experiment, the mean numbers of prey eaten were 3.5 at both trials. There were no significant differences in mean length or weight between the cannibals and the non-cannibals (Table 1).

Discussion

Arctic char establish social hierarchies when stocked at low densities (Christiansen et al. 1992, Jørgensen et al. 1993). The experiments carried out on char cannibalism here and by Amundsen et al. (1995), were conducted at moderate densities of predatory fish, and social interactions within the tanks may be expected. Social interactions could influence the feeding behaviour of char (Jobling and Baardvik 1994), and the cannibalistic responses of the individual fishes may thus have been affected by their social status within each experimental tank. However, when restocking the pre-classified cannibals and non-cannibals in separate tanks, the cannibals continued to feed on fish prey whereas the large majority of the non-cannibals did not. Social interactions are therefore not likely to have had a sig-

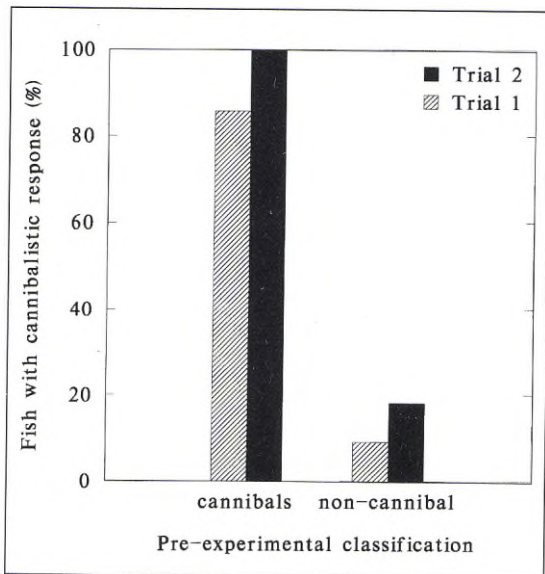nificant impact on the development of the observed pattern of individual feeding specialization of cannibalistic fish.

The individual specialization of cannibalistic char also appears to have a strong temporal persistence. After a three month period without any access to conspecific prey fish, all pre-classified cannibals resumed feeding on small char when given the opportunity, whereas most of the non-cannibals did not respond cannibalistically to prey fish. Strong and persistent prey specialization of individual fish has also been reported from *in situ* studies of natural populations of salmonids. By repeated observations of individually marked fish, Bryan and Larkin (1972) demonstrated individual feeding specializations in both brook trout (*Salvelinus fontinalis*), cutthroat trout (*Salmo clarki*) and rainbow trout (*Salmo gairdneri*), some of which persisted for half a year. Furthermore, strong relationships between intensity of parasite infection and the occurrence of the corresponding intermediate host in the stomach of individual fish, has also been taken to demonstrate persistent individual feeding specializations in natural populations of Arctic char (Curtis et al. 1995, Knudsen 1995).

A few individual char that had not been cannibalistic throughout the pre-experimental classification, developed cannibalistic feeding during the experimental trials. This may reflect a certain individual flexibility in relation to cannibalstic feeding. However, Arctic char are known to exhibit temporal changes in food intake rates (Pálsson et al. 1992), and these results may therefore also be related individual variation in feeding motivation throughout the experimental period. Some of the experimental fish showed external characteristics indicative of sexual maturation. Maturation and spawning may decrease food intake of fish (Jobling 1993), and some individuals may, thus, have experienced reduced feeding motivation, especially during autumn when the natural spawning occur. This was also the season when the pre-experimental trials were carried out. Nevertheless, only a small proportion of the fish changed their cannibalistic responses during the experimental trials. Most of the fish maintained their initial feeding strat-egy throughout the experiments, thus supporting the conclusion of a persistent individual feeding specialization of the char.

Several studies have reported individual feeding specialization within animal populations (e.g. Bryan and Larkin 1972, Bryan 1973, Heinrich 1976, Milinski 1982, Ringler 1983, Whitfield 1990, Amundsen 1995), but the ecological mechanisms producing specialization and the resulting consequences are poorly understood (Partridge and Green 1984, Holbrook and Schmitt 1992). The variation in feeding specialization between individuals of the same population has partly been attributed to differences in body size (Schmitt and Holbrook 1984, Werner and Gilliam 1984), gender (Selander 1966, Whitfield 1990) or ontogenetic stage (Osenberg and Mittelbach 1989). However, phenotypic variations in feeding preferences may also be the result of evolved morphological, physiological or behavioural adaptations of the individual predators. Feeding specializations may for instance be accompanied by differences in trophical apparatus and other morphological traits (Meyer 1987, 1990a,b, Wainwright et al. 1991, Magnan and Stevens 1993), or changes in the digestive and absorptive capacities of the gastrointestinal tract (Hofer 1979a, b, Buddington et al. 1987, Buddington 1992). Similarly there may be marked individual differences within a population both in foraging tactics (Ringler 1983, Bence 1986, Ehlinger and Wilson 1988, Ehlinger 1990, Kohda 1994) and in responses to particular chemical or visual cues (McBride et al. 1962, Clarke and Sutterlin 1985). Some of these adaptations merely reflect phenotypic plasticity, whereas others may have a genetic basis. In the present study with Arctic char, no significant differences in length or weight distributions were found between the cannibals and non-cannibals, which were all from the same age class. Apparently, the specialization for cannibalistic feeding is related to a predisposition of certain individuals, with the difference in cannibalistic response between the individuals being connected to phenotypic variation in behaviour, morphology or physiology that might be of a genetic nature. In fact, there is some evidence that cannibalism has a genetic basis in fish, since dif-

ferent strains of the same species have been shown to have different heritable cannibalistic tendencies (Dominey and Blumer 1984, FitzGerald and Whoriskey 1992)

In conclusion, the results of the present study strongly indicate that individual specialization for cannibalism is a significant behavioural feature of Arctic char, and does not appear to be a consequence of the social structure in the experimental tanks. Further, we show that the individual specialization for cannibalistic feeding is persistent for long periods in the absence of conspecific prey. Individual specialization of cannibalistic char may involve a genetically based predisposition to cannibalism, but conclusive evidence is lacking. It should also be emphasised that the phenomenon of strong individual feeding specialization is probably not restricted to cannibalism, but is more likely a behavioural feature related to piscivorous feeding in general. For Arctic char and most other fish species, fish prey are the largest and most mobile dietary items. Thus, fish are both difficult to capture and to handle. Predation on prey that requires a long pursuit and handling time is likely to promote specialized feeding by the predator, and this may provide an adaptive rationale for the observed individual feeding specialization of the cannibalistic char.

Acknowledgements

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Morphological Comparison of Natural Produced Atlantic Salmon (*Salmo salar* L), Anadromous Brown Trout (*S. trutta* L), and their Hybrids

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Abstract

Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and their hybrids are normally identified in the field by morphological differences such as maxilla length, thickness of caudal peduncle, degree of indentation of the tail, overall shape, fin heights, and coloration. This study quantifies 36 morphometric and 6 meristic characters and analyses their variation in electrophoretically identified wild produced individuals. In as much as 47.6% of the characters examined, there were no significant difference between the fish groups. Hybrids were mostly trout-like, and within the pure species many individuals were misclassified as hybrids or even members of the opposite species, when an hybrid-index was used to examine single characters. When summarising all characters by using a canonical discriminant analysis, hybrids and trout differed significantly from salmon but not from each other.

Keywords: Hybrids, morphology, Atlantic salmon, sea trout.

Introduction

Although natural selection should favour reproductive isolation, natural hybrids between Atlantic salmon (*Salmo salar*) brown trout (*S. trutta*) occur in many areas where the species lives sympatrically (cf. Elo et al. 1995, Hartley 1996). The frequency of hybrids is usually relatively low, but there are streams where hybrids appear to be common (cf. Jansson et al. 1991, Jansson and Öst 1997). Reasonably hybridization should be promoted when salmon and trout populations are significantly affected by human activities.

Salmonid body form has been demonstrated to be determined both genetically (Gjerde and Schaeffer 1989, Beacham 1990, Swain et al. 1991, Fleming et al. 1994) and environmentally (Winans 1984, Currens et al. 1989, Fleming et al. 1994), and characters such as body form (Taylor 1986,

Swain et al. 1991, Fleming et al. 1994) and fin morphology (Fleming and Gross 1989, Fleming et al. 1994) is known to be altered by culture. In addition, convergence in morphology may occur rapidly within as well as between fish species when faced similar environmental conditions (Meyer 1987, Brönmark and Miner 1992, Fleming et al. 1994). For these reasons, differences between hatchery produced trout, salmon and their hybrids may not be representative for natural produced fish. Comparisons of trout, salmon, and hybrid morphology have mostly been performed on hatchery reared fish (Day 1884, Jones 1947, Winge and Ditlevsen 1948, Alm 1955, Piggins 1964, 1966, Rogers et al. 1965, Mills and Hadoke 1987, Wilkins et al. 1994). These studies suggest that the overall shape of body, coloration, length of the maxilla, depth of the caudal peduncle and

degree of indentation of the caudal fin are the most reliable characters to use when identifying salmon and trout, although they appear to be very variable in hybrids. Deviations from morphological intermediary have been observed in many interspecific F1 hybrids from a variety of fish taxa (West and Hester 1964, Berry and Low 1970, Ross and Cavender 1981, Leary et al. 1985).

In this study we quantitatively examined a number of morphometric and meristic characters on electrophoretically verified wild salmon, trout and F1 hybrids. The fish was collected in the River Dalälven on the Swedish east coast, where the populations of salmon and anadromus brown trout to a large extent have been maintained by artificial breeding and release of 2+ smolts, and where the frequency of naturally breed hybrids have been demonstrated to be unusually high (Jansson and Öst 1997).

Material and methods

The study area and fish samples

The River Dalälven flows out into the Gulf of Bothnia. At Älvkarleby, ten kilometres from the river mouth, a dam construction of the hydroelectric power plant prevents upstream migration of anadromous fish. In 1989, a reproduction and nursery area for salmon and trout was improved by increasing the water discharge there during winter time from less than 0.5 m³/s to 3.0 m³/s, which probably increased the natural reproduction in the river. In October 1995 about 600 *Salmo* parr were collected by electro-fishing in that area. The collected parr were stored in a pen cage (9 m³) that was placed in the river, allowing them to feed nothing but natural prey items. In mid-November 1995, 103 individuals were sampled and transported to the Fishery Research Station in Älvkarleby, for age determination (scale and otolith reading) and for measurements and meristic counts.

Measurements

Morphometric measurements included total body length, lengths of the leading edges of the fins
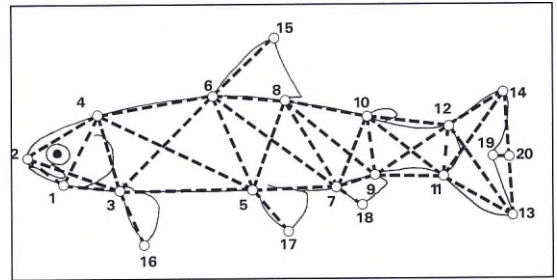
Fig. 1. Location of the morphometric landmarks (points) used. All landmarks, except 19-20, are described in detail by Winans (1984).

(fin heights), caudal peduncle length, and a truss network, a system of vertical, horizontal and oblique distances between anatomical landmarks (Fig. 1; after Strauss and Bookstein 1982). Fish were thawed and placed on a water resistant paper. Landmark positions were recorded by making holes with a needle in the paper alongside the location of each landmarks. Distance measurements were taken with digital vernier callipers between landmarks (holes). The measurement procedure is described in detail by Winans (1984) and Swain and Holtby (1989). Counts included the number of black and red spots located on three regions of the body, viz., (1) on the dorsal fin, (2) above, and (3) below the lateral line beneath the dorsal fin (within the demarcation of the landmarks 5, 6, 7 and 8 (cf. Fig. 1)). The spots were counted under a magnifying glass. All counts and measurements were made on the right side of the fish.

Electrophoresis

Starch gel electrophoresis of the diagnostic enzymes glucose-6-phosphate isomerase (GPI) and phosphoglucomutase (PGM) was performed by using muscle and adipose fin homogenates separated in a buffer described by Ridgway et al. (1970). The relevance of using GPI and PGM as diagnostic enzymes has earlier been shown by Verspoor (1988), Jansson et al. (1991) and Jansson and Öst (1997). Each parr conformed to the pattern expected for Atlantic salmon, or brown trout, or F1 hybrid.

Statistics

Analyses were performed using the Statistical Analysis System (SAS Institute Inc. 1987). Characters were adjusted using residuals from multiplicative regressions of the character on total body length. The variables were then analysed by using two methods. (1) Differences in characters between groups (salmon, trout, hybrids) and age-classes were examined by analysis of variance (ANOVA), followed by Tukey's *post hoc* test. The differences between groups were also analysed by using a canonical discriminant analysis, where all characters were included. (2) An hybrid-index *I* was calculated to express the relationship of some of the characters of the hybrids to those of salmon and trout (Hubbs 1943). The formula was;

$$\text{Hybrid Index } (I_i) = 100[(H_i - S_i)/(T_i - S_i)]$$

where *H* is the value of the character ($_i$) of the hybrid, *S* is the mean value of the character for the salmon and *T* is for the brown trout. In this study, a character of an individual having a hybrid index up to 30 was regarded as salmon-like, values from 30 to 70 as intermediate, and values above 70 as trout-like. The index estimates the morphological distance between hybrids and one parent as a percent of the distance between the parental species. Index was scored separately for four of the morphometric characters that are commonly used to identify hybrids, or putative hybrids (Jones 1947, Piggins 1964, 1966, Mills and Hadoke 1987, Wilkins et al. 1994); length of the maxilla (1-2, Fig. 1), depth of the caudal peduncle (11-12, Fig. 1), degree of indentation of the tail (19-20, Fig. 1) and counts of black and red spots on the dorsal fin. Non-parametric analysis were made following Hollander and Wolfe (1973).

Results

Seven out of the 103 sampled parr (6.8 %) were precocious males. These were excluded from the analysis because their morphology differ significantly from non-precocious conspecifics. Total

Table 1. Total body length and age of the brown trout (T), Atlantic salmon (S), and hybrids (H) used in this study. Means marked with the same letter were not significantly different according to Dunn's test (experimental error rate = 0.06).

Fish category	Sample size	Age (years)	Length (mm) mean±S.D.	Size range (mm)
T	32	1+	114 ± 18.2	77-156
T	23	2+	202 ± 19.3	169-233
S	2	1+	108	88-128
S	6	2+	151 ± 8.6	136-161
H	12	1+	95.9± 23.6	72-145
H	21	2+	160 ± 17.8	126-195

length of 1+ and 2+ hybrids differed from 1+ and 2+ trout, but not from salmon. Trout (2+) differed significantly from salmon (2+), but not from similar aged hybrids (Table 1).

Measurements

Hybrids and trout differed significantly from salmon but not from each other in 25% of the morphometric characters examined (Table 2a). Hybrids and trout had longer maxilla, larger head, shorter pectoral fin, shorter and deeper caudal peduncle, shallower indentation of the tail, and longer distance between head to dorsal fin. In one of the characters examined hybrids and salmon differed significantly from trout (hybrids and salmon had deeper mid-body). In 13.9% of the characters, significant differences were found only between hybrids and trout. Hybrids had longer distance between origin of dorsal fin to origin of anal fin, and larger caudal fin. In one case significant difference was found only between salmon and trout (salmon had longer distance between dorsal tip of dorsal fin to origin of adipose fin), and in one case between salmon and hybrids (salmon had longer distance between dorsal tip of anal fin to origin of upper tip of caudal fin). Finally, no significant differences were found between hybrids, trout or salmon in 52.8% of the morphometric characters examined.

Table 2 a. Morphometric characters in brown trout (T), Atlantic salmon (S) and hybrids (H). The fish catego-
ries are mentioned after their value of respective character; the category having the highest value is mention
first. Differences between the three groups are given as follows: S>H=T means that hybrids and trout differed
significantly from salmon, but not from each other. S≥H≥T means that salmon and trout differed significantly
from each other, but that neither species differed significantly from the hybrid. Differences between age classes
are expressed in a similar way. The significant values for the interaction between age class and categoy are also
indicated. Landmarks refer to Fig. 1. All values have been adjusted for size (body length); p.p. = posterior part.

a) Morphometric characters

Description	Landmarks	Diff. between categories	Diff. between age-classes	Interaction
maxilla length	1- 2	T=H>S	1+=2+	NS
maxilla to pectoral fin	1- 3	T=S=H	2+=1+	NS
head depth I	1- 4	T=H=S	1+=2+	NS
snout to pectoral fin	2- 3	T=H>S	2+=1+	NS
forehead length	2- 4	S=H=T	1+=2+	NS
head depth II	3- 4	H=T>S	1+=2+	NS
pectoral fin to pelvic fin	3- 5	S=H=T	1+=2+	NS
pectoral fin to dorsal fin	3- 6	T=H=S	1+=2+	NS
pectoral fin height	3-16	S>H=T	2+=1+	NS
oblique element I	4- 5	H=T>S	2+>1+	$P<0.041$ [1]
head to dorsal fin	4- 6	T=H>S	2+=1+	NS
body depth I	5- 6	S=H>T	1+=2+	NS
pelvic fin to anal fin	5- 7	H=T=S	1+=2+	NS
pelvic fin to p.p. of dorsal fin	5- 8	H=S=T	1+=2+	NS
pelvic fin height	5-17	S=H=T	1+=2+	NS
dorsal fin to anal fin	6- 7	H≥S≥T	2+=1+	NS
dorsal fin length	6- 8	H≥S≥T	1+=2+	NS
dorsal fin height	6-15	S=H=T	2+=1+	NS
anal fin to p.p. of dorsal fin	7- 8	H=S=T	2+=1+	NS
anal fin length	7- 9	H=T=S	1+=2+	NS
anal fin to adipose fin	7-10	H=S=T	1+>2+	$P<0.032$ [2]
anal fin height	7-18	S=T=H	1+=2+	NS
p.p. of dorsal fin to p.p. of anal fin	8- 9	H=T=S	2+=1+	NS
p.p. of dorsal fin to adipose fin	8-10	S≥H≥T	2+=1+	NS
body depth II	9-10	H=T=S	1+=2+	NS
caudal peduncle length	9-11	S>H=T	1+=2+	NS
anal fin to caudal fin I	9-12	S≥T≥H	1+=2+	NS
adipose fin to caudal fin	10-11	H=T=S	1+=2+	NS
anal fin to caudal fin II	10-12	S=T=H	1+=2+	NS
depth of caudal peduncle	11-12	T=H>S	1+=2+	NS
caudal fin length, lower lobe I	11-13	S=H=T	1+=2+	NS
caudal fin length, upper lobe I	11-14	H≥S≥T	2+=1+	NS
caudal fin length, lower lobe II	12-13	H≥S≥T	1+=2+	NS
caudal fin length, upper lobe II	12-14	H≥S≥T	1+=2+	NS
caudal fin height	13-14	S=H=T	2+=1+	NS
indentation of caudal fin	19-20	S>H=T	2+=1+	NS [3]

[1] 1+ salmon had higher value that 2+ salmon. For hybrids and trout the situation was reversed. [2] 2+ trout
had lower value that 1+ trout and 1+ hybrids. [3] This variable was not correlated with total length. Thus, an
ANOVA followed by Tukey's multicomparison test was performed.

Table 2 b. Meristic characters in brown trout (T), Atlantic salmon (S) and hybrids (H). (For more details see Table 2 a.)

b) Meristic characters

Description	Diff. between categories	Diff. between age-classes	Interaction
number of spots on dorsal fin	T>H>S	1+=2+	NS
proportion black spots on dorsal fin	S≥T≥H	2+=1+	NS
number of spots above lateral line	H=T>S	2+=1+	NS
proportion black spots above lateral line	S=T=H	2+=1+	NS[3]
number of spots below lateral line	T=H>S	1+=2+	NS
proportion black spots below lateral line	T>H>S	1+=2+	NS[3]

[3] This variable was not correlated with total length. Thus, an ANOVA followed by Tukey's multicomparison test was performed.

Meristics

The meristic characters showed greater differences between fish groups compared to the morphometric characters. Hybrids were intermediate to, and significantly different from, both salmon and trout in two of the six meristic characters examined (Table 2b). There were more black and red spots on dorsal fin, and proportionally more of black and red spots below the lateral line in trout than in hybrids and salmon. In two cases, hybrids and trout differed significantly from salmon. Counts of black and red spots, and the proportion of black spots, were higher above and below lateral line, respectively, in hybrids and trout. In one case the only significant difference was between hybrids and salmon (hybrids had a lower proportion of black rays on dorsal fin).There was no significant difference between hybrids, trout or salmon in the proportion of black spots above the lateral line.

Canonical discriminant analysis

The measured and meristic variation in hybrids and trout did not differ significantly when summarised (Mahalanobis squared distance between groups : $D=6.04$, $F=1.31$, $P=0.187$) (Fig. 2). In contrast, both hybrids and trout differed significantly from salmon (Mahalanobis squared distance between hybrids and salmon: $D=50.59$, $F=3.65$, $P<0.001$; between trout and salmon:
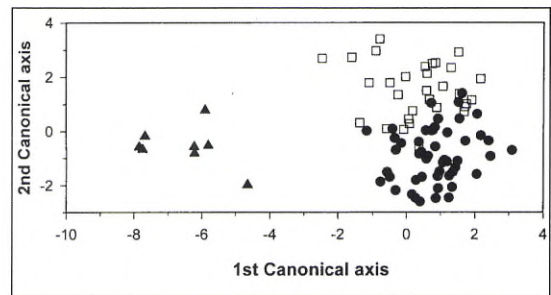
Fig. 2. Canonical discriminant function analysis using size-adjusted data. Scores for salmons are filled triangles, trout are filled circles, and hybrids are open squares. The first axis explains 77.1% of the variation and the second 22.9% (the length of the axis are about proportional to their explanatory level). The loading of the characters on the axes are given in Table 3.

$D=54.21$, $F=4.24$, $P<0.001$). Proportion of black spots below lateral line, and counts of black and red spots on dorsal fin, depth of caudal peduncle, and length of pectoral fin explained most of the variation between fish groups. The loadings of the characters on the first and second canonical axes are given in Table 3.

Hybrid index

Salmon and trout phenotypes were observed in each of the four characters examined (i.e. counts of black and red spots on dorsal fin, length of maxilla, depth of caudal peduncle, and degree of

Table 3. Loadings of the measurements and counts on the first and second canonical axes. Characters as in Fig. 1 and Table 2; p.p. = posterior part.

Description	Landmarks	Loading on first canonical axis	Loading on second canonical axis
maxilla length	1- 2	0.242	0.015
maxilla to pectoral fin	1- 3	-0.042	-0.022
head depth I	1- 4	0.091	0.126
snout to pectoral fin	2- 3	0.249	0.037
forehead length	2- 4	-0.024	0.129
head depth II	3- 4	0.343	0.153
pectorial fin to pelvic fin	3- 5	-0.165	0.044
pectorial fin to dorsal fin	3- 6	0.058	-0.029
pectoral fin height	3-16	-0.416	0.092
oblique element	4- 5	0.151	0.065
head to dorsal fin	4- 6	0.187	-0.106
body depth I	5- 6	-0.116	0.187
pelvic fin to dorsal fin	5- 7	0.038	0.070
pelvic fin to p.p. of dorsal fin	5- 8	-0.005	0.086
pelvic fin height	5-17	-0.271	0.017
dorsal fin to anal fin	6- 7	-0.012	0.160
dorsal fin length	6- 8	0.029	0.258
dorsal fin height	6-15	-0.110	0.096
anal fin to p.p. of dorsal fin	7- 8	-0.058	0.006
anal fin height	7- 9	0.200	0.139
anal fin to adipose fin	7-10	0.018	0.208
anal fin height	7-18	-0.108	0.005
p.p. of dorsal fin to p.p. of anal fin	8- 9	0.006	-0.016
p.p. of dorsal fin to adipose fin	8-10	-0.140	0.131
body depth II	9-10	0.290	0.114
caudal peduncle length	9-11	-0.211	-0.045
anal fin to caudal fin I	9-12	-0.225	-0.195
adipose fin to caudal fin	10-11	0.136	0.067
anal fin to caudal fin II	10-12	-0.250	-0.086
depth of caudal peduncle	11-12	0.429	0.033
caudal fin length, lower lobe I	11-13	-0.035	0.050
caudal fin length, upper lobe I	11-14	0.087	0.277
caudal fin length, lower lobe II	12-13	0.025	0.199
caudal fin length, upper lobe II	12-14	0.062	0.194
caudal fin height	13-14	-0.057	0.139
indentation of caudal fin	19-20	-0.309	0.154
number of spots on dorsal fin		0.428	-0.110
proportion black spots on dorsal fin		-0.251	-0.213
number of spots above lateral line		0.353	0.175
proportion black spots above lateral line		-0.070	-0.202
counts of spots below lateral line		0.634	0.197
proportion black spots below lateral line		0.795	-0.169

Table 4. Proportion of individuals showing salmon-like, intermediate and trout-like phenotypes for four morphological characters according to Hubb's hybrid index. Index-values are calculated as described in Material and methods.

Fish category	Character	per cent of fish showing index values of		
		Salmon-like	Inter-mediate	Trout-like
T	Maxilla, 1-2	16.4	16.4	67.3
	Peduncle, 11-12	10.9	14.6	74.5
	Caudal fin, 19-20	27.3	14.5	58.2
	Spots	14.6	16.3	69.1
S	Maxilla	75.0	12.5	12.5
	Peduncle	62.5	25.0	12.5
	Caudal fin	62.5	25.0	12.5
	Spots	75.0	0.0	25.0
H	Maxilla	27.3	12.1	60.6
	Peduncle	12.1	27.3	60.6
	Caudal fin	30.3	18.2	51.5
	Spots	21.1	18.2	60.6

indentation of the caudal fin) (Table 4). Individual fish showed the phenotype of the opposite species in a relatively large number of instances. For trout, this was especially pronounced in degree of indentation of the caudal fin, in which 27.3% of individuals showed the salmon phenotype, and 25% of salmons showed the trout phenotype in number of black and red spots on the dorsal fin. In hybrids 60.6% showed a trout-like appearance in three of the four characters examined.

Discussion

The morphology of hybrids appeared to be more similar to trout than to salmon. First, hybrids and trout differed significantly from salmon but not from each other in 11 (26.2%) of the characters examined; corresponding pattern for hybrids/salmon to trout was found for only one character (2.4%). Second, hybrids were classified as trout in as much as 60.6% in three of the four characters examined by using the hybrid-index; corresponding figures for hybrids classified as salmon were only 12.1%, 21.2%, 27.3%, and 30.3%. Third, the canonical discriminant analysis con-

firmed that hybrids and trout differed significantly from salmon but not from each other. Studies on hatchery-reared fish have also reported the hybrids to be trout-like in a majority of characters (Jones 1947, Piggins 1964, 1966, Wilkins et al. 1994), although there are exceptions in which the appearance of hybrids was considered about equally often as trout-like as salmon-like (Alm 1955), or mostly as intermediate (Winge and Ditlevsen 1948). It has been suggested that deviations from morphological intermediacy in hybrids may be effects of genetic dominance (Simon and Noble 1968), modifier genes (Ross and Cavender 1981), and/or delays in developmental rate (Leary et al. 1983).

In a recent study on naturally produced hybrids from the River Dalälven, and apparently representing the same breeding population as the present study, Jansson and Öst (1997) found that all hybrids had brown trout mitochondrial DNA genotypes. Because the mitochondria genome is inherited from the mothers, the hybrids were all progeny of female trout and male salmon. An alternative explanation for the hybrid-trout-similarity is, hence, that morphological characters are

maternal inherited and not inherited through genetic dominance, modifier genes or delay in developmental rate.

When using the hybrid index, a significant proportion of individuals of the pure species exhibited characters of the other species. Among the four characters examined, i.e. length of maxilla, thickness of caudal peduncle, degree of indentation of the caudal fin, and counts of black and red spots on dorsal fin, at least 12.5% of salmon and 10.9% of trout were classified as members of the other species. Similar findings have been reported from studies in which single characters have been analysed in a quantitative way (Piggins 1964, 1966, Rogers et al. 1965, Wilkins et al. 1994). The hybrid index also revealed that as much as 60.6% of the hybrids exhibited a trout-like character in three of the four characters examined. These results show that characters used on its own may result in a large proportion of misclassified hybrids, a feature common for all of the previous studies on the subject (e.g. Day 1884, Jones 1947, Winge and Ditlevsen 1948, Alm 1955, Piggins 1964, 1966, Rogers et al. 1965, Wilkins et al. 1994).

Compared to salmon and trout, hybrids usually took a numerically, but not statistically significant, intermediate position. While hybrids showed numerical intermediacy in 20 characters, corresponding figures for trout and salmon were 13 and 9, respectively. A significant intermediacy was found in only two of the characters examined: counts of black and red spots on the dorsal fin, and proportion of black spots below the lateral line. In both cases the hybrids were between their parental species. In field surveys, and as a complement to electrophoretic confirmation and other visible characters, the colour and counts of spots on body and fins may be helpful attributes to identify natural Atlantic salmon × brown trout hybrids amongst their parental species.

To conclude, in nature there is no "fool proof" morphological character separating trout, salmon and their hybrids. However, in this study hybrids was more similar to trout than to salmon and in fact, a canonical discriminant analysis showed that both hybrids and trout were separated from salmon.

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Screening of Descending Atlantic Salmon (*Salmo salar* L) Smolts from a Hydropower Intake in The River Orkla, Norway

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Abstract

A hydropower station was built downstream from major salmon rearing areas in the River Orkla. Studies of salmon smolt behaviour during descent were conducted prior to regulation for hydropower production. The smolt run was heavily correlated to water discharge, and most smolts migrated during increasing and high discharges. The smolts migrated in the top water layer in the main current of the river. The intake at the hydropower station was designed to prevent descending smolts from entering the turbines. An extended intake 50 m long and 1.5 m high diverts water from the lower layers for hydropower generation. A hypothesis on low mortality during the smolt run was tested in the salmon producing areas of River Orkla. Mortality of smolts passing through the turbines was also tested. Carlin-tagged smolts were stocked in groups at different sites along the entire salmon producing stretch of the river (88 km). A turbine mortality of 73% was estimated for smolts released into the intake at the power station. No differences in smolt survival were found between hatchery reared, Carlin-tagged smolts stocked at different sites upstream and downstream from the intake. Turbine and predation related smolt mortality was insignificant in 5 of 6 years. The screen constructed in the River Orkla seems to function well, and prevent smolts from entering the turbines in periods of high river flow. However, during smolt migration in periods of low flow diversion of water should be omitted, or diversion for hydropower generation should probably not exceed more than 20% of the river flow.

Keywords: Atlantic salmon smolt, screening, turbine mortality, predation.

Introduction

Smolt descent in rivers is reported to be a hazardous period in the life history of salmon (Ruggles 1980). The passage of dams, water falls, desmoltification and predation from different fishes, birds and mammals are assumed to be the main sources of mortality for migrating smolts. Physical damage to fish when passing through turbines is a major source of mortality (Von Raben 1957, Monten 1964). Technologies developed for passage of downstream migrating smolts has been difficult to manage and are generally not very successful (Cada et al. 1994, Francfort et al. 1994). The River Orkla was regulated for

hydropower production in 1982-83. The salmon producing stretch is 88 km long and an intake to divert water was built 51 km downstream from important salmon nursery grounds (Fig. 1). Salmon smolt behaviour was studied prior to the regulation (Hesthagen and Garnås 1986). The smolt descend in the top water layer, in the main current, at night and at increasing and high water discharges. Newer analysis have confirmed the positive relation between water discharge and smolt migration (Hvidsten et al. 1995). Based on the early smolt behavioural studies a specially designed intake screen was built to prevent smolts from passing through the turbines (Fig. 2). The intake diverts water from the bottom layers tak-
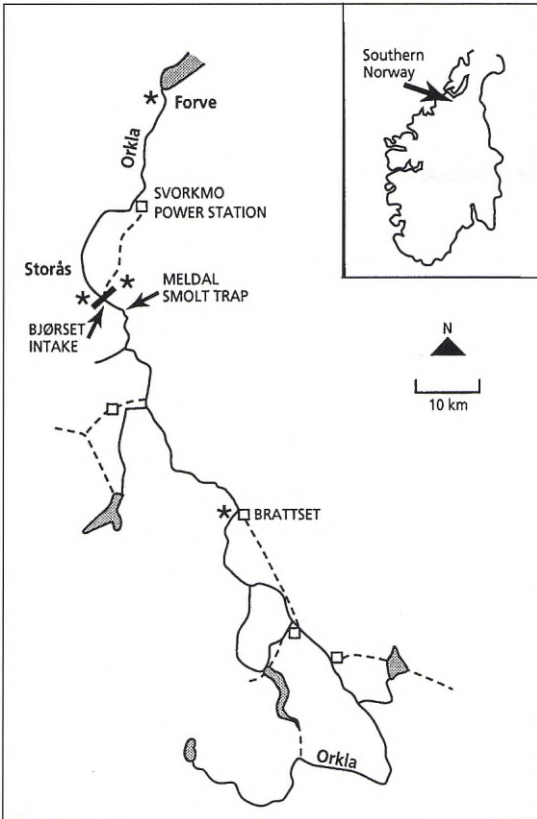
Fig. 1. Map showing the River Orkla, releasing sites (*) and site of smolt capture.

ing notice of the surface smolt migration. To evaluate the effectiveness of the intake screen groups of Atlantic salmon smolt were released upstream, downstream and into the power station. Two hypothesis were formulated;

1) Smolts released upstream and downstream from the inlet have the same survival rate.
2) Smolts released directly into the inlet at the power station have the same survival rate as smolts released upstream and downstream from the inlet.

Study area

The River Orkla was regulated for hydropower production in 1982-83. Mean discharge throughout the year is 64 m^3s^{-1}. The annual catch of adult

salmon in the Orkla is normally 10-20 tons, and consists of grilse, 2 and 3 sea-winter fish. The salmon producing stretch is 88 km long and an intake to divert water was built 51 km downstream from important salmon nursery grounds (Fig. 1). The screen is a 50 m long concrete wall parallel to the river bank (Fig. 2a). A horisontal opening at the river bottom is 1.5 m high (Fig. 2b). Svorkmo power station was opened in 1983 and has two Francis turbines, with 27 and 43 m^3s^{-1} capacities respectively. The total water fall in the power station is 99 m.

Fig 2. a) The river intake for hydro power generation in the River Orkla, the total opening is 1.5 x 50 meters along the river bottom. b) The smolt screen deflector is seen in cross section perpendicular to the river side.

Table 1. Year and site of release of hatchery reared smolts in the River Orkla. Mean and maximum smolt lengths are given.

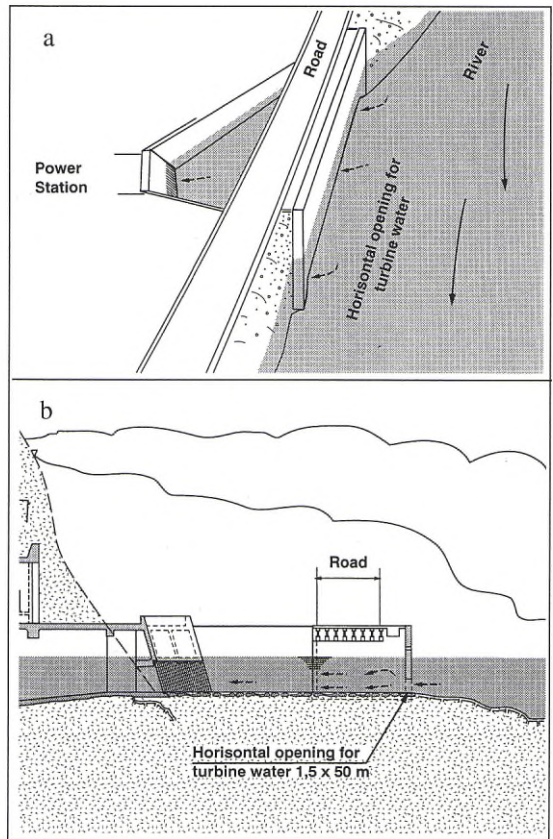| Year	Brattset		Bjørset, intake		Storås		Forve	
	mean	max	mean	max	mean	max	mean	max
1984	17.8	22	17.7	23	17.5	22	17.4	21
1985	17.6	22	17.5	24	17.3	24	17.3	22
1986	16.8	26	16.6	23	16.8	22	17.0	25
1987	17.1	23	16.7	21	16.6	20	16.4	20
1988	16.2	20	17.0	21	16.3	22	17.1	20
1989	16.6	20	16.9	21	16.9	21	17.2	21

Methods

During the period from 1984 through 1989, four groups of Atlantic salmon smolts were released at different sites in the River Orkla. The smolts were released at Brattset, Bjørset, Storås and Forve (Fig. 1). The smolts released at Bjørset were released into the inlet of Svorkmo power station. Smolts were tagged with Carlin-tags and transported about 40-70 km from the Lundamo Hatchery to the releasing sites. All the smolts were 14 cm or larger (Table 1), and there were no differences in average fish size between the four groups released the same year. The smolts were released between the 13th and 15th of May each year (Table 2). Smolts were stocked in the period of the wild smolt run. Tagging and handling procedures used were identical throughout the period. A total of 33,529 specimens of hatchery reared salmon were tagged and released in the River Orkla in the period from 1984 through 1989 (Table 3). 7,833 smolts were stocked at the

Table 2. Date of release () and numbers and dates of recaptures of hatchery reared Carlin-tagged smolts at Meldal after releases at Brattset. Discharge in the River Orkla and the proportion of diverted water to the Svorkmo Power station at Bjørset intake are given. * = Highest number of recaptures.

Date recapt.	1984 (14 May)			1985 (15 May)			1986 (15May)			1987 (13 May)			1988 (13 May)		
	n	m^3s^{-1}	%	n	m^3s^{-1}	%	n	m^3s^{-1}	%	n	m^3s^{-1}	%	n	m^3s^{-1}	%
15 May	5	130	21.8	0	125	18.4	0	100	27.0	0	63	66.7	4	186	7.0
16 "	12*	219	0.9	1	134	14.9	0	90	35.6	0	70	60.0	1	154	15.6
17 "	0	274	0	0	137	15.3	1	105	22.9	6	98	34.7	5	152	15.8
18 "	0	265	0	2	139	14.4	1	79	45.6	13*	151	12.6	4	106	32.1
19 "	0	287	0	4	135	15.6	0	79	49.5	9	140	17.1	1	82	52.4
20 "	0	243	0	8*	138	15.2	2	82	43.9	4	112	28.6	0	68	60.3
21 "	0	181	4.4	0	152	13.2	2*	82	46.3	0	100	36.0	0	57	59.7
22 "	0	228	0	4	160	6.9	0	93	32.3	5	98	35.7	1	52	55.8
23 "	0	208	0.5	0	101	30.7	0	68	48.5	4	118	22.9	0	56	57.1
24 "	0	183	9.3	2	81	50.6	0	52	53.9	5	155	14.2	0	57	63.2
25 "	1	179	9.5	2	94	37.2	0	43	53.5	4	137	19.7	1	68	63.2
26 "	0	155	18.1	2	114	29.8	0	41	56.1	4	151	17.2	2	77	54.6
27 "	0	210	6.2	1	68	10.7	0	41	41.5	2	109	33.9	10	99	42.4
28 "	0	279	0	0	242	0	0	33	48.5	0	77	57.1	15*	147	20.7
29 "	0	224	4.9	0	263	0	0	32	43.8	0	69	63.8	2	150	18.0
30 "	0	157	19.1	0	107	25.2	0	30	40.0	1	65	66.2	0	125	29.6
31 "	0	116	42.2	0	80	50.0	0	28	-	0	71	60.6	0	113	29.2

Table 3. Number of released smolts and number of recaptures of adult salmon from the different releasing sites in the River Orkla. (The smolts were released 18th of May 1989.)

Year	Brattset			Bjørset, intake			Storås			Forve		
	release	recap	(%)	release	recap	(%)	release	recap	(%)	release	recap	(%)
1984	1971	134	(6.8)	1890	41	(2.2)	987	52	(5.3)	986	70	(7.1)
1985	1984	49	(2.5)	1946	11	(0.6)	984	35	(3.6)	993	31	(3.1)
1986	1998	13	(0.7)	999	6	(0.6)	1928	28	(1.5)	1000	17	(1.7)
1987	1867	38	(2.0)	998	4	(0.4)	1998	60	(3.0)	1000	22	(2.2)
1988	2000	37	(1.9)	1000	7	(0.7)	2000	45	(2.3)	1000	31	(3.1)
1989	1000	12	(1.2)	1000	3	(0.3)	1000	17	(1.7)	1000	9	(0.9)
Total	10820	283	(2.5)	7833	72	(0.8)	8897	237	(2.9)	5979	180	(3.0)

two Francis turbines. At the time of smolt releases, engines were producing at or near full efficiency.

In order to study smolt descent near the screen, smolts were caught at Meldal bridge using two traps according to methods described by Hesthagen and Garnås (1986). The distance from the traps to the inlet of the hydropower station is 4 km. The traps were not operated in 1989.

Recoveries of tagged adult salmon are reported by commercial fishermen in the sea and anglers in the river(s). Recapture rates were expressed in percent of the numbers released. Recaptures varied considerably between years and thus deviation (ln transformed) from the mean recapture rate of each year were used as recapture variable in the ANOVA statistics.

Results

The recapture rate of adult salmon from Brattset, Storås and Forve areas was the same, and averaged 2.5, 2.9 and 3.0% respectively in the period from 1984 through 1989 (Table 3). The releases at Storås and Forve are both downstream from the dam for hydropower intake situated at Bjørset. The numbers of recaptures from the upstream and downstream areas were indifferent (ANOVA, $P>0.05$). Thus hypothesis no 1 was confirmed. However, recapture rate from Brattset was lower than recoveries from Storås and Forve in 1986 (Chi-square = 6.1, $P<0.025$), when water dis-

charge during the smolt run was low. In 1986, the diverted water flow from Orkla at Bjørset was 46% of the total discharge on the date of the peak migation of hatchery reared smolts passing Meldal (Table 2). The water flow diversion at peak migration of hatchery reared smolts varied between 0.9 in 1984 as the lowest, and 20.7% in 1988 as the highest in the other years (Table 2).

Smolts stocked in the intake of the power station at Bjørset gave an average recapture rate of 0.8% adult salmon (Table 3). This figure was significantly lower than for groups released at the three releasing sites in the river (ANOVA, $P<0,001$). Thus hypothesis no 2 was rejected. Turbine mortality averaged 73.0 ($\pm$12.0) per cent per year in the period from 1984 through 1989.

Discussion

The recapture rates of the group of smolts which were released directly into the turbines show that mortality of smolts passing the Svorkmo Power station was high. Von Raben (1957) and Monten (1964) explain the reasons for fish mortality when passing turbines. These are mechanical-, pressure-induced-, shearing action- and cavitation damage. Carlin quoted by Ruggles (1980) estimated smolt mortality of 50-70% for Francis turbines. It is difficult to compare mortality from different types of Francis turbines (Ruggles 1980). The mortality of the hatchery reared smolts released in the turbines in River Orkla was

within the figures given by Carlin. Small turbines (small openings) in the Orkla, increases the probability of touching the fish and thereby mortality (Monten 1955 and Von Raben 1957). Larger fish are more vulnerable to hit the turbine than small fish. The wild smolts in the River Orkla are smaller in length than the hatchery released smolts, and mortality therefore is probably less for the wild than for hatchery reared smolts.

In 5 of 6 years, returns of salmon upstream and downstream from the intake did not differ. This means that few smolts are diverted into the power station at normal water regimes and that the screen operates satisfactorily. Smolts migrate with the current in the top layer, passing in the main river and thereby avoid the inlet. In years with low river discharge, when a high proportion of the water flow is diverted for hydropower generation, the number of smolts passing the turbines increases (Hvidsten 1990).

Low returns of adult Atlantic salmon from smolt stockings upstream compared to downstream in rivers, are reported by many authors. These results contradict results from the River Orkla. When releases are performed in the upstream areas of rivers draining into the Baltic, predation by fishes such as burbot (*Lota lota*) and pike (*Esox lucius*) resulted in heavy mortalities (Larsson and Larsson 1975, Larsson 1977, Jacobsson and Järvi 1977, Larsson 1985). The topography at releasing sites is important for smolt survival. Releases in areas with low water velocity make smolts more vulnerable to predation by fish (Bakshtansky et al. 1976) and mammals (Heggenes and Borgstrøm 1988). Mills (1964) reported a 10% smolt mortality due to predation from pike in two hydropower dams in a Scottish river. In Norway, lower returns of released smolts are reported from upstream releases compared to downstream areas in the River Glomma (Hansen 1980). Predation from pike, hydropower dams, as well as possible desmoltification due to long migratory distances were discussed as possible causes of differences in adult salmon recoveries after smolt releases in the River Glomma (Hansen 1980). Hansen and Lea (1982) reported higher recaptures from downstream releases than upstream releases in the Rana

and Vefsna rivers in Norway. Difference in recaptures of adult salmon in the River Vefsna are probably caused by high water falls. In the River Rana, water falls and hydropower stations could explain the increased mortality of the smolts stocked upstream. The fauna of the River Rana includes potential predators such as migratory char (*Salvelinus alpinus*), in addition to brown trout. Migratory brown trout in the River Bondalselv were observed eating presmolts/large parr (own observations) in April. There are some minor water falls situated upstream from the intake in the River Orkla. However, no significant mortality was found for Atlantic salmon smolts passing the five meter high Anti Dam in East River Sheet Harbour, Nova Scotia (Ruggles 1980). Mortality from turbines and predation in the River Orkla seems to be low when water discharge is high.

Hansen and Jonsson (1985) reported that the hatchery reared smolts began their migration immediately after release, and the downstream migration speed depended on water velocity. Descent was slower than the water velocity in the River Imsa (Hansen and Jonsson 1985). In the River Orkla the released smolt migration speed is dependent on water discharge, and may obviously be much slower than the water velocity at low water discharges (Table 2). The low recapture rates for Carlin tagged smolts in the smolt traps at Meldal (Table 2) in 1986, might have been caused by the low water discharge, and that catch efficiency in the traps was low. A significant difference in the recapture rate of adult salmon from releases at Brattset compared to the releases downstream from the turbine intake, indicates mortality during a period of low water discharge (Table 2). Normal recaptures of adult salmon from downstream releases also indicate that the smolts from Brattset experienced no special desmoltification problems as they were triggered by the same water regime. Predation should not differ significantly in the upstream and downstream areas in a single year.

Six years of releases yielded no significant differences in the recapture rates of smolts released at the different sites from upstream to downstream areas of the River Orkla. Mortality

due to turbine passage and predation by fishes, birds and mammals within the period of the smolt run, was therefore insignificant in 5 of 6 years. The intake built to divert descending smolts seems to protect smolts from passing through the power station in most years. This construction operates successfully when smolt descent occurs during high water discharge, and the bulk of water is kept within the river. In periods of low water discharge during smolt migration water divertion should be omitted, or probably restricted to less than 20% of the river flow for use in hydropower generation.

Acknowledgements

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Effects of Instream Habitat Enhancement on Fish Populations of a Small Norwegian Stream

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Abstract

Weirs and pools were created by using an excavator on a 200 m long experimental section in a small tributary (mean discharge 0.95 m³/s) of the River Glomma in southeastern Norway. The experimental section was once dredged to facilitate timber floating. The most abundant fish species in the stream were brown trout (*Salmo trutta*), bullheads (*Cottus poecilopus*) and minnows (*Phoxinus phoxinus*). Four weirs, placed in two pairs, were constructed to create 10 m wide, 15 m long and approximately 1.5 m deep pools. Small pools, 2-3 m wide and 0.7 m deep, were distributed in the stream bed between the two pairs of weirs. The density of brown trout was annually estimated by means of the mark-recapture method for the first two years (1986-87) and by successive removal the last year before enhancement (1988) and annually during six years after the enhancement (1989-96, except in 1993-94). A reference section was sampled simultaneously, except in 1989. The mean density of brown trout on the experimental section was 18.3 per 100 m prior to enhancement, and increased by 200% after the construction of weirs. The increase was due to increased number of specimens >10 cm, whereas number of specimens <10 cm (agegroups ≤1+) decreased. In 1996 the density was reduced close to the conditions before enhancement, and this was probably caused by a heavy flood in 1995, deteriorating the weirs followed by a cold winter with thin snow layer and a thick ice cover. Age group 2+ dominated in the pooled sample, and low representation of agegroups ≤1+ indicated that the brown trout stock on this section must be recruited by immigration from sections upstream.

Keywords: Habitat, enhancement, weirs, brown trout, minnow, size distribution, migration.

Introduction

The brown trout (*Salmo trutta*) is a territorial species like many other salmonids, and prefers specific types of habitat. Preferences depend on the size of the fish (Kalleberg 1958, Allen 1969, Bohlin 1977, Heggenes 1988, 1996). Discharge, current velocity, depth, substrate and occurrence of pools determine density and size distribution of fish in a river section. These factors may even be used to predict fish abundance by means of multivariate, empirical models (Milner et al. 1985, Winstone 1993, Barnard and Wyatt 1995). Experimental habitat enhancement by physical alterations in running waters to increase the number of territories, has been done in several countries (Tarzwell 1937, Saunders and Smith 1962, Hunt 1969, Burgess and Bider 1980, Eronen and Shemeikka 1985, Linløkken 1988, Näslund 1989, Brittain et al. 1993, Jungwirth et al. 1993, Riley and Fausch 1995). Habitat enhancement may be a successful and sustainable way of increasing natural recruitment, and an alternative to stocking artificially reared fish, which involves risks of introducing diseases (Ståhl 1987, Egidius et al. 1991) as well as genetic interference (Ryman and Ståhl 1981, Skaala et al. 1990, Hindar et al. 1991).

Territories may be formed by altering the physical structure of shores and river bed in different ways. Duration of a constructed pool or weir is probably related to the resources allocated to the construction. The aim of this work is to monitor the effects compared to the cost of an enhancement done with an excavator. The density of brown trout and the relative abundance of other fish species were monitored before and after the enhancement, and data was compared with results from a reference section.

Methods

Study area

Letjern is a small tributary to the River Glomma in southeastern Norway (Fig. 1). The catchment is 68 km² and the mean discharge is 0.95 m³/s. The catchment is dominated by moraines covered by coniferous forest and in the upper parts, bogland. The water quality is characterized by low salt content; κ = 1.9-2.6 mS/m, [Ca^{2+}] = 2.0-4.3 mg/l and is slightly acidified during periods of high flow; pH = 5.2-6.3 due to low alkalinity; 39-145 µekv/l. Brown trout (*Salmo trutta*), European minnow (*Phoxinus phoxinus*) and bullhead (*Cottus poecilopus*) are the most abundant fish species in the stream. Grayling (*Thymallus thymallus*) spawns in Letjern during May and fry migrate down to the Glomma in the summer. In the River Glomma there are several other species, including pike (*Esox lucius*), perch (*Perca fluviatilis*), burbot (*Lota lota*) and several cyprinides (Borgstrøm and Løkensgard 1984).

Until the 1960's, the stream was used for timber floating, and the bottom and shores were dredged to remove obstructions for timber. Such encroachments are known to affect the fish habitat negatively (Chapman and Knudsen 1980, Jutila 1985, Doloff 1986). The extent of dredging was greatest in the lower part, extending some 300 m upstream from Glomma, and the physical habitat was very homogeneous on this section. The gradient and thus the stream velocity was lower here than on the above sections; 1.5% compared to 2.0%. Twohundred meters of this lower section was chosen as an experimental section for the habitat enhancement project.
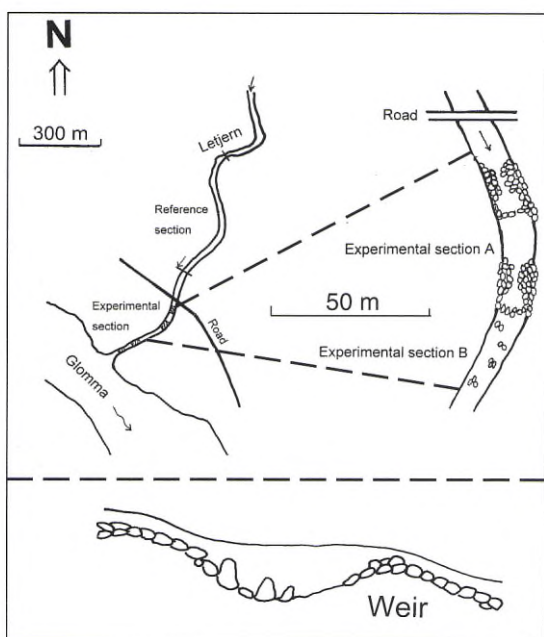
Habitat enhancement

In the autumn of 1988, pools were created on the experimental section by construction of four weirs with an excavator (Fig. 1). The four weirs, placed in two pairs, created 10 m wide, 15 m long and approximately 1.5 m deep pools, at normal discharge. Stream deflectors were constructed upstream, to narrow the stream and increase the water velocity into the pool. The purpose was to create a rapid which could maintain the water depth of the pool downstream by erosion, and thus avoid/reduce sedimentation. The deflectors and the weirs were built of rocks sorted out from the riverbed. Most of the rocks had a maximum size of <50 cm, but some were 50-100 cm. Rocks were also placed in the pool to increase the physical heterogenity and thereby increase the number of territories and hiding places for the brown trout. More moderate enhancement was done on the 30 m long section between the two pairs of

Fig. 1. Sketch map of the study area, showing details of the sampling site on the experimental section, and a principal sketch of a weir.

weirs by digging 2-3 m wide and 0.7 m deep pools, with groups of boulders on the upper side. In periods of high discharge and water velocity, rocks were gradually removed from the stream deflectors and deposited in the pool downstream. An extremely high flow in June 1995 caused considerable deterioration, and the depth was then reduced to less than 1 m in the weir pools. The winter 1995-96 was extremely cold with little snow, causing a thick ice cover on the stream during the winter.

Sampling

Sampling was done using a portable electro fishing apparatus in July 1986-87 and in August 1988-96. Density of brown trout was determined by mark-recapture experiments (Ricker 1975) in 1986 and 1987 and by successive removal (Bohlin 1984) annually in the periods 1988-92 and 1995-96. Prior to enhancement density was determined on the entire 200 m long (dredged) experimantal section, and on a reference section, starting 100 m above the experimental section. The sampling on the reference section always started from the same point, but the length of the section sampled varied; 400 m in 1986 and 1987, 280 m in 1988. After enhancement, the sampling was done on a 50 m section covering the two upper weirs, called the experimental section A, and on a 100-150 m reference section, except in 1989, when no sampling was done at the reference section. In 1990 and 1991, the section with small pools, called the experimental section B, was also sampled. Each sample from a section was anesthetized, measured, weighed, scales were collected, and the fish were kept in a tub of water until the last sampling was done. The brown trout were then released on the section on which they were captured. In 1988, 1992, 1995 and 1996 all the brown trout captured were killed for age determination based on otoliths.

Analysis

The density, expressed as number of specimen per 100 m, and the size distribution on the experimental and reference section were compared.

Differences in brown trout density were tested for significance by Wilcoxon-Mann-Whitney test (Siegel and Castellan 1988), and differences in size distribution were analysed by χ^2-test (given on the figures). Annual variations on the reference section express natural variation, and a regression model was calculated for the relationship between discharge and density of brown trout. The density and size distribution on the experimental section A and B were computed and compared to the density and size distribution before enhancement. Age determination was based on scales picked from anesthetized fish and otoliths from killed fish. Relative abundance of other species was expressed as a percentage in number of the total catches. Catchability varies with fish size. Samples from all years and sections of successive removal were pooled, and abundance and catchability of each age group was calculated to compute a selection curve. The estimated catchability was used to adjust age distibution in the total material. As sampling date varied from year to year, empirical growth could not be compared between years. Growth therefore had to be analysed by comparing samples from the experimental and the reference section caught at the same period.

Results

Density

The density on the experimental section was an average 18.3 brown trout per 100 m before enhancement. After enhancement the mean density was 66.2 per 100 m during 1989-95 on the experimental section A (weir section), which was significantly higher ($P[W_X < C_L] = 0.0179$) than the density before enhancement, and implies a 200% increase (Fig. 2). There was a peak on the weir section in 1991, and a low in 1992 and especially in 1996. On the reference section the density varied between 22.9 and 46.1 brown trout per 100 m, and there was a peak in 1991 and a low in 1992 like on the experimental section, but not in 1996. The mean density was 35.6 specimens per 100 m, which was 100% higher than the density on the dredged section and 70% of
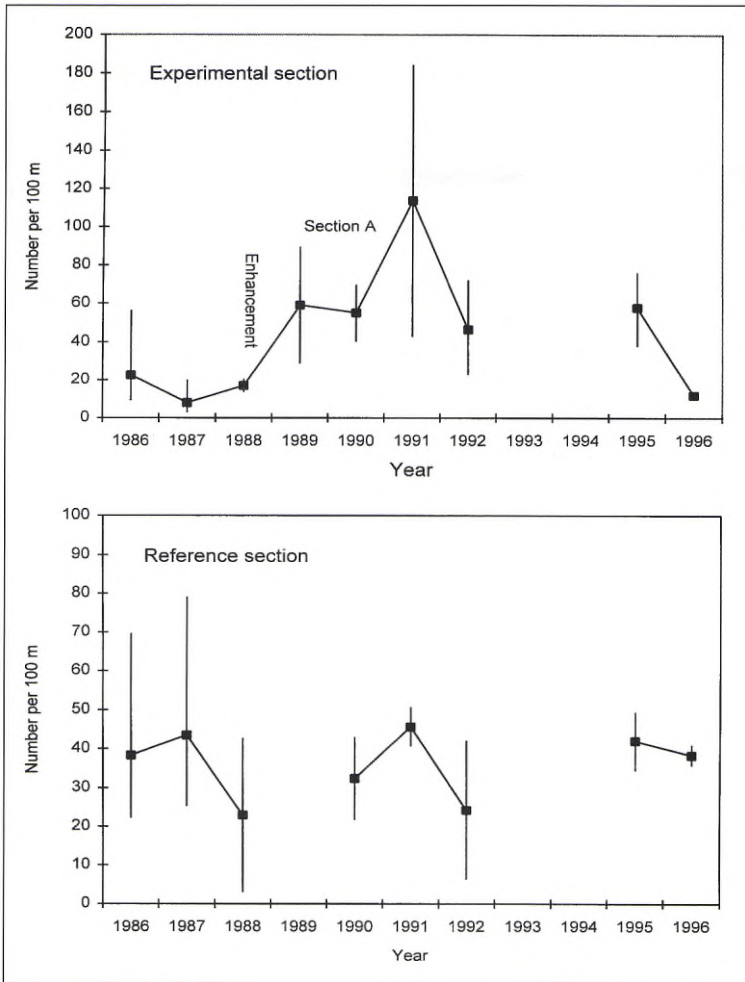
the density on the weir section. The mean density on the reference section, before and after the enhancement downstream, was very similar; 34.9 and 36.9 brown trout per 100 m, respectively. Number of specimens per 100 m on the reference section was positively correlated to mean discharge in June (r^2=0,722, P<0.05). No significant correlations were found between density and discharge during other periods. On the experimental section B (small pools), density was 65.9 (C.L.=40-147) in 1990, which differed significantly (P<0.05) from the denisty in 1987 and 1988, as both estimates are outside the other estimate's 95% C.L. (Snedecor and Cochran 1987). Density decreased to 28.7 (C.L. = 11-47) in 1991,

as the small pools were partly filled with gravel. This was considerably lower than on the experimental section A, but higher compared to the density when it was dredged.

Species composition

On the experimental section the fraction of brown trout varied from 16-20% before and increased to 20-45% after enhancement (Fig. 3). The fraction of bullheads varied from 60-70% before the enhancement and decreased to 33-61% afterwards, whereas the fraction of minnows increased from 10-15% before to 8-46% after enhancement, peaking in 1995 and 1996. On the reference sec-
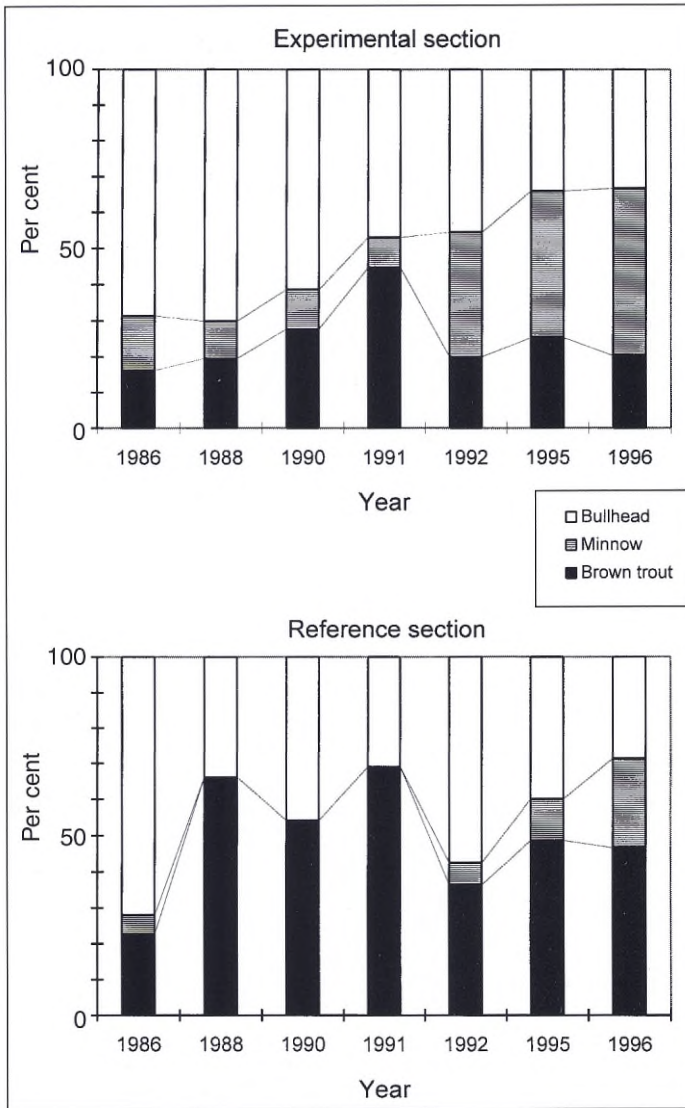
Fig. 3. Species composition in numbers in the total catches in Letjern. In 1987 and 1989 only brown trout were counted, so these years were omitted.

tion the fraction of brown trout was 23-69%, with a low in 1986 and a peak in 1991. The fraction of bullheads was higher than on the experimental section; 29-72%, whereas the fraction of minnows was lower; 0-25%, but it increased in 1995 and 1996.

Size and age

There were no systematical differences in mean lengths between samples from the experimental and the reference section neighter before nor af-

ter enhancement (Table 1). No differences were significant. Brown trout grew about 5 cm annually the first two years, and 3-4 cm annually the following two years. Specimens in size group <5 cm were 0+, size group 5-10 cm were 1+. Those in the size group 10-15 cm were mainly 2+, some 1+ and some 3+, and those >15 cm were ≥3+. Males matured from age 3+ and females from 4+.

Differences in size distributions reflected differences in age distribution as the growth rate was similar on both sections. The size distributions on the two sections were significantly different

Table I. Mean length (L. cm). standard deviation (SD) and number of specimens (*N*) of brown trout caught on two sections in Letjern 1987-95 (- = no data).

		Experimental section						Reference section				
		Age						Age				
	Date	1+	2+	3+	4+	5+	Date	1+	2+	3+	4+	5+
	08.07.87						17.07.87					
L		8.0	12.6	16.7	18.4	-		8.1	12.4	17.3	19.9	22.0
SD		0.71	1.37	0.47	1.77			0.73	1.11	2.05	2.12	0
N		8	6	3	5			7	21	15	9	1
	28.07.88						26.10.88					
L		9.2	12.8	19.5	20.0	-		9.9	14.0	17.3	20.4	23.0
SD		0.53	0.90	1.78	1.0			0.97	1.19	1.79	1.51	1.0
N		6	4	3	2			5	11	13	8	2
	13.07.89											
L		9.7	12.8	15.8	22.5	-		-	-	-	-	-
SD		2.21	0.67	0.87	0							
N		8	9	5	1							
	22.08.90						22.08.90					
L		11.2	15.1	18.8	22.8	-		11.3	14.6	19.7	21.5	25.0
SD		1.00	0.84	0.75	0.75			1.19	1.13	1.17	1.00	0
N		8	12	2	2			10	9	5	2	1
	06.08.91						06.08.91					
L		10.7	13.7	17.8	22.0	28.0		10.5	14.2	17.8	21.2	26.9
S.D		0.15	1.34	1.42	2.04	0		0.80	1.46	2.13	1.78	0.35
N		2	16	10	7	1		7	39	8	5	2
	05.08.92						05.08.92					
L		9.9	13.3	16.5	24.0	-		10.3	13.2	16.0	-	24.0
SD		0.6	0.85	1.20	0			0.63	1.03	1.00		0
N		8	3	6	1			9	3	12		1
	16.08.95						16.08.95					
L		9.2	13.1	16.3	20.8	-		10.3	13.5	17.0	21.8	-
SD		0.58	1.56	1.23	2.02			0.70	0.88	1.10	2.40	
N		3	11	6	3			8	18	6	2	

before enhancement, and the fraction of brown trout <5 cm was practically absent on both sections (Fig. 4). Size groups 5-15 cm dominated on the experimental section (dredged), whereas the size group 10-25 cm dominated and very few were <10 cm on the reference section. The first year after enhancement the size distribution on the experimental section A (weirs) had changed significantly, and was very similar to that on the reference section. During 1990, 1991 and 1992 there were no significant differences between the two sections. In contrast, size distributions differed significantly in 1995 and 1996, and on the experimental section A, brown trout <10 cm became

more numerous, and those >15 cm were less numerous than on the reference section, like it was before enhancement. On the experimental section B (small pools), the fraction of brown trout <15 cm was significantly higher than on the experimental section A.

Survival and recruitment

The age distribution in the pooled material was adjusted for the size selectivity of the sampling method, but the 1+ group was still poorly represented (Fig. 5). The 0+ group was practically absent, and therefore not included in these cal-
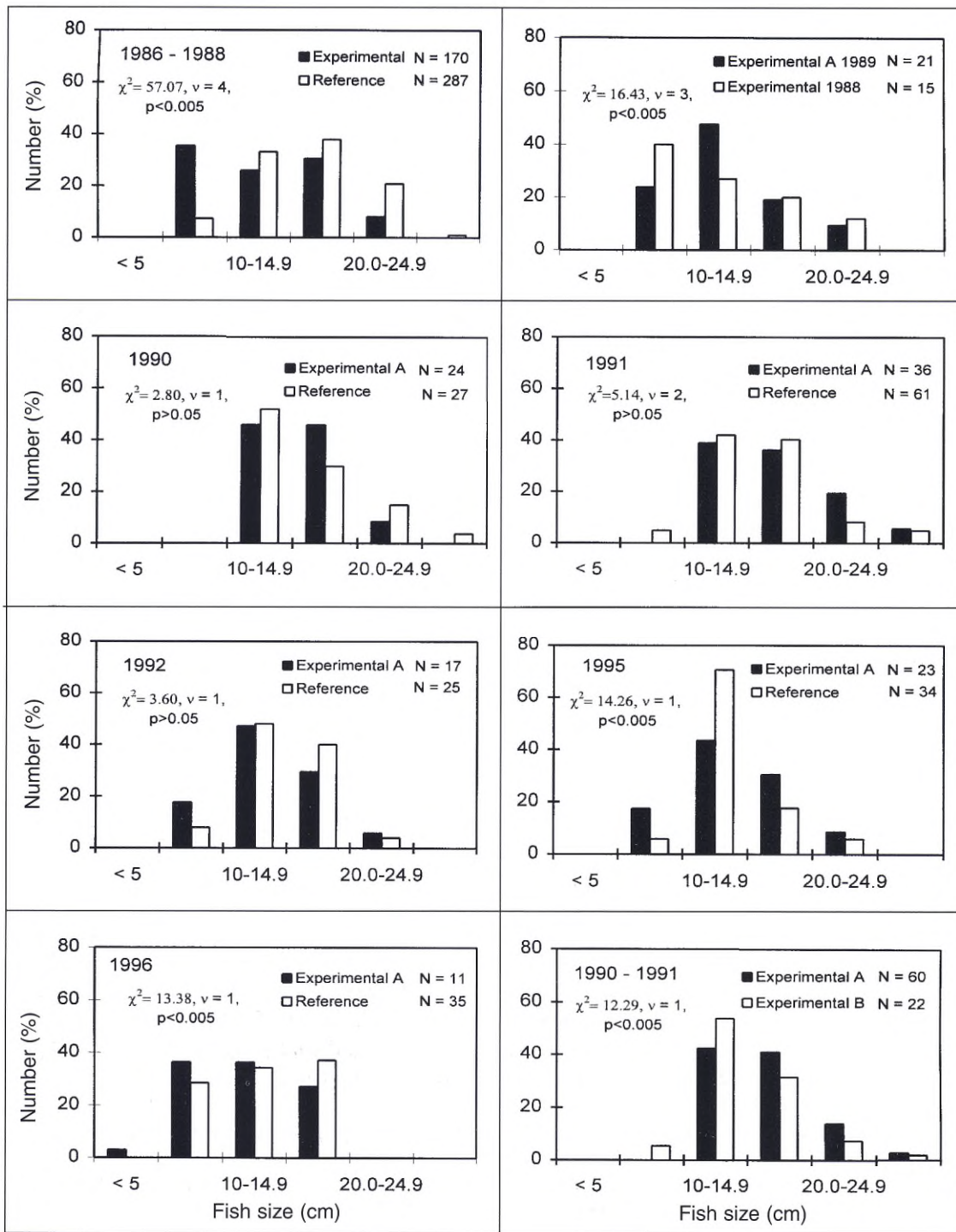
Fig. 4. Size distribution in the samples of brown trout from Letjern 1986-96.
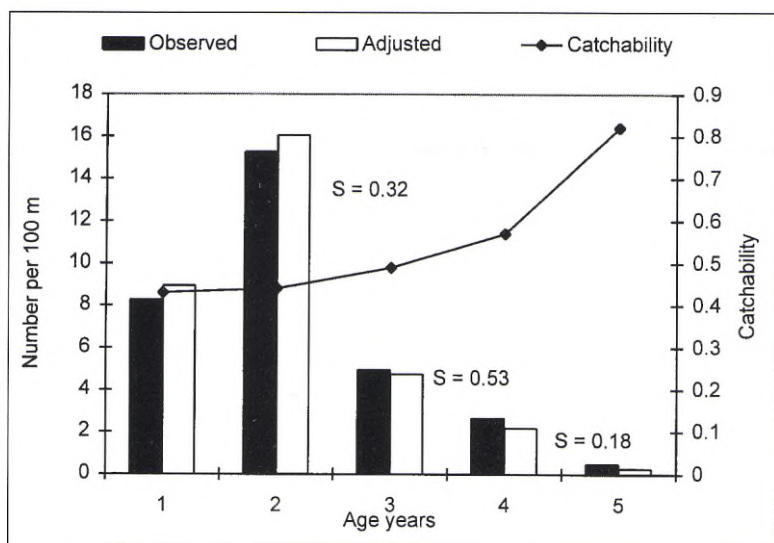
Fig. 5. Age specific catchability curve, observed and adjusted age composition in the total samples of brown trout from Letjern in 1986-95.

culations. Age group 2+ was the most numerous. Survival according to age distribution was S=0.32 for 2+ and S=0.53 for 3+ brown trout, in mean S=0.38. Total annual mortality + netto emigration of age 2+ and 3+ was A=1-S=0.62. To support a stable population the annual recruitment must equal A, which means that 62% of the stock must be replaced every year to maintain the population.

Discussion

The physical streambed alteration by construction of weirs increased brown trout densities by 200%, and the size group >10 cm (≥2+) was favoured. The increase corresponds to results from similar experiments in Sweden (Näslund 1989). The Swedish project was carried out in a stream with a slightly higher discharge and a higher density of brown trout than Letjern, and boulder dams, not unlike the weirs in Letjern, also increased density by 200%. The density also increased on the section of small pools, but less than on the weir section, and the effect declined rapidly, as the flow filled the excavations with gravel.

The duration of the weirs also seemed limited. A high flow seven years after enhancement detorated the weirs and filled the deepest parts

of the pools with rock and gravel. The density estimated two months after the high flow was still at a high level, but the following cold winter with thick ice cover, probably caused the reduction in 1996, to a level close to that prior to the enhancement. To increase the duration, rocks or boulders with maximum >1 m should be used in constructions, and placed at erodable spots at the deflectors to avoid deteriorations like those oberved in Letjern.

The size group 15-20 cm dominated in the weir section before detoration, like in the reference section, whereas the size group 10-15 cm was more numerous in the small pools. The size group <10 cm, which was numerous before enhancement, became sparse. These differences were due to size dependent habitat preferences (Kalleberg 1958, Bohlin 1977), and suggest the possibilities for influencing size and age distribution in the brown trout stock by using physical alterations. Brown trout prefer higher current velocity and depths with increasing size. The distribution of pool size and depth in the stream bed will therefore structure the size and age compostion of the brown trout stock. Dominance of shallow areas would favour production of fry and 1+, which then can recruit areas of bigger streams or lakes. Dominance of weirs and deep pools would favour brown trout of catchable size (>20 cm). Al-

though the samples were small, the growth rate of brown trout in Letjern seemed unaffected by the enhancement, as was the case in the Swedish project (Näslund 1989), and other surveys (Riley and Fausch 1995).

Lower gradient and stream velocity in the experimental section probably caused the observed higher fraction of minnows and lower fractions of brown trout and bullheads compared to the reference section. After enhancement, minnows seemed to prefer the weir pools, as their abundance increased. The increased abundance of minnows on the reference section may be due to imigration from the the enhanced section downstream, during low summer flow, and this may cause increased competition for the youngest brown trout.

Annual emigration and mortality of A=0.62 and a mean density of 66 brown trout per 100 m, gives an annual recruitment or production of 66•0.62=41 (Ricker 1975) specimen of 2+ and 3+ after enhancement, compared to 18•0.62 = 11 before. The age distribution in the total material relates that 0+ and 1+ brown trout must be recruited in shallow head water areas where minor streams run together. Although all the brown trout caught in 1988 and 1995 were killed, the density was high in 1989 and 1996, except from the weir section in 1996. This indicate a rather immediate imigration from upstream areas where there must be an excess of recruits. Similar migrations of young brown trout are reported from other studies (Elliot 1987, Näslund 1989, Gowan et al. 1994).

An unknown fraction of the recruits enter the River Glomma and some of them returns to spawn later years. Brown trout of 50 cm size from the Glomma have been observed as spawners in Letjern, and brown trout of 15-20 cm fish have been Floy-tagged in Letjern and recaptured in Glomma (Linløkken and Solvang 1994).

The price of a river enhancement of this kind may vary according to planning and preparation prior to execution. Several projects have been worked out in similar streams in this region at a cost of $200-300 per 100 m (Tore Qvenild pers. comm.). The annual production increase of 30 specimens per 100 m, yields a total increase of

210 specimens per 100 m during 1989-95, at a price of $1-1.5 per speciemen. Prices from hatcheries vary from $1.5-3 for 1+-3+ brown trout, depending on size. Habitat enhancement in this case would be a less expensive way of increasing the number of brown trout, and the quality of the fish is probably better than when artificially reared fish are used. If habitat enhancement should be used as an alternative to stocking, it will be a problem to estimate the increased contribution, in this case to the River Glomma, from Letjern after enhancement, as the fractions of emigration and mortality are unknown.

Acknowledgements

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The Physiological Effects of Salmon Lice Infection on Sea Trout Post Smolts

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Abstract

The physiological consequences and mortal impact of salmon lice infections were tested by artificially infecting hatchery-reared post smolts of sea trout (mean weight 91 g) with infective copepodids. Late chalimus stages of the lice caused minor osmoregulatory disturbances in the fish. However, infected fish had high levels of the stress hormone cortisol and a significantly reduced lymphocyte-leukocyte ratio, even at early chalimus stages. After the first preadult stage of the lice had appeared, the infected fish contracted severe osmoregulatory problems and anemia. The plasma chloride levels increased and the hematocrit levels decreased significantly in the infected compared to the control fish, thereby leading to mortality with high infection. Thus, infection intensities above 90 salmon lice copepodids may result in mortality of small sea trout post smolts (60 g) after the lice have reached their preadult stages.

Keywords: salmon lice infections, stress reaction, osmoregulatory problems, mortal impact.

Introduction

Salmon lice (*Lepeophtheirus salmonis* Krøyer) are one of the most serious pathogens of sea farmed Atlantic salmon (*Salmo salar* L.) (Wootten et al. 1982, Pike 1989). Even though salmon lice epizootics on wild salmonids have been reported (White 1940, Johnson et al. 1996), salmon lice have normally been found in low numbers (Boxhall 1974, Wootten et al. 1982, Berland 1993). However, annually, between 1989 and 1996, epizootics have occurred on wild sea trout (*Salmo trutta* L.) both along the coast of Ireland and along the coast of Norway, and have been associated with significant host pathology (Anon 1993, Tully et al. 1993a,b, Grimnes et al. 1996a, Birkeland and Jakobsen 1997). Several cases such as increased number of hosts in fish farms, increased temperatures in sea and changed host attraction have been discussed (Grimnes et al. 1996a). A combination of these factors seems

to be relevant to the increased number of salmon lice on sea trouts (Grimnes et al. 1996a).

The infection of chalimus larvae of salmon lice has not been shown to cause severe physiological consequences for post smolt of Atlantic salmon (Grimnes and Jakobsen 1996). However, heavy infection of these stages has induced a primary stress response of Atlantic salmon and Arctic charr (*Salvelinus alpinus* (L)) (Grimnes et al. 1996b). Furthermore, preadult and adult stages of salmon lice can cause considerable damage to the fish and in some cases even mortality of the fish (Wotten et al. 1982, Pike 1989, Grimnes and Jakobsen 1996, Grimnes et al. 1996b).

Experimental studies on Atlantic salmon and Arctic charr indicate that 30 to 50 chalimus larvae of salmon lice, with time, may cause death of a 40 gram post smolt (Grimnes and Jakobsen 1996, Grimnes et al. 1996b). Similar experiments have not been performed on sea trout. The connection between salmon lice infection and pri-

mary and secondary stress responses have not yet been evaluated. Thus, the significance of the observed epizootics on wild sea trout has not been established.

Bjørn and Finstad (1998) describe the developmental and survival rate, distribution on the host and the pathogenicity caused by salmon lice on sea trout post smolts. In the present study we aim to experimentally investigate the physiological effects of different developmental stages and variable numbers of salmon lice to sea trout post smolts.

Materials and methods

Fish and fish maintenance

The experiment was carried out on 320 hatchery-reared two year old first generation sea trout smolts from the River Halselva in Talvik, northern Norway (70°05´N, 22°55´E). The initial weights of the fish were 93.1±11.2 gram (Mean ± SE, N=10). The fish were randomly split into one infected and one control group and placed in separate 800 L fiberglass tanks. The fish were gradually acclimated to sea water over a period of 16 days, and kept at sea water (34 ‰ salinity at 9.7±0.4 °C) for a week before the start of the experiment. The fish were automatically fed to satiation with commercial food pellets every 30 minutes throughout both day and night under continuous light conditions.

Salmon lice culture and artificial infection

Ovigerous salmon lice were collected from gill-netted wild Atlantic salmon. The salmon lice were incubated in sea water (35 ‰ salinity) at low temperature (+ 4 °C) for approximately 24 hours at sampling locality and during transportation before reaching the research station in Talvik, where the experiments were performed. Egg strings were then removed from the lice and reared in a net (mesh size 125 μm) covered chamber (10 L) at a temperature and salinity similar to that in the fish tanks. The egg strings were allowed to hatch for two days. Two to four days old copepodids were

used to artificially infect the sea trout. The fish in the infected group were exposed to infective copepodid larvae by adding a calculated number of 20,320-28,160 (95% CL) copepodids to the tank. The infection was carried out at reduced water level (100 L), aeration but no water flow. After four hours of exposure, the water flow was restarted. The water level in the control tank was reduced and the fish were treated similarly, but without adding any copepodid larvae to the tank.

Sampling procedures

Infected and control fish were sampled at 7, 14, 19, 24, 29 and 38 days post infection (p.i.). Twenty fish from each group were collected at each sampling date, and individually anaesthetized in a metomidate solution (Marinil ™, 12.5 mg × 1^{-1}). After sampling 0.5 ml blood from the caudal vein, the fish were killed by a blow to the head and weight (g) and length (total length in mm) were measured. The blood samples were temporarily kept on ice while the fish were frozen individually in plastic bags at -20 °C for later examination.

Moribund and dead fish were removed daily. Fish were classified as moribund when found hyperventilating at the bottom of the tank without reacting to physical disturbance. These fish were examined in the same way as sampled fish, except that no blood was collected from dead fish. Groups of moribund fish consist of moribund and dead fish removed from the tank during the experimental period and split at 22-25 (N= 10), 26-29 (N= 6) and 30-38 (N=12) days p.i. in order to compare samples.

Analyses and registration

Blood hematocrit was measured on all blood sampled fish by a Compur microspin microhematocrit centrifuge. Blood cell analyses were made by studying smears (blood drop of about 10 μl) from ten randomly selected blood samples from the infected and control group at each sampling date. Smears were Giemsa stained as described by Amin et al. (1991). The blood smears were analysed by differential-counting of white blood cells

according to Wedemeyer and Yasutake (1977). The counting was conducted along a randomly sampled horizontal stripe on the smear and minimum 200 blood cells were counted per smear. The results are given as the ratio of lymphocytes to the total number of leukocytes.

Blood plasma was separated in centrifuge at 5000 rpm for five minutes and stored at -20 °C until plasma chloride and plasma cortisol values were analysed. Plasma chloride content was assayed on all blood sampled fish by coulometric titration (Radiometer CMT 10 chloride titrator). Cortisol analyses were performed on blood plasma from only the ten first sampled fish from the infected and control group because of sampling disturbances (Pickering et al. 1982), and analysed by a RIA-method described by Simensen et al. (1978), as modified for fish (Olsen et al. 1992).

The body surface, fins and gills of all infected, moribund and control fish were examined for lice and the frequencies of each developmental stage were recorded. Lice at chalimus stages 1 and 2 and chalimus stages 3 and 4 were pooled in two groups called ch 1 and ch 3, respectively. Older stages were classified and sex determined according to Johnson and Albright (1991) and Schram (1993). Condition factor of the fish was calculated as $(100 \times W) \times L^{-3}$ where W is weight in g and L is total lenght in cm.

Statistical treatments and handling of data

Statistical tests were done on a SPSS 6.0 computer program. A Shapiro and Wilk test for normality combined with normal plots and detrended normal plots were used to evaluate departure from normality, and a Levene test was used to evaluate homoscedasticity among all samples.

Due to lack of normal distribution and homoscedasticity among samples, nonparametric tests were chosen for analyses of statistical differences in infection parameters, plasma chloride, hematocrit and plasma cortisol levels. A Kruskal-Wallis test was used to test for statistical differences between samples of each group with time, and between infected, moribund and control fish. If

significant differences were detected, a multiple comparison test decribed by Zar (1984) was used to locate the differences. A Mann-Whitney test was used to test for statistical differences between two groups from the same sampling date.

Parametric statistics were chosen to analyse for differences in lymphocyte frequency, weight, length and condition factor due to normal distributions and homoscedasticity, or only minor departures from normality. A One-way ANOVA was used to evaluate statistical differences between samples of each group with time, and between infected, moribund and control fish. If significant differences were detected, a Tukey HSD test was used to locate the differences. A *t*-test was used to analyse for statistical differences between two groups from the same sampling date.

Spearman rank correlations were used to test the relationship between relative density and plasma chloride values. The terms' prevalence and infection intensity are used as recommended by Margolis et al. (1982). To adjust for the effect of host size on the physiological consequences of the salmon lice infection, a parameter termed relative density was calculated according to Frandsen et al. (1989) as: number of lice ÷ fish weight (g). In all tests, a probability level of ≤0.05 was considered significant.

Results

Copepod development and infection parameters

Only early chalimus stages (ch 1) were found at day 7 p.i. (Fig. 1). One week later almost all lice had developed into late chalimus stages (ch 3). At day 19 p.i. approximately 80% of the lice had developed into the first preadult stage. Five days later, most males had reached the second preadult stage while females still were at their first. At 29 days p.i. second preadult females dominated together with adult males. Adult lice dominated at 38 days p.i. As males developed faster than females after moulting to the first preadult stage, this resulted in a biased sex ratio within each developmental stage present at each sample day. However, after all lice had reached the first
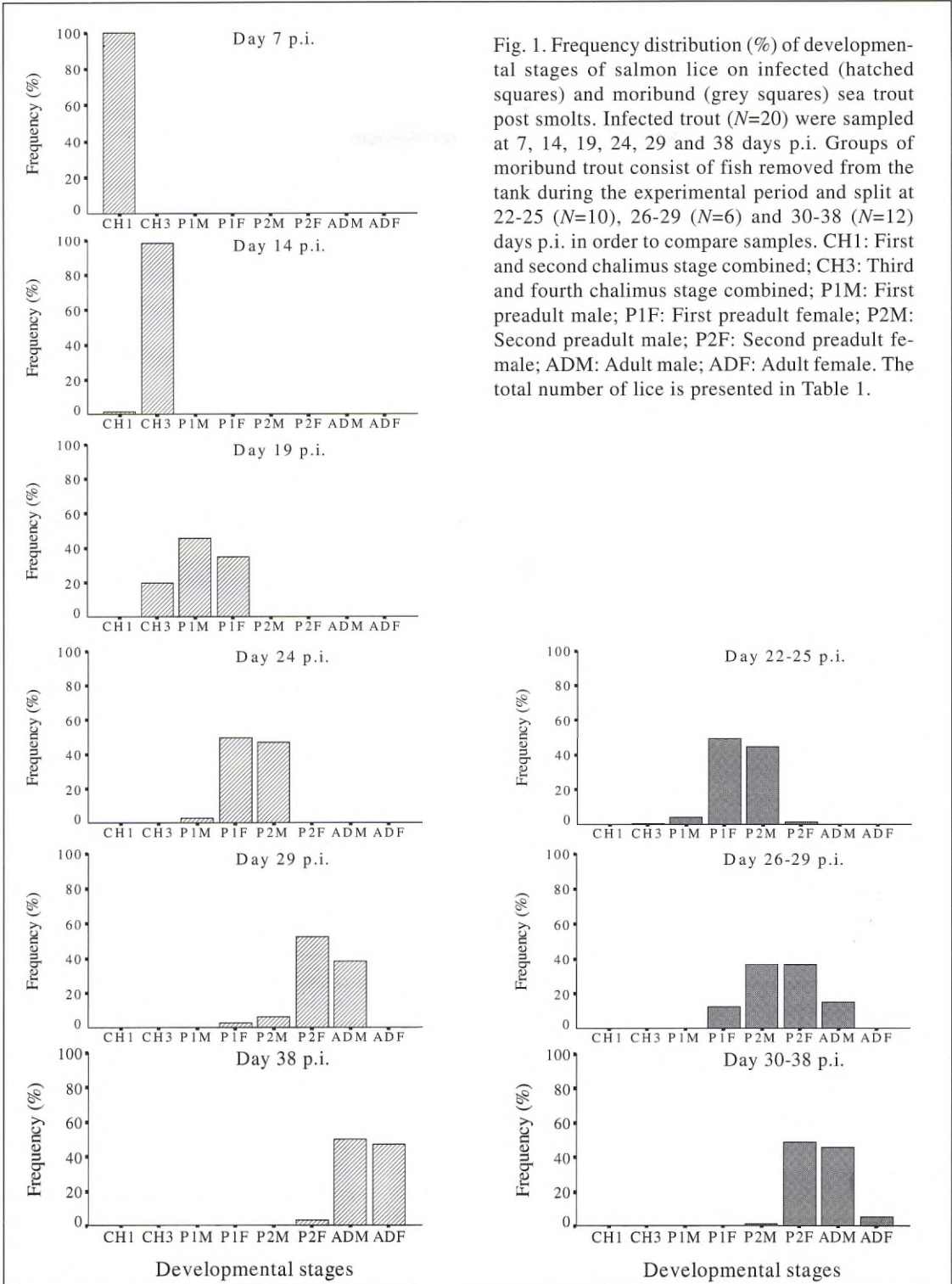
Fig. 1. Frequency distribution (%) of developmental stages of salmon lice on infected (hatched squares) and moribund (grey squares) sea trout post smolts. Infected trout ($N=20$) were sampled at 7, 14, 19, 24, 29 and 38 days p.i. Groups of moribund trout consist of fish removed from the tank during the experimental period and split at 22-25 ($N=10$), 26-29 ($N=6$) and 30-38 ($N=12$) days p.i. in order to compare samples. CH1: First and second chalimus stage combined; CH3: Third and fourth chalimus stage combined; P1M: First preadult male; P1F: First preadult female; P2M: Second preadult male; P2F: Second preadult female; ADM: Adult male; ADF: Adult female. The total number of lice is presented in Table 1.

Table **1a**) Infection intensity (number of lice per fish) of salmon lice <u>infected</u> and **1b**) <u>moribund</u> sea trout post smolts during the experimental period. Infected trout (N= 20) were sampled at 7, 14, 19, 24, 29 and 38 days p.i. Groups of moribund trout consist of fish removed from the tank during the experimental period and split in order to compare samples. N=number of fish; tot= total number of lice found on the fish; SD=standard deviation.

1a)

Days post infection	N	tot	mean	SD
Day 7	20	1757	88	38
Day 14	20	1946	97	48
Day 19	20	1640	82	29
Day 24	20	1309	66	25
Day 29	20	1211	61	16
Day 38	20	769	38	10

1b)

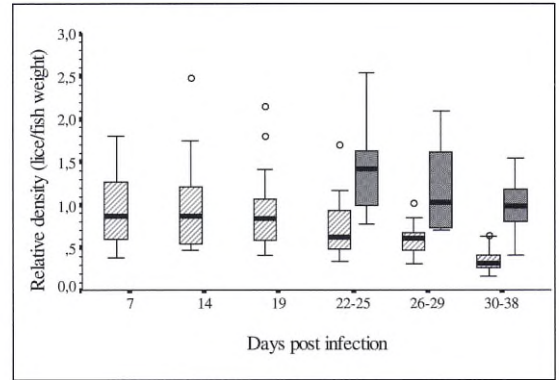| Days post infection	N	tot	mean	SD
Day 22-25	10	704	70	23
Day 26-29	6	390	65	23
Day 30-38	12	644	54	20

Fig. 2. Box-and-whiskers plot showing the relative density (number of lice per gram fish weight) throughout the experiment on salmon lice infected sea trout (hatched squares) and on moribund sea trout (grey squares). Medians are indicated by fat horisontal lines. The lower and upper hinges gives the 25 th and 75 th percentile. Outliers (O) are presented, and the whiskers gives the largest and smallest observed values that are not outliers. 20 infected trout were sampled at 7, 14, 19, 24, 29 and 38 days p.i. Groups of moribund trout consist of fish removed from the tank during the experimental period and split at 22-25 (N=10), 26-29 (N=6) and 30-38 (N=12) days p.i. in order to compare samples.

preadult stage, the preadult and the adult combined gave about 50% males and 50% females. There was no clear difference in the frequency of developmental stages of lice between the randomly sampled and the moribund fish (Fig. 1).

All sea trout, except controls, were salmon lice infected throughout the experiment. The infection intensity of the infected fish differed significantly with time (Kruskal-Wallis test; $P<0.001$), and tended to decrease from late chalimus stages (day 14 p.i.) and throughout the experiment (Table 1a). However, only the last sampling occasion (day 38 p.i.) was significantly different from day 14 p.i. (multiple comparisons; $P<0.05$). If the decreasing number of lice per fish was due to mortality of lice only, the mean lice survival would be approximately 63% (95% CL=55-70) from late chalimus larvae (day 14 p.i.) to second preadult females and adult males (day 29 p.i.). From late chalimus larvae to adult stages (day 38 p.i.), the mean survival was approximately 40%

(95% CL=35-44). The infection intensity on the moribund fish also tended to decrease with time (Table 1b), but not significantly (Kruskal-Wallis test; $P=0.28$).

The relative density showed the same pattern with time as the earlier described infection intensity (Fig. 2), and was significantly reduced in infected fish with time (Kruskal-Wallis test; $P<0.001$). The three first samples had significantly higher relative densities than the last sample (multiple comparisons; $P<0.05$). The relative density of moribund fish did not change significantly with time (Kruskal-Wallis test; $P=0.22$). However, the median relative density decreased successively from 1.44 lice per gram body weight at 22-25 days p.i. to 0.99 lice per gram body weight at 30-38 days p.i. Groups of moribund fish had significantly higher median relative densities (Mann-Whitney U-test; $P<0.05$) than infected fish at all comparable sampling occasions.

Fish weight and condition factor

The average body weight did not change significantly with time for the infected (ANOVA; $P=0.47$), the moribund (ANOVA; $P=0.97$) and the control (ANOVA; $P=0.06$) groups of trout (Fig. 3). The trout in control group, however, tended to increase in weight with time. Infected and control fish did not differ in weight at any of the three first sampling occasions (t-test; $P>0.05$). The moribund fish were significantly smaller than the infected and the control fish at each of the three last sampling occasions (Tukey test; $P<0.05$).

The average condition factor did not change significantly with time for the infected (ANOVA; $P=0.053$), the moribund (ANOVA; $P=0.059$) and the control (ANOVA; $P=0.73$) fish (Fig. 4). Infected and moribund fish tended, however, to get a reduced condition factor with time, but the infected and the control fish did not differ significantly at any of the three first sampling occasions (t-test; $P>0.05$). At the two latest sampling occasions, infected fish had a significantly lower condition factor than control fish (Tukey test; $P<0.05$). The infected fish, however, were slightly

Fig. 4. Condition factor of salmon lice infected (○), moribund (□) and control sea trout (●) sampled throughout the experiment. The results are given as the mean value with 95% confidence interval. 20 infected and 20 control fish were randomly taken out at 7, 14, 19, 24, 29, and 38 days p.i. Groups of moribund trout consist of fish removed from the tank during the experimental period and split at 22-25 ($N=10$), 26-29 ($N=6$) and 30-38 ($N=12$) days p.i. in order to compare samples.

shorter than the control fish at the second last sampling (day 29 p.i.) (t-test; $P<0.05$), but not at the final sampling occasion (day 38 p.i.) (t-test; $P>0.05$). Moribund fish had a significantly lower condition factor than both infected and control fish at all comparable sampling occasions (Tukey test; $P<0.05$).
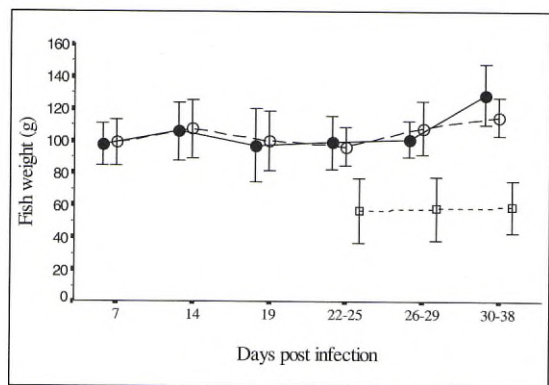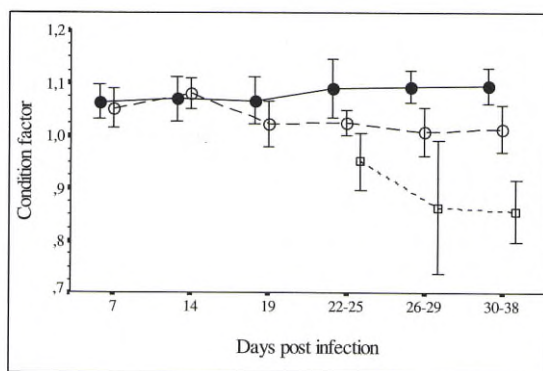

Fig. 3. Body weight of salmon lice infected (○), moribund (□) and control sea trout (●) sampled throughout the experiment. The results are given as the mean value with 95% confidence interval. 20 infected and 20 control fish were randomly taken out at 7, 14, 19, 24, 29, and 38 days p.i. Groups of moribund trout consist of fish removed from the tank during the experimental period and split at 22-25 ($N=10$), 26-29 ($N=6$) and 30-38 ($N=12$) days p.i. in order to compare samples.
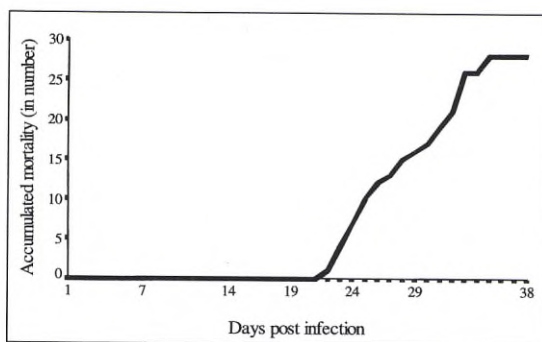

Fig. 5. Accumulated mortality (number of fish) of salmon lice infected sea trout post smolts throughout the experimental period. 28 out of 160 infected fish were removed as dead or moribund before taken out by sampling procedure, and 12 fish were terminated at the end of the experiment. There was no mortality in the control fish.
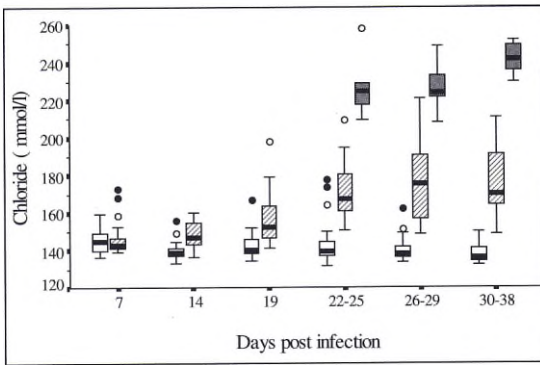
Fig. 6. Box-and-whiskers plot showing plasma chloride levels of salmon lice infected (hatched squares), moribund (grey squares) and control sea trout (open squares) sampled throughout the experiment. Medians are indicated by fat horisontal lines. The lower and upper hinges gives the 25 th and 75 th percentile. Outliers (O) and extremes (●) are presented, and the whiskers gives the largest and smallest observed values that are not outliers. 20 infected and 20 control fish were sampled at day 7, 14, 19, 24, 29 and 38 p.i. Groups of moribund sea trout consist of fish removed from the tank during the experimental period and blood sampled at 22-25 (*N*=6), 26-29 (*N*=5) and 30-38 (*N*= 6) days p.i. in order to compare samples.

Fish mortality

There was no mortality of control fish. Infected fish became moribund and started to die 2-3 days after the lice had reached their preadult stages (day 22 p.i.). Thereafter, moribund and dead fish appeared almost daily throughout the experimental period (Fig. 5).

Plasma chloride and hematocrit level

The plasma chloride levels changed significantly with time for the infected fish (Kruskal-Wallis test; *P*<0.001) (Fig. 6). The median plasma chloride levels increased significantly from the two first to the three last samples (multiple comparisons; *P*<0.05), all of which had median levels above 160 mmol/l. The plasma chloride levels also changed significantly with time for the control fish (Kruskal-Wallis test; *P*<0.05), but a post-hoc multiple comparison test failed to locate the differences (*P*>0.05), and the median values were below 145 mmol/l at all sampling occasions.

There was no significant correlations between weight of the control fish and plasma chloride levels at any sampling occasion (multiple comparison; *P*>0.05).

The infected fish had significantly higher plasma chloride levels than the control fish at all sampling occasions (Mann-Whitney U-test; *P*<0.05), except at day 7 p.i. (Mann-Whitney U-test; *P*=0.92). Moribund fish appeared from day 22 p.i., and had significantly higher plasma chloride levels than comparable groups of infected and control fish (multiple comparison; *P*<0.05). Significant correlations between relative density and plasma chloride levels of infected fish (Spearman rank test; *P*<0.05) were found from day 14 p.i. and throughout the rest of the experiment (Fig. 7).

The hematocrit levels changed significantly with time for the infected (Kruskal-Wallis test; *P*<0.001) and the moribund (Kruskal-Wallis test; *P*<0.05), but not for the control fish (Kruskal-Wallis test; *P*=0.55) (Fig. 8). A post-hoc multiple comparison test failed, however, to locate differences between samples of moribund fish (*P*>0.05). The hematocrit levels of infected fish were significantly reduced from the first three to the last two sampling occasions (multiple comparisons; *P*<0.05). At the four last sampling occasions, the infected fish had significantly lower hematocrit levels than the control fish (multiple comparisons; *P*<0.05). There was no significant difference in the hematocrit levels between the infected and the moribund fish (multiple comparisons; *P*>0.05).

Plasma cortisol level and lymphocyte-leukocyte ratio

The plasma cortisol levels of infected fish did not differ significantly among samples (Kruskal-Wallis test; *P*=0.12) (Fig. 9). The levels changed, however, with time and peaked at 24 days p.i. whereafter it levelled off. The plasma cortisol levels of control fish differed significantly among samples (Kruskal-Wallis test; *P*<0.05), but a post-hoc multiple comparison test failed to locate the differences (*P*>0.05).
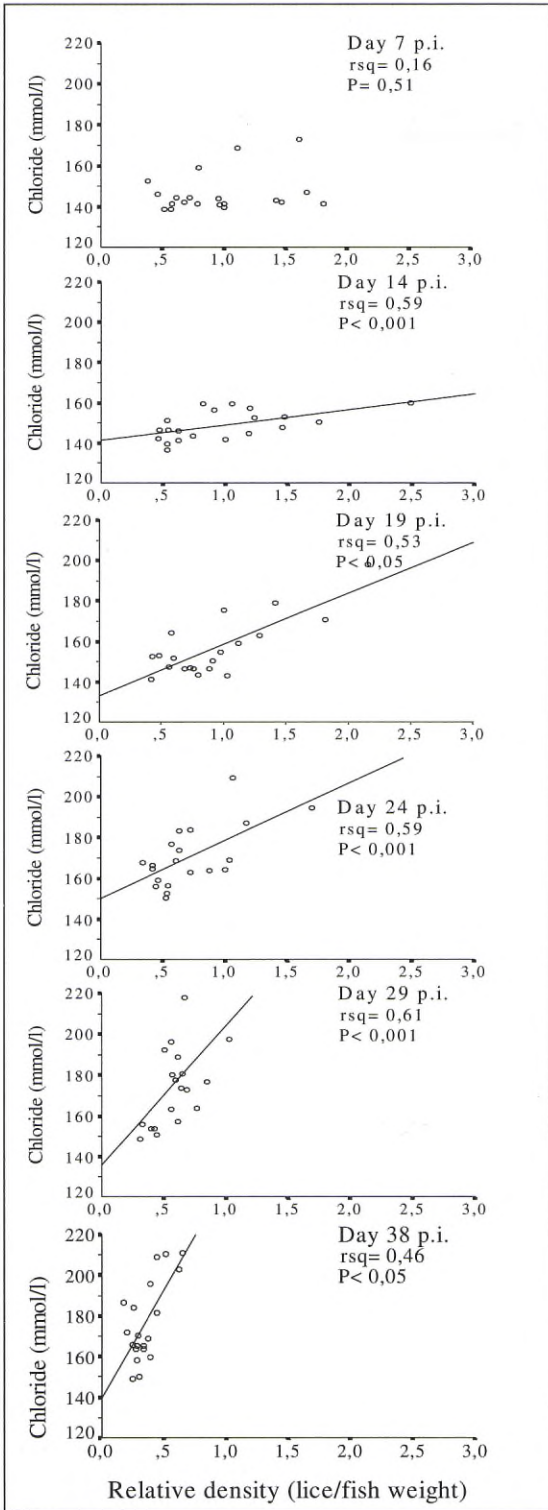
The infected fish had significantly higher median plasma cortisol values compared to the control fish at all sampling occasions (Mann-Whitney U-test; *P*<0.05), except at day 7 and 14 p.i. However, even at chalimus stages (day 7 and 14 p.i.) the infected fish had median plasma cortisol values close to 100 nmol/l. The comparable median values for the control fish were below 10 nmol/l.

The infected fish had a significantly reduced percentage lymphocytes of the total number of white blood cells (leukocytes) compared to the control fish, even at early chalimus stages (day 7 p.i.) (*t*-test; *P*<0.001) (Fig. 10). The percentage
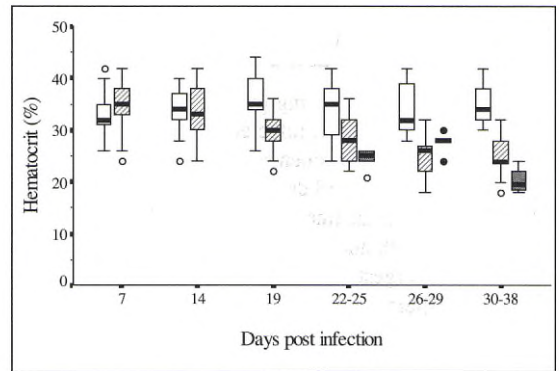

Fig. 8. Box-and-whiskers plot showing hematocrit levels of salmon lice infected (hatched squares), moribund (grey squares) and control sea trout (open squares) sampled throughout the experiment. Medians are indicated by fat horisontal lines. The lower and upper hinges gives the 25 th and 75 th percentile. Outliers (○) and extremes (●) are presented, and the whiskers gives the largest and smallest observed values that are not outliers. 20 infected and 20 control fish were sampled at day 7, 14, 19, 24, 29 and 38 p.i. Groups of moribund sea trout consist of fish removed from the tank during the experimental period and blood sampled at 22-25 (*N*=6), 26-29 (*N*=5) and 30-38 (*N*= 6) days p.i. in order to compare samples.

Fig. 7. Relationship between relative density (number of lice per gram fish weight) and plasma chloride levels for salmon lice infected sea trout post smolts sampled at 7, 14, 19, 24, 29 and 38 days p.i. Moribund fish are not included.
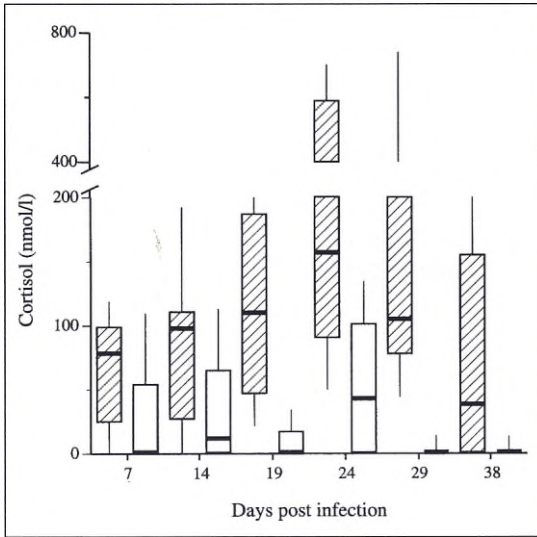
Fig. 9. Box-and-whiskers plot showing plasma cortisol values (nmol/l) in 10 salmon lice infected (hatched squares) and 10 control sea trout (open squares) sampled at day 7, 14, 19, 24, 29 and 38 days p.i. Medians are indicated by fat horisontal lines. The lower and upper hinges gives the 25th and 75th percentile, and the whiskers gives the largest and smallest observed values that are not outliers.
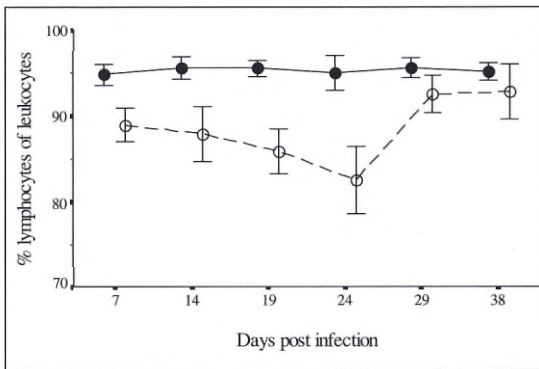

Fig. 10. Percentage of lymphocytes of the total number of white blood cells (leukocytes) of 10 salmon lice infected (O) and 10 control (●) sea trout each sampled at 7, 14 , 19, 24, 29 and 38 days p.i. Mean values and 95% confidence interval are given.

lymphocytes of the infected group were reduced further and significantly with time (ANOVA; $P<0.001$). A minimum level, significantly different from the two first and the two last sampling occasions, was reached at 24 days p.i. (Tukey test; $P<0.05$). However, at the last sampling occasion, there were no significant differences between the infected and the control fish (t-test; $P=0.14$). The lymphocyte percent of the control fish did not differ significantly among samples (ANOVA; $P=0.90$).

Discussion

The present study showed that salmon lice caused cortisol release and a significantly reduced lymphocyte-leukocyte ratio of infected sea trout post smolts. The stress responses occurred already at chalimus stages of the lice. Combined with minor osmoregulatory disturbances, these results imply that heavily salmon lice infected fish may experience physiological problems a long time before it eventually dies. There were sudden increases in osmoregulatory disturbances and mortality among heavily infected sea trout when the lice reached their preadult and adult stages. This indicates that preadult and adult lice are more pathogenic than the former chalimus stages.

This sharply contrasted with the control fish, which had median plasma chloride levels within the normal range at all sampling occasions which is between 130-150 mmol/l (Hoar 1988, Sigholt and Finstad 1990). The significant difference in plasma chloride levels between the infected and the control fish occurred already at late chalimus stages (day 14 p.i.). This differs from experiments with Atlantic salmon where such differences first appeared after the salmon lice had reached preadult stages (Grimnes et al. 1996b, Grimnes and Jakobsen 1996). Moreover, there was a positive correlation between plasma chloride levels and relative densities of late chalimus larvae. This indicates that late chalimus larvae can cause minor osmoregulatory disturbances in heavily infected sea trout.

Infected sea trout developed serious osmoregulatory problems after preadult lice stages appeared (day 24 p.i.). This is most probably due to the increased feeding activity by mobile preadult lice and thereby increased skin damages (Kabata 1974, Pike 1989, Bjørn and Finstad 1998). By this time, most infected fish had plasma

chloride levels above the normal range, whereas the moribund fish suffered from a completely osmoregulatory breakdown and had plasma chloride levels comparable to dying fish (Finstad et al. 1989, Sigholt and Finstad 1990, Grimnes and Jakobsen 1996). There was also a significant correlation between plasma chloride levels and relative density of preadult and adult stages of lice at all sampling occasions, confirming that heavily infected fish suffered the most.

By the same time as the osmoregulatory problems occurred, the hematocrit levels of infected and moribund fish were reduced. The reduction may have been caused by leakage of blood components (bleeding) through feeding activity of preadult and adult lice, possibly in combination with erythrocyte shrinkage (dehydration). Similar results were observed in salmon lice infected Atlantic salmon (Grimnes and Jakobsen 1996).

In contrast to the control fish, the infected fish tended to have higher cortisol levels already at early chalimus stages, and significantly higher levels from preadult stages and throughout the experiment. The elevated cortisol levels, which is comparable to levels found in acutely stressed brown trout (Pickering et al. 1982, Pickering and Pottinger 1989) and also generally found in teleostean fish in response to stressful stimulies (Barton and Iwama 1991), suggests that the sea trout experienced the lice infection as a discomfortable situation. A General Adaptation Syndrome, GAS, (Selye 1936, 1984, Schreck 1981) is therefore expected to be elicited, and include a release of the stress hormones adrenaline, noradrenaline and cortisol (Mazeaud and Mazeaud 1981, Barton and Iwama 1991). However, since the hypothalamic-pituitary-interrenal axis is very sensitive to any stressor, it is also sensitive to sampling disturbances (Pickering et al. 1982). This might explain the high plasma cortisol values of some control fish. The median plasma cortisol levels were, nevertheless, below 10 nmol/l at nearly all sampling occasions, which is within the level reported from unstressed salmonids (Pickering and Pottinger 1989). The majority of the control fish may thereby be considered as unstressed. Similar results have been found in heavily infected Atlantic salmon, which tended to have increased plasma cortisol levels at early chalimus stages and throughout the experiment (adult stages) (Grimnes et al. 1996b).

By the same time as the cortisol levels first tended to increase, the infected fish had a significantly reduced lymphocyte-leukocyte ratio (day 7 p.i.), which also has been found in chronically stressed Arctic charr (Brunsvik et al. 1996). This further increased and reached nadir co-occuring with the plasma cortisol peak. Changes in the plasma cortisol levels are detected by cortisol receptors of the leukocytes (Maule and Schreck 1990, 1991). Stress has been shown to cause a reduction in the number of monocytes and lymphocytes, as well as an increase in the number of neutrophil cells both in fish and mammals (Ellis 1981). Even slightly elevated cortisol levels (10-14 ng/ml) have been found to reduce the number of antibody-secreting cells (Maule et al. 1987), suppress the mitogen response of lymphocytes (Tripp et al. 1987) and predispose salmonids to pathogens (Pickering and Pottinger 1989, Nylund et al. 1991, 1992, 1993). Moreover, the infected fish contracted a reduced, and a significantly lower condition factor than the control fish with time. This is probably caused by maladaptive stress responses (Pickering et al. 1991, Pickering 1992, 1993) and dehydration of the fish.

The present study showed that heavily infected fish suffered most from salmon lice attacks and some died. Moribund fish had a significantly higher relative density and were significantly smaller than randomly sampled infected fish. The observed difference in relative density between the infected and the moribund fish may have been increased by migration of mobile stages of lice from healthy to less healthy fish (Bruno and Stone 1990). There was, however, no correlation between plasma chloride values and weight of the control fish, which could have indicated that moribund fish were parr infected by lice after becoming moribund.

The relative density found on moribund fish, further indicate that more than 1.0 lice per gram body weight, or 50 preadult and adult lice per fish, may cause death of small sea trout post

smolts (60 g). Given an average lice survival of 63%, a lethal relative density of approximately 1.6 chalimus larvae per gram fish weight, or more than 90 larvae on a small sea trout post smolt (60 g), can be suggested.

The present study on hatchery reared smolts in a laboratory experiment, can not be directly compared to wild migrating smolts. Factors as differences in the environment, condition and fish genetics, may have implications. However, in a field study, wild sea trout infected with a median of 61.5 preadult lice (IQR=37.0, *N*=10), also developed physiological problems and started to die shortly after preadult lice stages appeared on the fish (Birkeland and Jakobsen 1997). Infection intensities above 90 lice larvae may then be expected to kill wild as well as hatchery reared sea trout (60 g), and infection intensities above this level have frequently been observed on sea trout post smolts prematurely returning to fresh water both in Ireland and Norway (Urdal 1992, Anon 1993; Tully et al. 1993a,b, Birkeland and Jakobsen 1994, Finstad et al. 1994, Karlsbakk et al. 1994, Finstad 1995, 1996, Birkeland, 1996, Birkeland and Jakobsen 1997). In addition, sea trout, suffering from lepiophtheiriosis may have increased susceptibility to secondary infections and may be more easily predated. This may contribute to an increased severity of the salmon lice epizootics.

Acknowledgements

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A Retrospective on Baltic Salmon (*Salmo salar* L.) Biology and Fisheries

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Abstract

Human intervention in the biology of Baltic salmon has been some of the most intensive in the history of world salmon populations. Within the last century hatchery-reared salmon have nearly replaced wild populations in the Baltic, in spite of policies that would suggest that wild populations are important and worthy of protection. Despite the magnitude of human intervention in the Baltic, the production of Baltic salmon fisheries has remained as high or higher than most recorded history. For the most part, this has been due to successful smolt rearing projects in Sweden and more recently in Finland. Only in Japan has the replacement of wild salmon for hatchery production been achieved on a scale of intervention that exceeds the Baltic although other nations are following the same path (Beamish et al. 1995). Intense mixed stock fisheries in the Baltic have harvested hatchery and wild stocks with little regard for variations in productivity. Not only has the production of wild salmon been replaced by hatchery reared salmon, but the habitats that formerly supported wild salmon have been eliminated by hydroelectric dams. It is not clear that the trends can ever be reversed.

As late as 1995, the quality of stock-specific assessments of stock status in the Baltic is limited by data quality and technical problems. While individual laboratories may be more accurate than others, it is not possible to provide reliable ages of Baltic salmon throughout the various national agencies involved. It is difficult to determine the proportion of hatchery or wild salmon in samples and it is difficult to provide reliable estimates of stock composition in mixed stock fisheries. The historical large-scale fluctuations in salmon abundance remain unexplained and as a consequence, it seems unlikely that we will be able to recognize conditions that will produce future variations.

Why should there be so much concern? Unfortunately, the increased production has been achieved at great cost to the salmon and its environment. Fishery managers forgot, or perhaps never understood, that they were responsible"for managing the genetic material in the fish; the basis of future evolution and adaptation. Fish are just packages containing the thing of lasting (hopefully) importance.

The future of Baltic salmon research and management will involve better systems for collecting, storing, accessing, and manipulating basic biological data; more emphasis on population structure within and among rivers through the application of recent genetic techniques, a strong emphasis on stock identification (perhaps a tractable problem in the Baltic), model development and application, and with a modicum of luck, healthier salmon populations producing harvestable surpluses and fishing opportunities.

Introduction

*"What circumstances determine the changes in
the result of fisheries?
And which among these are caused by man,
and which not?"*
...translated from Dr. Rudolph Lundberg,
Stockholm, 1883.

Wherever they occur in their global distribution, anadromous salmonids are valued by humans for commercial, recreational, social and ceremonial purposes. Many of these species occur in great abundance and form the basis of great commercial enterprises. Their anadromous life histories provide easy access to those who exploit them. Human demand for salmonids, their economic value, and their requirement for relatively undisturbed habitat put wild salmonids at considerable risk. In combination, these factors create a need for fishery management and research to support conservation objectives.

Anadromous life history strategies create difficulties for fisheries management because of extensive use of multiple ecosystems. Not only must the fisheries exploitation be regulated, but the ecosystems that sustain the species need to be protected, managed, restored, and enhanced. Conflicting human uses of land and water resources create management and administrative complexities that at times seem to defy comprehension. Management complexity is compounded even further by the underlying effects of global climate change.

The Baltic salmon is a genetically distinct form (Ståhl 1987) of Atlantic salmon (*Salmo salar* L.) whose geographic distribution is almost exclusively restricted to the Baltic Sea (Karlsson and Karlström 1994). Historians of the Baltic salmon fishery (Christensen and Johansson 1975, Christensen and Larsson 1979, Eriksson and Eriksson 1993, Christensen et al. 1994, Karlsson and Karlström 1994) described the destruction of natural spawning habitat due to extensive hydroelectric developments on many large salmon rivers, the extirpation of wild stocks from some regions, and the replacement of wild salmon with hatchery production. Extinctions and the replacement of wild salmon with hatchery production have not attracted as much attention as they might have had there not been a significant mitigating hatchery program to keep salmon at high abundance. Since 1993, extreme mortalities caused by the reproductive disorder, M74, are threatening hatchery production as well as natural stocks (ICES 1994) throughout much of the Baltic and the general level of concern for Baltic salmon has risen.

Concerns about the management of Baltic salmon are not new. Lundberg (1886) noted that fishermen were complaining about declining numbers of salmon with increasing numbers of seine nets. It seems that two extreme views of Baltic salmon management are possible. On one hand the catches of salmon have been sustained at high levels since 1945 and the highest recorded levels were in recent years (Karlsson and Karlström 1994). For some, this is considered successful fisheries management. On the other hand, what has been necessary to achieve these high catches has been a nearly complete replacement of diverse natural production with hatchery production from a few large hatcheries. This strategy is not new. It has been used successfully for a century to manage chum salmon (*Oncorhynchus keta* W.) in Japan. The major concern is that human intervention seems inherently more risky for the long term viability of the animal.

Not surprisingly, one of the major issues in salmon management is the conservation of wild Baltic salmon. Because they now form such a small proportion of the overall production, their interaction with hatchery salmon is an important consideration in management and research. Unfortunately, conservation of wild salmon is not so easily achieved, in part, because it is difficult to obtain some of the basic biological data for assessing salmon production and stock status.

The purpose of this report is to provide a retrospective examination of Baltic salmon biology, to examine current topics in salmon research and management as they apply to Baltic salmon, to compare the situation in the Baltic with other jurisdictions, to review the current status of Baltic salmon and the quality of information on which the assessments are based, and to identify opportunities to improve our knowledge of Baltic salmon.

Distribution in the sea

The absence of salmon fisheries in the Sound and on the west coast of Sweden led Lundberg (1886) to conclude that Atlantic salmon of Baltic origin did not migrate from the Baltic. Regional variations in the types of fish hooks used in Baltic salmon fisheries led to initial hypotheses concerning the importance of the northern Baltic rivers to the fisheries in southern Sweden. Studies of the recoveries of marked smolts of known origin, in combination with the studies of fish hook recovery patterns, allowed Alm (1934) to confirm that Baltic salmon from northern rivers migrated to the southern Baltic, remained there for several years, then returned to spawn in their natal rivers. This general pattern was accepted as the normal model of salmon distribution in the Baltic. Swedish Baltic salmon migrated to the southwestern Baltic during their first winter at sea and tend to remain there, or move to the southeastern Baltic with increasing age, before beginning their first spawning migrations to the north (Alm 1934). Finnish salmon from northern rivers migrated to the southeastern Baltic and remained there until the onset of maturity (Alm 1934).

Christensen and Larsson (1979) summarized many of the historical reports on postsmolt migration in the Baltic. Most postsmolts entering the Gulf of Bothnia followed the main oceanic currents. Alanärä (1988) analyzed recoveries of tagged hatchery postsmolts from the Luleälven, Ångermanälven, and Dalälven. He concluded that postsmolt migration for Luleälven and Dalälven stocks was passive. The pattern of recoveries and the distances and times of travel were consistent with a hypothesis of passive migration that followed the oceanic circulation in the Baltic. The pattern of recovery of postsmolts from the Ångermanälven suggested that this stock undergoes a more active migration to the feeding areas in the central Baltic. No evidence of passive migration was found in this stock.

The general tendency of Baltic salmon postsmolts to migrate to the Main Basin may vary within stocks. Salminen et al. (1994) reported that greater proportions of large postsmolts from the Iijoki remained in the Bothnian Sea and they hypothesized that large postsmolts will remain in the Bothnian Sea, rather than migrate to the Main Basin, if: 1) they are large enough to have switched to a piscivorous diet, and 2) there are adequate forage fish (primarily herring) available in the Bothnian Sea.

That the northern rivers dominate salmon production in the Baltic has influenced the thinking about migration and distribution in the sea. Deviations from this general pattern exist and have been known for some time (Christensen and Larsson 1979). Tag recovery data indicated that salmon released from rivers in the Gulf of Finland remain resident in the Gulf (ICES 1995). One of the more important research findings is that there is an apparent genetic basis to the migration patterns of Baltic salmon stocks (Kallio-Nyberg and Ikonen 1992). Release experiments demonstrated that the migratory distance is stock-specific for two stocks in the Baltic. The degree to which this is generally applicable is open to debate.

Distribution of the spawning populations

The number of rivers supporting naturally spawning populations of Baltic salmon has been reduced significantly in the last 2 centuries. At present, 12 of 44 rivers in the Gulf of Bothnia that have produced salmon are still producing salmon, as are two rivers entering the Main Basin (ICES 1993). These include the Simojoki and Tornionjoki in Finland, the Torne, Kalix, Pite, Vindel, Råne, Åby, Byske, Sävarån, Öre, and Lögde rivers in northern Sweden, and the Emån and Mörrumsån in southern Sweden. Transplant attempts have recently been made in some Swedish rivers (Sangis, Töre, Lillpite, Kåge, Rickleån, and Hörnån) but the success has not been monitored (ICES 1993).

The Vindelälven is unique among Baltic salmon rivers. It originates in the mountains in northwestern Sweden and flows, uninterrupted, for over 300 km until it joins the Umeälven about 20km from the coast, just above the terminal dam.

It supports both naturally reared and hatchery fish. The latter have been finclipped since the early 1970's. A fish ladder at the terminal dam allows a near complete assessment of the spawning migrants to the system. Between 1974 and 1991, as many as 716 (1974) and as few as 87 (1987) naturally reared females returned to the system to spawn (McKinnell et al. 1994). Between 1974 and 1984, hatchery production accounted for 48% of the annual return to the river (McKinnell et al. 1994).

Spawning migration/run timing

The spawning migration from the Main Basin begins in late March or April (Christensen and Larsson 1979) as salmon begin a rapid migration to their natal rivers. Karlsson et al. (1994) discovered that the mean catch date of returning salmon in the Lule älv, Ångermanälven, and Indalsälven was negatively correlated with sea temperature (3 m depth) in the spring. Warm springs resulted in earlier catches in rivers in central and northern Sweden. Mean March and April temperatures explained 77% of the interannual variation in the mean catch date. From 1974 to 1991, McKinnell et al. (1994) found that arrival date of grilse male salmon was significantly (negatively) correlated with pre-midsummer river temperatures in the Umeälven. Although there was a similar trend for other strata, the relationships were not significant.

McKinnell et al. (1994) examined the run timing of hatchery and wild salmon in the Umeälven from 1974 to 1991 and concluded that the median day of passage through the fish ladder at Norrfors was determined by size, sex and origin. Larger, and presumably older, female salmon of wild origin arrived the earliest and hatchery origin grilse males arrived the latest. There was some evidence to suggest that larger individuals took longer to pass from the estuary into Norrfors fish ladder.

Fecundity

Most models that assess salmon population productivity (eg. spawner-recruit) have ignored the effects of variations in fecundity. Nonetheless, accurate estimates of fecundity are useful for modeling salmon populations. Egg deposition, not numbers of females or numbers of spawners, is a better index of 'initial conditions' of a salmon population model. The number of eggs/kg of female varies from year to year. Christensen and Larsson (1979) reviewed the literature on fecundity of Baltic salmon stocks. Values ranged from 1,014 eggs/kg in the Ljusnan to 1,720 eggs/kg in Latvian rivers. There was some evidence to suggest that the number of eggs/kg diminished with sea age in the Ljusnan.

Seaward migration

There was a general 'rule of thumb' that smolt migration in the Baltic begins when water temperatures reach approximately 10°C. Österdahl (1969) concluded temperature was not likely the causal effect using river temperature and smolt migration data from the Rickleån River. A number of studies of smolt migration in the Umeälven have indicated that the smolt migration occurs when water temperatures are approximately 10°C (Fängstam et al. 1993). There was a strong diel migration pattern in the Rickleån River (Österdahl 1969). The early part of the smolt run was made up of nocturnal migrants while the latter part of daytime migrants. The definition of nocturnal at the latitude of the Rickleån River (64° 05'N) during the smolt run (June) is somewhat clinical; there is no darkness. Österdahl (1969) was able to conclude that nocturnal migrants were not influenced by the same environmental factors as daytime migrants and that variations in the strength of the daytime migration probably resulted from factors related to light (radiation) intensity.

Survival

Since hatchery-reared salmon first began returning as mature adults to hatcheries, managers have been aware of interannual variations in survival. A lack of understanding of the factors responsible for the survival of hatchery-reared salmon led to the design of experiments in Canada (Bilton et

al. 1982, 1984), Sweden (Lundqvist et al. 1988, 1994, Eriksson 1988) and Finland (Salminen et al. 1995) to study the effects of variations in hatchery release date and smolt size and maturity on survival. Bilton et al. (1982, 1984) identified that both release date and smolt size and their interaction had an effect on coho salmon (*O. kisutch*) survival and that optimum conditions changed as the season progressed. Large smolts released early and smaller smolts released late produced optimum survivals.

Murdoch and Peterman (1992) were critical of Bilton's date and size at release work because it lacked temporal or spatial replication. Although this criticism would seem unwarranted for those who must plan, budget, and execute experiments in the real world, the benefits of replication are important. A single experiment carried out in one year will not test whether the survival response is invariant. Those who use the results for hatchery management probably will assume it. Lundqvist et al. (1988, 1994) was able to obtain sufficient funding to support two multi-year release experiments. These results will be significantly more valuable than any single experiment.

In part, these experiments have set the stage for future work that will identify the source of mortality. The date, size, and maturity at release are not the sources of mortality. They are indirect measures of what is causing the mortality. In British Columbia, Canada, influxes of mackerel and hake into Barkley Sound in 1992 are thought to have caused the worst survival of chinook salmon smolts released from the Robertson Creek hatchery. Chinook smolts migrate through Barkley Sound on their way to the coastal Pacific Ocean. Had a release experiment included the period of rapid predator buildup, it would have demonstrated a strong effect of release date on survival. Those escaping before the mackerel arrived would have survived in much larger numbers. Only the sampling in Barkley Sound identified the cause of the mortality. Skilbrei et al. (1994) discovered that smolt size and date of release were critical determinants of migratory behavior of cultured Atlantic salmon smolts in Norway. Larger smolts were found to migrate quickly from the release area whereas smaller

smolts remained near the area of release. This difference decreased at later release dates. Only smaller smolts were found in the stomachs of predators sampled near the release site area. In the Baltic, Eriksson (1988) found that delaying the release date for 2 or 3 months led to significantly higher survivals (Eriksson 1988) but this has not been replicated elsewhere.

Larsson (1985) reported a 35% mortality of Carlin-tagged wild smolts during an 8 km downstream migration in the River Mörrumsån and a 50% mortality during a 22 km downstream migration in the River Emån. Spicer et al. (1995) found that only 3% of radio tagged smolts were tracked over distances exceeding 40 km downstream in the Penobscot R. (Maine, USA). They concluded that the migration of the radio signals could have resulted from discontinuous smolt migration in the river, predation on smolts, or inadequate battery life. Predation by double-crested cormorants (*Phalacrocorax auritus*) and freshwater fishes (*Esox niger* and *Micropterus dolomieu*) could have been important. Approximately 50-70% of a hatchery smolt release in the Luleälven were consumed by burbot (*Lota lota*), pike (*Esox lucius*) and other predators Larsson (1985).

In repeated experiments, spaced over a decade apart, Lundqvist et al. (1988, 1994) demonstrated the importance of release date, smolt size and life history type on survival of Baltic salmon. Survival of immature males and females was from 5 to 8 times higher than previously mature male parr. The survival of larger, immature smolts was a constant feature in these experiments, however, there were indications that optimum release dates may not be fixed from year to year.

In the Umeälven hatchery stock, an annually variable proportion of the male juvenile population becomes sexually mature prior to smoltification. One result of early sexual maturation is a smaller body size (Lundqvist et al. 1988). Sexual maturation favours gonadal growth over somatic growth. As a result, early maturing hatchery-reared males are about 1 cm shorter in length in early spring than immature males and females of the same age (Lundqvist et al. 1988). The smaller size is likely partly responsible for

their lower survival but it is not likely the major factor. Lundqvist et al. (1989) showed that androgens can impair seawater adaptability in Baltic salmon smolts. Berglund et al. (1992) showed that there was a bimodal smoltification pattern in previously mature males. One portion of the population had an osmoregulatory ability equivalent to that of immature males and females while one portion had a poorer ability in seawater challenge tests.

Berglund et al. (1994) demonstrated how early sexual maturation in males can affect the migratory inclinations of smolts. In spite of documentation indicating that both wild and hatchery Baltic salmon stocks can experience very high frequencies of early maturing male parr, recent models (Ackefors et al. 1991) of Baltic salmon production did not include this component. Lundqvist et al. (1994) demonstrated the potential loss in fishery yield due to this life history strategy.

At least 2 techniques have been used to describe the survival response to varying sizes and dates of release and maturity state. Bilton et al. (1982) used response surface analysis (eg. Schnute and McKinnell 1984) and Lundqvist et al. (1994) used probit regression analysis. What has not yet been done is an assessment of the degree to which the fitted surfaces, i.e. the models, fit the observed data. This could be important because the data (releases and recoveries) are not evenly distributed throughout the sampling design. In particular, there are normally few large fish in a release strata while there will be many fish released at sizes near the mean. Some simple Monte Carlo simulations with the fitted model should detect whether models fit to the observed data are appropriate within the entire range of the design.

Age and ageing

Without a reliable method for determining the age of salmon, it is not possible to assess the performance (survival or growth) of a stock through time in any detailed way. Samples taken from the catch or the escapement cannot be attributed to any particular brood year without age. One of the earliest and most comprehensive biological sampling projects for a salmonid was established by Gilbert (1914). He used the pattern of rings laid down on salmon scales to determine freshwater and ocean age in sockeye salmon (*O. nerka* W.). Scales have routinely been used for many salmonids to provide acceptable estimates of age. Otolith samples are frequently collected from spawning ground samples as scales are resorbed during the maturation process in freshwater.

Age determination from salmon scales is not a precise science and considerable judgment is required when assigning ages. Not surprisingly, the skill and experience of the scale reader can affect the results. As many laboratories, agencies, and nations are responsible for determining salmon ages, a critical component of reliability is the standardization of techniques. For Atlantic salmon in the Atlantic, guidelines were developed in 1984 and revised in 1988 (ICES 1992). In the Baltic, scientists are discovering how difficult this can be (ICES 1995). The collection and reading of salmon scales to determine age has a long history in the Baltic. Over 60 years ago, Alm's (1934) treatise on salmon in the Baltic precincts relied exclusively on age determinations from 5,249 scales as did Järvi's (1938) response from Finland and his follow-up report (Järvi 1948).

Alm (1934) noted the general trend of increasing smolt age with increasing latitude and noted that results from Finland and Norway were consistent with Swedish data. The mechanism was thought to be limited food supply in northern rivers reducing growth and increasing age at smoltification.

Alm (1934) estimated that the freshwater age distribution of spawners returning to the Umeälven was:

Year	2	3	4
1915-16	54.1%	43.2%	2.7%
1930	33.6%	63.6%	2.8%
1931	21.4%	71.5%	7.1%

Alm (1934) reported that, of the maiden spawners, males mature at both younger and older ages than females. More males than females ap-

peared as grilse and as 4 year old maiden spawners than females. He also noted that the age at first spawning was older at higher latitudes but that this was mainly due to the older age at smoltification in northern rivers. In fact, northern rivers were reported to have a large quantity of small salmon of 1 sea winter. In the Umeälven the age distribution of spawners was 0.3% 3 year old, 6.1% 4 year, 54.6% 5 year, 35.6% 6 year, and 3.4% 7 year old. Alm (1934) noted a correlation among the sea age of spawners from different rivers and concluded that this was evidence that factors outside of the native river were acting to produce the observed result. He speculated that the sea temperature and salmon abundance were responsible.

Some of the first recommendations of the recent ICES salmon and sea trout working group were related to salmon scale reading (ICES 1960). A symposium was convened to consider the topic. The inconsistent results presented at the symposium convinced the salmon and trout committee that the papers should not be published (ICES 1961). Nevertheless, additional work on scale reading was recommended (ICES 1962). Progress toward solving some of the important technical questions of salmon biology in the Baltic has been slow. Despite years of endeavor, existing methods still do not allow independent scale readers to provide consistent salmon ages (ICES 1995).

Size frequency analysis (MacDonald 1979, Schnute and Fournier 1980) has been used to circumvent some of the problems associated with directly ageing individual fish. Direct ageing of fish is laborious, it can be inaccurate, and verification studies are required. Size frequency analysis, on the other hand, can be done quickly with commonly available data, fish lengths for example. It can provide information on mean size and variation at age, age composition, growth, and survival parameters simultaneously.

The underlying method is based on solving a mixture of normal distributions problem (Hasselblad 1966). The basic model is then augmented to add growth structure (Schnute and Fournier 1980), mortality (Breen and Fournier 1983), repeated samples (Fournier et al. 1990). As the models are non-linear in the parameters, a search algorithm (eg. Nelder and Mead 1965) is used to solve for the model parameters. The input data are size frequencies from random samples of a population. Size at age is assumed to be normal. The mean size at age can be unconstrained or it can be assumed to lie along a von Bertalanffy growth curve. Variation in size at age can be parameterized in any number of ways. It can be assumed to be constant at age, independent, or some increasing or decreasing function of age, to name a few. The method exploits the fact that size at age can be strongly modal, particularly for fast growing species. Fitting the model to strongly modal data is a fairly simple task as there are few competing solutions for the data.

Normally, only one type of size (either lengths or weights) is analyzed. Length data are available more frequently because of their ease of collection. In the Umeälven, individual weights of Baltic salmon have been collected for many years (McKinnell et al. 1994). Lengths are available only for brood stock for most years, but in recent years (1993-95), both lengths and weights have been collected for large numbers of migratory fish. Baltic salmon increase in length more rapidly than weight as juveniles and the reverse as adults. This produces the curvlinear weight/length relationship seen in Baltic salmon. This suggests that when the method is applied to salmon, it might be preferable to develop a model that simultaneously analyses both length and weight. Length will provide most of the resolution for young individuals and weights for older individuals. The greatest improvements will likely be in the estimates of proportion at age.

Sex

On the basis of sampling from 1925 to 1933, Alm (1934) concluded that females form about two-thirds of the spawning migration with the highest proportions occurring in rivers in central Sweden. In the Umeälven, 63.8% were females. This has changed significantly. From 1974 to 1991, males were routinely more abundant in the spawning migration than females (McKinnell et al. 1994). There are 2 major factors that will affect the returning sex ratio: the maturity schedules of

the sexes, and the fishery. The main causes of variation in the annual proportion of males are likely interannual variation in the proportion of early maturing males in the smolt run, and interannual variation in the proportion of grilse (males). The fishery takes the females and large males. The grilse suffer much lower exploitation because of their smaller size. They mature before recruiting to the driftnet fishery.

Growth

Stock- and age-specific variations in body size of Baltic salmon are available for many stocks for varying periods of time (Alm 1934, Järvi 1938, 1948). The most notable change in salmon body size in the Baltic occurred in the 1939 smolt year class. Järvi (1948) had developed a method of assigning ages to salmon based on fixed weight intervals. In 1942, he discovered that assigning age using historical weight-classes was inappropriate because of significant decreases in the size-at-age of returning adults. It was later shown that the size-at-age of Baltic salmon had apparently undergone some fundamental decrease (Lindroth 1965) beginning with the 1938 or 1939 smolt year-class. The decrease in size at age during this period was not equally distributed among age-classes. There was no evidence that the size of grilse was affected by whatever caused the change. In fact, the magnitude of the decrease in size-at-age seems correlated with sea age i.e. the oldest fish were most affected. The most common explanation for variations in adult body size of salmon is density (Rogers 1980, Peterman 1984, McKinnell 1995) although ocean temperature is also correlated (Rogers 1986). Is a density-dependent growth response a plausible mechanism for the changes in size-at-age observed in the Baltic beginning in the late 1930s? Certainly, there is a historical precedent.

Henking (1913) reported the catches at the Raattii salmon weir on the Oulujoki for the period 1869 to 1912. The data included the number and total weight (kg) of small salmon (salmon weighing less than 4 kg), the number and weight of large salmon (greater than 4 kg), and the number and weight of seatrout. From these, one

can compute the average weight of salmon and seatrout returning to the Oulujoki on an annual basis. Salmon counts and weights are only available for combined weight classes from 1907 to 1909. Järvi (1938) added catch and biological data for the years 1921 to 1935 from the combined fishing areas of the Pyhäkoski Rapids on the Oulujoki.

The mean weight of large salmon was significantly lower in years when catches of large salmon were high. The mean weight of small salmon was significantly higher in years when the catches of large salmon were high. Neither the mean weight of small salmon, nor the mean weight of large salmon was affected by the abundance of small salmon. The mean weight of all salmon (weight classes combined) was significantly lower in years of greater salmon abundance. The mean weight of seatrout was not affected by the abundance of seatrout or salmon.

Is there evidence that juvenile abundance in the rivers increased significantly in the late 1930's? Unfortunately, there are no observations on this point. Is there evidence that salmon were more abundant in the sea in the early 1940's? That catches were maintained near or even greater than historical levels during the early 1940's is remarkable given the unstable political situation in Europe during that period. It seems reasonable to conclude that catch data obtained between 1940 and 1945 were not equivalent indices of abundance gathered prior to or following that period. What we do know is that when political hostilities ceased and the salmon fleets moved into the Baltic, the catches were significantly higher than any other period in the 20th century (Karlsson and Karlström 1994). There is no *a priori* reason to rule out that possibility that the abundance of salmon that appeared in the catches following 1945 was not present some years earlier.

Shifts in survival have occurred in other salmon populations. Van Hyning (1973) found that chinook salmon (*O. tschawytscha*) survival decreased suddenly in 1948 and remained at lower levels. Francis and Hare (1994) also identified 1948 as the year when a significant increase occurred in the world's largest sockeye salmon (*O. nerka*) populations in Bristol Bay, Alaska. For

the most part, these large scale shifts in abundance have gone unexplained but climatic effects are considered to be important.

Salmon and climate

Schlesinger and Ramankutty (1995) identified a global temperature oscillation with a period of 50-88 years in the North Atlantic Ocean and its bordering continents. Their temperature anomaly series for each of North America, the North Atlantic, and Eurasia indicated trend reversals (shifts) in the 1890's and the 1940's. The pattern of sea surface temperature anomalies at Harmaja in the Gulf of Finland indicated that the northern Baltic was cool during the first 30 years of the 20th century, followed by a warm period of about 38 years, followed by a slightly cooler than average period up to 1990 (Haapala and Alenius 1994). The warm anomalies were the result of warmer summer temperatures, particularly during the 1930's. The 1930's are unique in the time series because of the near absence of cool anomalies.

River catches peaked in the mid-1880s and by 1900, the rapid decline in catches was causing great concern. Catches remained low through the first half of the 20th century (increasing somewhat around 1920) until the mid-1940's. Following end of World War II, the catches of salmon were substantially higher than before the war and average catches have remained high through the end of the 20th century.

The early and mid-20th century were periods of rapid change in Baltic salmon abundance; the former a decline and the latter, an increase. The intensity and duration of scientific focus on the effects of the environment on fish growth and survival have varied over most of this century. The greatest recorded decline in the salmon fishery in the Baltic took place in the late 19th century (Henking 1913, Alm 1928a). Alm (1928 a,b) concluded that the fluctuations in the performance of the fishery and the great decrease in the fishery in 1900 was due to the effects of climate variability during the late 19th century. From 1890 to 1900 variations in river discharges were greater than normal, the rainfall during that dec-

ade was higher than normal, and the temperatures were warmer than normal for that decade Alm (1928b). The fluctuations in salmon abundance in the southern Baltic were not subject to the more extreme variations that were observed in the northern Baltic (Alm 1928a).

Perhaps some of the most intensive discourse on the effect of climate on salmon was undertaken by Lindroth (1957,1962) and Svärdson (1955, 1957). Svärdson (1955) reported that salmon abundance (measured by catches at the Svärtö weir, Luleälven) rose 4-6 years after harsh winters (determined by the extent of ice cover in the Baltic) and 2-3 years after mild winters. He hypothesized that the variations in salmon abundance were due to the exclusion of porpoises from the Baltic. Although Lindroth (1957) agreed with Svärdson's observation that climate was somehow related to salmon abundance, he argued against the porpoise effect because: 1) he did not consider the Svärtö weir to be representative of salmon abundance in the northern Baltic, 2) none of the linkages between environmental conditions had been adequately demonstrated, and 3) overestimation of the effects of porpoise hunting. In his reply, Svärdson (1957) examined catch data from a second source in the Luleälven (Gäddvik 1891-1956) and from the Umeälven (Norrfors 1887-1924) to provide additional evidence of a statistical correlation between harsh winters and salmon production but he continued to pursue the argument that porpoise mortality in harsh winters was the cause. In what appears to have been the final paper in this discussion, Lindroth (1962) sampled 50 porpoise stomachs and found no evidence of salmon in the diet. Although the discussion may have ended, the link between climate and salmon abundance has not been identified. After investigating the pattern of variation in abundance of Atlantic salmon stocks in various regions of the North Atlantic (Canada, Norway, Scotland), Lindroth (1965) concluded pattern of variation in abundance of Baltic salmon was not correlated with the pattern of variation in Atlantic salmon stocks outside of the Baltic. As a result, he concluded that the causes of the variations must be found within the Baltic.

Stock identification

The development of techniques to identify the origin of salmon revolutionized the science, management, and politics of salmon. Interest in salmon stock identification ranges over broad geo-political scales. Universal recognition of the stock concept in salmon led to the entrenchment of legal rights of nations to salmon based on their origin (UNCLOS II, 1982). As a result, salmon producing nations have been keenly interested in techniques that identify the origin of salmon. International agencies such as the former International North Pacific Fisheries Commission, the Pacific Salmon Commission, the International Council for the Exploration of the Seas, have devoted considerable energies and resources to the science of identifying salmon. Within nations, the domestic management of some salmon species are dependent upon stock identification to assess the status and production of hatchery and wild salmon and international agreements have provided the mechanism and funding support to exchange stock identification data where the salmon ignore national borders.

The characteristics used to identify salmon can be generalized into two general classes: those using natural biological traits and those using applied marks. Natural marks include parasites (Margolis 1963), morphometric and meristic traits (Fournier et al. 1984), scale patterns (Messinger and Bilton 1974), age composition, and more recently genetics including protein allozymes (Utter et al. 1987, Beacham et al. 1987), mitochondrial DNA, and nuclear DNA (Taylor et al. 1994). The potential to use population-specific DNA for solving stock identification problems is one of the most active areas of stock identification research at present. Applied marks include external tags (Carlin 1955), internal coded wire tags (Jefferts 1963) and PIT tags, thermal otolith marks, and elemental marks (Mulligan et al. 1983).

In addition to the discovery of many kinds of natural and applied marks, there was a concomitant development of analytical techniques for solving stock composition problems (Pella and Milner 1987). Discriminant function analysis was and is commonly used for solving stock composition problems based only on scale pattern data. For genetic data, or combinations of genetic and non-genetic data, maximum likelihood is the preferred technique for estimating stock composition problems (Fournier et al. 1984, Millar 1987). The reduction in cost of computing power allowed for the extensive testing, via simulation, of the factors that affect the precision and accuracy of stock composition estimates (Wood et al. 1987). Simulations have now become routine procedures prior to the analysis of observed mixed fishery data.

Genetic data have not been used to examine stock composition problems in the Baltic until recently (Koljonen 1995) although some information had been previously reported. Using protein allozymes, Ryman and Ståhl (1981) identified genetic heterogeneity in Baltic salmon among 4 river drainages in Sweden: Byske, Lögde, Kalix, and Torne. Within the Torne drainage, a sample from the tributary Lainio was significantly different from one taken in the Torne mainstem. Genetic data have been used extensively for national and international fisheries problems in the Pacific (Beacham et al. 1987). Genetics have played a pivotal role in the United States National Marine Fisheries Service discussion of the Endangered Species Act and in the development of policies to protect salmon populations at risk. The genetic structure of salmon populations required that the Endangered Species Act consider taxonomic structures other than 'species' and led to the development of the *evolutionary significant unit* (Waples 1991) for salmon. As a result, individual *esu*s have been listed for protection under the act (Waples 1995).

The Fisheries

The first salmon fishing in the Baltic targeted maturing salmon in rivers as they migrated upstream (Christensen and Larsson 1979, Karlsson and Karlström 1994). In-river fisheries accounted for most of the catch until the latter part of the 19th century. In southern and eastern Skåne, coastal fishermen used floating nets, longlines and seine nets (Lundberg 1886). Toward the end of

the 19th century, declining catches focused attention on the increase of coastal catches by seine nets. In 1881, 125 vessels were involved in the Skåne coastal salmon fisheries. By around 1930, coastal fisheries accounted for most of the catch. The Bothnian Bay was the most important region for salmon fishing in Finland (Järvi 1938) where most fishing was in the lower reaches of rivers. In southern Finland, the Bothnian Sea and the Gulf of Finland were historically important (Järvi 1938). A major shift in the nature of the fishery occurred in 1945. Fleets moved offshore accounting for up to 80% of the catch although it has declined somewhat in recent years (Karlsson and Karlström 1994). The offshore driftnet fisheries for Baltic salmon are some of the largest fisheries on any salmonid species in the world.

Conservation

In addition to the threats to conservation due to the fishery, hydroelectric power dams, pollution, timber floating, and lowering lake levels affect the freshwater habitat of salmon in the Baltic (Alm and Hamilton 1949). The approach taken by the Swedish government was to compensate for these effects using the most efficient and cheapest methods (Alm and Hamilton 1949). A number of institutions were established to undertake the necessary research including the Fishery Board of Sweden, regulation associations, the Migratory Fish Committee, and the Swedish Salmon and Trout Association (Alm and Hamilton 1949). The major focus of policy and research was to mitigate for lost spawning and rearing habitat through the most cost effective means.

When the Swedish government established the large scale compensatory hatchery production of smolts in the Baltic, it was considered a salmon conservation policy (Lindroth 1963, 1965). The goal of the program was to replace natural production lost due to the construction of hydroelectric facilities on major salmon spawning rivers. Forty years after the program began, hatcheries surrounding the Baltic now release, on average, 5.33 million smolts into Baltic rivers while wild smolt production is thought to be about 0.4 million (Karlsson and Karlström 1994). Even some

of the remaining wild production is maintained by hatchery augmentation (Karlsson and Karlström 1994). The major criteria for success of the compensatory release program as a conservation policy was the survival of the species and to that end, it has been successful. Unfortunately, that adage that *you should be careful what you ask for, you might just get it* seems applicable. The criteria established in an earlier era are no longer applicable. Karlsson and Karlström (1994) report that the current situation is serious for the wild stocks and they appear to be advocating change.

In the intervening years between the initiation of the Swedish compensatory rearing program, the buildup of Finnish rearing programs, and the demise of wild salmon populations in the Baltic, there has been considerable evolution in thinking about salmon fisheries and their management. Much of this evolution has been driven by advances in our understanding of the genetic basis for differences between salmon populations (Ryman and Utter 1987) and the need to consider conservation at that level (Thorpe et al. 1995). Definitions of salmon conservation are now being expanded to more fully reflect conservation concerns for the complex structure of salmon stocks (Rice et al. 1995). Concerns for the value and the management of Baltic salmon genetic resources are being given new prominence in some jurisdictions (de Maré and Berntsson 1994) while others maintain their focus on carving up the remaining pie (Aro 1994).

One notable exception to the world wide concern for wild stocks remains. The highly successful (to date) system for producing chum salmon (*O. keta*) in Japan is based exclusively on hatchery production. Approximately 2 billion fry are released from Japanese hatcheries each year producing an average catch of about 50 million adult chum salmon (Kaeriyama 1994). No wild chum stocks remain in Japan. To date there have been no collapses in this fishery to vindicate the proponents of wild stocks. Nonetheless, there is concern. The mean size at age of Japanese chum salmon has been decreasing (Kaeriyama 1994) as have other Asian chum stocks (Ishida et al. 1993) and some North American stocks (Helle

and Hoffman 1995). The mean age of Asian chum salmon has been increasing (Ishida et al. 1993, Kaeriyama 1994) since large-scale releases of chum salmon began in the early 1970's and there is evidence that these changes are founded in density-dependent growth in the North Pacific. Regardless of its current success, reliance on hatchery production seems inherently more risky, particularly in a time of global climate change. Both the diversity of environments and the diversity of salmon will be needed.

Scientific Advice

The major forum for the exchange of information on the status of Baltic salmon is and has been the ICES Baltic salmon and trout working group and its predecessors which date back to 1903 (Christensen and Johansson 1975, Christensen et al. 1994). The collapse of Baltic salmon fisheries around 1900 would have warranted considerable attention. In 1957, the ICES Baltic-Belt Seas Committee and the Salmon and Trout Committee met to consider salmon problems in the Baltic (ICES 1959). Their concerns focused on varying yield from the fishery and increasing reliance on Swedish hatchery production. Their recommendations focused on the regulation of the fishery. Recommendations concerning programs of study for the advancement of scientific knowledge for the same period (ICES 1960) focused on the collection of biological and fishery data that are important for assessing the status of stocks and for understanding variations in the fishery. Tagging, the analysis of scale characteristics, and modeling have been consistent themes throughout the history of the group.

The early reports of the working group identified the potential for wild populations to be replaced by hatchery production (ICES 1959). Their concerns were well founded. Originally, 44 rivers flowing into the Gulf of Bothnia supported wild salmon populations. By the mid-1980s, this number had been reduced to 14 (ICES 1988). Over-exploitation was the only apparent cause. Ninety-seven to 99% of all recoveries of tagged salmon occurred in the sea (ICES 1988). In 1989, the working group began making strong state-

ments about the state of the stocks in the Baltic (ICES 1989) based on what appears to have been a reconsideration of *safe biological limits*. Concerns expanded to include the genetic resources (ICES 1990) although by 1991, the focus shifted strongly from conservation to preservation (ICES 1991). Under a single annual TAC management regime for Baltic salmon, safe catch limits designed to protect wild stocks precludes any offshore fisheries. Strong management measures to reduce or radically alter fisheries have been a common theme of recent assessments (ICES 1991, 1992, 1993, 1994, 1995).

Modeling salmon production

Models of salmon biology are not models of reality. Models are simplifications of complex interacting processes that can barely be imagined. If the modeller is fortunate, her/his models capture some of the major forcing elements, interactions, or limiting factors in nature. Despite their shortcomings, models of populations are useful for assessing a biologist's impression of reality. If nature behaves according to some imagined reality, what then is the likelihood of a given set of observations according to that reality. For that purpose alone, models can be valuable.

General models of salmon production in the Baltic were begun by Carlin (1962) and developed further by Lindroth (1962), Larsson (1975), and Ackefors et al. (1991). These models attempted to portray 'average' conditions in the Baltic by following the disposition of salmon biomass of a cohort from entry into the sea until spawning and/or mortality. For the most part, they relied on tagging data from hatchery releases to provide information on growth and mortality. These models have been useful for understanding large-scale variability in salmon biomass in the Baltic but they leave the impression that all one must do to keep salmon in the Baltic is add water and stir. This is clearly not the case. Although variations in Baltic salmon production are correlated, this is not sufficient justification for managing salmon as something like a unit stock. Stock-specific variations in life-history types, migration, vulnerability to fisheries and reproduc-

tive disorders suggest that future models will need to encompass considerably more specificity in an attempt to capture stock-specific variations in biological parameters.

Rivers such as the Ume/Vindelälven system are good candidates for modeling because of their history of detailed observations. Models that consider life history variation are needed such that hypotheses about the factors regulating salmon abundance, growth, mortality, and distribution can be compared analytically with the historical observations of salmon abundance and biology. The annual returns of salmon are determined by stock size, sex-specific life history characteristics, genetic inclinations, environmental influences, competition, predation, disease, habitat, and fishery patterns.

A Baltic salmon simulation model should allow researchers to experiment with and control salmon biological parameters of survival, growth, fecundity, age at maturity, etc. by species and stocks. The model may be made spatially explicit such that species and stock interactions can be studied based on our current knowledge of stock distributions and migrations. Models can be used to challenge current beliefs or to develop new ones on topics such as:

- What is the effect of long-term variations in climate on salmon life history and abundance?
- How does fishing (eg. gear selectivity) affect salmon populations?
- How does assessment advice change depending on whether one assesses stock status based on numbers of spawners, numbers of females, or numbers of eggs.
- Simulation is probably the only means to examine the confounding effects of size-selective mortality and density-dependent growth on mean size at age in salmon.
- Why has there been no trend in the abundance of wild salmon in the Vindelälven in the past few decades? The theory suggests that if 2 stocks of different productivities are subjected to intensive mixed stock fisheries with very high exploitation rates, the less productive stock will decline in abundance.
- Density-dependent growth of salmon has been observed in the Pacific Ocean, a substantially

larger expanse of ocean than the Baltic. To what degree are the current stocking densities in the Baltic Sea affecting the growth or fecundity of Baltic salmon?
- Are strong interannual variations in sex ratios of returning salmon due solely to the maturation schedule of males or are other factors involved?

Conclusion

At the beginning of this document, I quoted from Lundberg (1886) where he posed the question of whether humans or other factors were the cause of variations in the fisheries of Sweden. I was not trying to answer that question in this work, but after reviewing much of the history of the Baltic salmon fisheries, the mark of human intervention is unmistakable.

Acknowledgement

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Guide to authors

General editorial practice

Submit the manuscript in triplicate.

All manuscripts submitted are considered for publication on the understanding that they have not been published, submitted, or accepted for publication elsewhere.

Manuscripts are submitted to reviewers for evaluation of their significance and soundness. Authors will generally be notified of acceptance, rejection, or need for revision within three months.

Decisions of the editor is final.

Manuscripts are edited to improve communication between the author and the readers.

Authors will receive one set of first proofs.

Authors are recommended to keep their papers short.

Fifty reprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for reprints are sent with proofs.

Manuscripts

Language

Manuscripts should be in English. Linguistic usage should be correct. Write in a clear style. Avoid extensive reviews in the Introduction and Discussion. Cite only essential sources of a theory or opinion.

Title

The title should be brief and contain words useful for indexing and information retrieval.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article.

Keywords

Five keywords should be given for indexing and information retrieval.

Text

The first page should contain only the title and author's name and address. Begin the text on page two. The manuscript should be type-written, double-spaced with wide margins and on one side only of good quality paper. Word processor generated manuscripts should be in upper and lower case letters of typewriter quality font. Manuscripts printed by 7 x 9 or 9 x 9 dot matrix printers will not be accepted for publication or review. Underlinings in the text should be avoided. After re-submission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program (e.g. wp 5.1, ws, ms-world).

Illustrations

Submit each diagram, graph, map or photograph in one original and three copies. All illustrations should bear author's name. Tables and legends of illustrations should be written on separate sheets. Do not incorporate the legend in the figure itself. Tables and illustrations should be comprehensible without reference to the text.

Colour plates may be included at the author's expense.

Plan your illustrations for the smallest size possible. Figures, letters, and other symbols on illustrations should be drawn so large that they will be at least 1.5 mm high in the final print.

Units

Use SI units as far as possible.

Nomenclature

Binomial Latin names should be underlined and used in accordance with International Rules of Nomenclature.

References

In the list of references the following usage should be conformed to:

Journal

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.

Book

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology. An evolutionary approach. Third edition. - Blackwell Scientific Publications, Oxford. 482 p.

Chapter

Krebs, J.R. and R.H. McCleery. 1984. Optimization in behavioural ecology. p. 91-121. - In: Krebs, J.R. and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Second edition. Blackwell Scientific Publications, Oxford.

In the text references are given:

Svärdson (1976) or, at the end of a sentence (Svärdson 1976).

Titles of journals should be abbreviated according to the World List of Scientific Periodicals. If in doubt, give the title in full.

Do not refer to unpublished material.

Acknowledgments
Keep them short.

Symbols and Abbreviations

The following symbols and abbreviations, as well as others approved for the Systeme International d'Unités (SI), are used in this journal without definition. Any others must be defined in the text at first mention, as well as in the captions or footnotes of tables and in fiugres or figure captions. A variable divided with another variable should be noted as the following example L per min is L min^{-1}.

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min", and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Prefixes

giga	(10^9)	G
mega	(10^6)	M
kilo	(10^3)	k
milli	(10^{-3})	m
micro	(10^{-6})	μ
nano	(10^{-9})	n
pico	(10^{-12})	p

Time and Temperature

day	d
degrees Celsius	°C
hour	h
(spell out for diel time)	
kelvin	K
minute	min
second	s

Spell out year, month, and week.

In Table and Fig.:

year	yr
month	mo
week	wk

Weights and Measures

centimeter	cm
gram	g
kilogram	kg
kilometer	km
liter (exception to SI)	L
meter	m

Spell out hectare and tonne.

Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations base of

natural logarithm	e
common test statistics (F, t, etc.)	
correlation or regression coefficient (multiple)	R
correlation or regression coefficient (simple)	r
degree (angular)	°
degrees of freedom	df
expected value	E
intercept	α
logarithm (specify base)	log
minute (angular)	'
not significant	NS
percent	%
probability	P
probability of type I error (false rejection of null hypothesis)	$P\alpha$

probability of type II error (false acceptance of null hypothesis)	$P\beta$
radian	rad
sample size	N
second (angular)	"
standard deviation	SD
standard error	SE
variance	V or var

Physics and Chemistry

all atomic symbols	
alternating current	AC
ampere	A
becquerel	Bq
candela	cd
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)	
coulomb	C
dextro	D
direct current	DC
electron volt	eV
equivalent	eq
farad	F
gray	Gy
hertz	Hz
hydrogen ion activity (negative log of)	pH
joule	J
levo	L
lumen	lm
lux	lx
molar	M
mole	mol
newton	N
normal	N
ohm	Ω
ortho	o

para	p
pascal	Pa
per mille (per thousand)	‰
siemens	S
tesla	T
trishydroxymethyl-aminomethane	tris
volt	V
watt	W
weber	Wb

General (some are restricted)

compass directions (maps and coordinates):	east	E
	north	N
	south	S
	west	W
et alii		et al.
et cetera		etc.
filial generation		F
for example		e.g.,
international unit		IU
months (tables, figures): first three letters (Feb, Jun, etc.)		
ploidy		n
sex (tables, figures, hybrid crosses):	female	♀
	male	♂
that is		i.e.,

Word List

The spelling of the following words is frequently inconsisten in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

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