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Nordic Journal of Freshwater Research is a modern version of the Report of the Institute of Freshwater Research, DROTTHINGHOLM. The journal is concerned with all aspects of freshwater research in the northern hemisphere including anadromous and catadromous species. Specific topics covered in the journal include: ecology, ethology, evolution, genetics, limnology, physiology and systematics. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models within the field of ecology. Descriptive and monitoring studies will be acceptable if they demonstrate biological principles. Papers describing new techniques, methods and apparatus will also be considered.

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A Study of Interactions between Fish Species in Streams using Survey Data and the PCA-Hyperspace Technique

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Abstract

Data from extensive electrofishing surveys were used to investigate the presence of biotic interaction between five predominant fish species (brown trout, bullhead, European minnow, burbot and northern pike) in small low-order streams in Sweden. The environmental variables were reduced to five major abiotic components using Principal Component Analysis (PCA). Using the value of each electrofishing locality on these components only localities within all five species-extreme values for each component were chosen, thus forming a PCA-hyperspace. It was suggested that all five species studied could exist within this reduced set of localities. Absence/presence and abundance of the five fish species in this reduced set of localities were then studied using traditional parametric linear methods. Although abiotic factors seemed to be the major mechanisms regulating the fish fauna in streams of low order, predation probably also played a significant role. However, no indication of competition was found, which may be due to the methods used. There were negative correlations between yearlings of brown trout and the piscivorous burbot, and between larger brown trout and the piscivorous northern pike.

Keywords: Species interactions, PCA-hyperspace, fish assemblages in streams, electrofishing, fish distribution, predation.

Introduction

Swedish streams have a low diversity of fish and a variable habitat, with large climatic fluctuations. It has been argued and shown that stream fish species/assemblage occurrence depends mainly on abiotic factors (Karlström 1977, Cech et al. 1990, Meffe and Sheldon 1990, Power 1990, Rachel and Hubert 1991, Degerman and Sers 1992). It has also been suggested that predation and competition between species (Degerman and Appelberg 1992, Degerman and Sers 1992, Greenberg 1992, Strange et al. 1992) or within species (Bohlin 1977, 1978) affect species occurrence and dominance, but on a lesser scale. Species interaction leading to interactive segregation has been shown to be the major mechanism regulating assemblage structure in larger and thus more stable streams

and rivers (Zaret and Rand 1971, Ross 1991). Freeman et al. (1988) conclude that interactive segregation could only be a dominating factor if the assemblages are persistent and resilient, i.e. in a stable habitat and not in small streams.

Degerman and Sers (1992) suggested a division of the fish fauna in small Swedish streams into four major assemblages; **the headwater fish assemblage, the stream fish assemblage, the sea-run fish assemblage and the lake fish assemblage**. This division accords with the old idea of a succession along with increasing stream order (Vannotte et al. 1980), disrupted in the parts where lakes are located. In other words, as one moves downstream the headwater fish assemblage is gradually replaced by the stream fish assemblage, which is in turn replaced by the sea-run fish assemblage. At locations with lakes or slow-flowing river-like

sections this succession is disrupted and fish that only utilise the streams for a certain period of their life cycle predominate.

At extreme locations certain species are excluded by abiotic factors such as climate and colonisation probability, but there are seldom sharp boundaries between fish assemblages (Appelberg and Degerman 1991, Degerman and Sers 1992). At the same locality in a stream variations over the year in water flow and temperature might temporarily change the fish fauna (Erman 1986, Freeman et al. 1988, Strange et al. 1992), e.g. from a stream fish assemblage to a lake fish assemblage and back (Degerman et al. 1990). At locations where the physical factors may allow several species to occur biotic interactions between species should be pronounced. It is here suggested that species interactions in the variable stream environment should be studied in these localities. Absence of a species in a locality where its environmental requirements are fulfilled, i.e. a locality within its environmental and dispersal range, ought to be due to biotic interactions.

The close correlation between various abiotic variables and also between fish species means that it is seldom possible to assess the impact of a single abiotic or biotic variable on a single species or population. Instead, the combined effect of different variables on the species within the fish assemblage must be considered (Appelberg and Degerman 1991). One step towards an understanding of this is a descriptive study of abiotic variables in order to reduce them to a few major components (op.cit.). If possible, it is also desirable to choose localities which do not display marked environmental differences. Interaction within and between species may then be observed and quantified.

The purpose of the present study was to study the abundance of fish species in small streams using electrofishing survey data from Sweden. It was suggested that although abiotic regulation dominates, biotic interaction (predation and competition) could play a role in species regulation. In the present paper the environmental components were ordinated using PCA (Principal Components Analysis) to reduce them to a minimum of compo-

nents. In addition, PCA was used to isolate localities where the environmental requirements for the five predominant fish species in Swedish streams were met, i.e. their environmental niche. Within this reduced set of localities common parametric linear methods were applied to detect effects of possible biotic interactions.

Methods

Electrofishing data was obtained from a national database established 1989 containing electrofishing results in Sweden (Sers and Degerman 1992). Electrofishing generally involved the successive removal of fish and the absolute abundance could be estimated (Bohlin 1981). Data was available from 1,110 localities fished during the period June - October 1983-91. The physical data recorded were geographical position (latitude, longitude and altitude), stream width, average depth and maximum depth at the sampling locality. The bottom substrate was classified into six categories (fine, sand, gravel, rocks, boulders, large boulders), coarser particles being given a higher value. The substrate was used as an indirect measure of the average water velocity. Additional information included annual average air temperature, average air temperature in January and July, size of catchment area upstream of the sampling locality and proportion of the catchment area consisting of lakes, the distance from each sampling locality to lakes upstream and downstream and the total distance to lakes, both upstream and downstream ('lake distance'). It was also noted whether each locality was located above or below the highest sea level occurring since the last ice age. Finally, the length of the plant growing season, expressed as the number of days with an average air temperature above 5°C, was added. All variables were transformed using \log_{10} . The population parameters included were discrete (absence/presence) and continuous (the number of individuals of each species per 100 m²). The latter variable was transformed ($\log_{10}(x+1)$) in order to normalise data.

The electrofishing localities included in this study are located throughout Sweden. The size of the localities studied was generally 100-500 m².

Their altitude average 172 m above sea-level with extremes of 1 and 795 m. The stream order was generally low: 1-4. The average stream width was 8 m (0.5-175 m), and the average depth 0.29 m (0.04-2.6 m). The substrate was predominantly coarse gravel. Only 14% had soft bottoms (mud-sand), 56% had gravel (0.002-0.02 m) or rocks (0.02-0.2 m) and 28% boulders (>0.2 m) as the predominant substrate. The majority of the localities (62%) were located below the highest sea level after the last glaciation. The size of the catchment area upstream of most localities was 10-100 km² and the proportion of lakes in the catchment area averaged 5-10%.

The environmental variables were reduced by principal component analysis (PCA). The primary ordination factors were subsequently rotated using varimax rotation and Kaiser normalisation. The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and Bartlett's test of sphericity were

computed to check the accuracy of the PCA. Only components with eigenvalues above 1 were accepted.

In order to confine the study to the localities where the five most numerous species could exist according to environmental conditions a reduced set of localities was chosen. The lowest and highest value for each species was noted along each PCA-axis. The narrowest common span for the five most frequent species was then chosen on each axis (Fig. 1). By joining the resulting five stretches on the five PCA-axes a multidimensional space, PCA-hyperspace, was formed. Factor scores for each sampling locality were computed for each of the five components using the regression method. All localities within this space were chosen for further analysis. This resulted in a sub-sample of 228 localities out of the 1,110 initially included in the analysis.

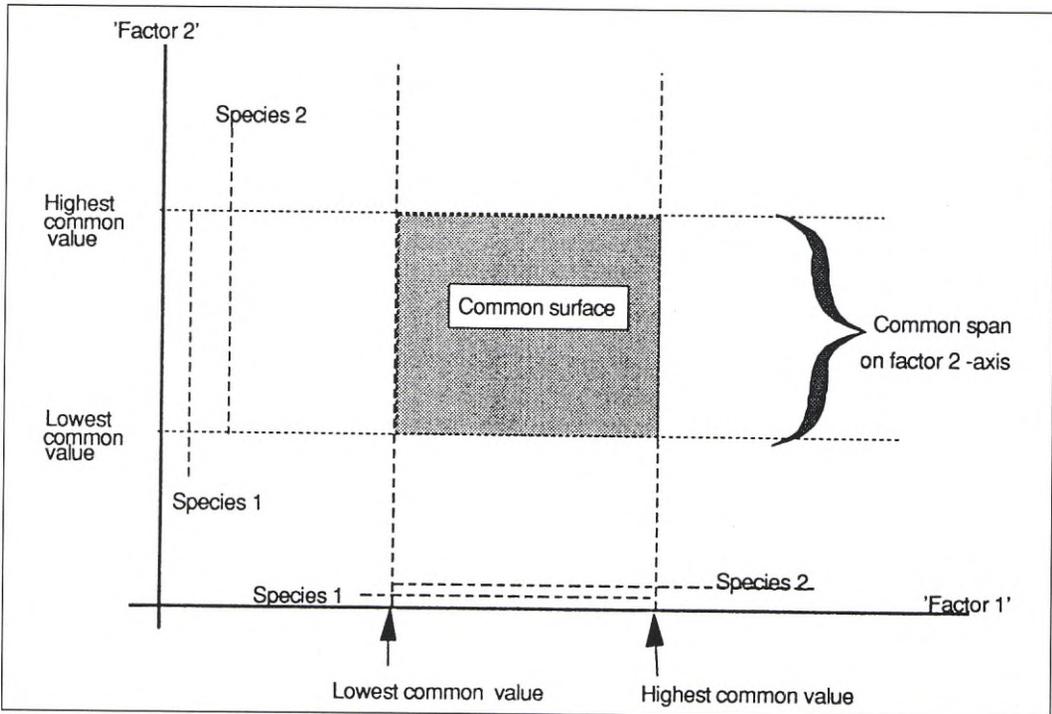


Fig. 1. The principles for selecting the common span of species on a PCA-axis and the resulting common area when two PCA-axes are combined. The span of a single species is the span between the most extreme localities where that species was found. Combining the common space for several PCA-axes creates a common PCA-hyperspace for the species.

The occurrence and abundance of fish species within this reduced set of localities were then studied using common parametric methods; discriminant analysis, stepwise multiple regression and factorial analysis of variance with the aid of SPSS statistical package (ver. 4.0, SPPS Inc., Chicago, Illinois) on a PC.

Results

The PCA of the 18 environmental variables resulted in five components that explained 78% of the variation (Table 1). The KMO index of adequacy was 0.69, indicating an acceptable ordination. The resulting five components were interpreted as "climate", "colonisation probability", "stream order", "habitat depth" and "lake distance".

Brown trout (*Salmo trutta*) was the predominant species and was noted at 79.1% of the locali-

ties. Other common species were European minnow (*Phoxinus phoxinus*) (31.4%), burbot (*Lota lota*) (26.3%), northern pike (*Esox lucius*) (22.5%) and bullhead (*Cottus gobio*) (21.0%). Other species were found at fewer than 20% of the localities. The number of species averaged 2.4 per sampling location, with extremes of 0 and 9. No fish were found at 7.9% of the localities, and five or more species at 4.0%. Thus, the number of species was generally low and 35.5% of the localities had only one species, usually brown trout (31.0%).

From this material localities were extracted where all the five most numerous species could exist (see Methods). As expected, the localities extracted had a higher number of fish species (3.2) than the whole material (2.4). The number of individuals averaged 46.5 per 100 m². The abundance of bullhead constituted 49% of the average abundance, brown trout 22% and the other species

Table 1. Factor loadings for the PCA of environmental variables. Only loadings above 0.5 are shown (Degerman and Sers 1992).

	Environmental components				
	Factor 1 "climate"	Factor 2 "colonis. prob."	Factor 3 "stream order"	Factor 4 "hab. depth"	Factor 5 "lake dist."
Temperature (Jan)	0.91				
Annual temperature	0.91				
Growing period	0.90				
Latitude	-0.89				
Longitude	-0.60				
Highest shoreline		-0.85			
Temperature (Jul)		0.77			
Altitude		-0.76			
Stream width			0.84		
Catchment area			0.81		
Substrate			0.56		
Max. depth				0.91	
Average depth				0.82	
Cross-section area				0.81	
Lake distance (upstream)					0.87
Lake distance (total)					0.84
Proportion of lakes					-0.68
Lake distance (downstream)					0.52

less than 22%. Brown trout occurred at 70% of the localities, bullhead at 57%, burbot at 43%, European minnow at 32% and northern pike at 30% of the localities.

Species occurrence

Species occurrence was studied by means of discriminant analysis. The variables included were absence/presence of each of the five species and the five abiotic principle components (Table 1). The occurrence of bullhead could be described using only abiotic variables, of which colonisation probability was the most important (Table 2). Yearlings of brown trout occurred more often at localities where northern pike was absent; colonisation was difficult for other species, and stream order was low. Low frequency of northern pike was also beneficial for the occurrence of older brown trout, but a cold climate was the major factor influencing the difference between localities where brown trout was present or absent.

European minnow was more frequent at localities without northern pike and brown trout after compensation had been made for the effect of stream order and climate (Table 2). Burbot and northern pike were more frequent in deeper habitats. The occurrence of the latter species was favoured by a warm climate and easily accessible sites, whereas the occurrence of the former species could not be explained by these factors.

Species abundance

Variables included in the stepwise regression of species abundance were the \log_{10} -abundance of each species as well as the five environmental PCA-components: climate, colonisation probability, stream order, habitat depth and lake distance (Table 3).

The explained variance was generally low for the regression of single species on other species and the environmental components. There were negative correlations between yearlings and burbot and between older brown trout and northern pike (Table 3). To test if this effect was independent of the stream order, with which there was also a correlation, a factorial ANOVA was performed. The PCA-axis labelled "stream order" consisted principally of three variables: stream width, catchment area and predominant substrate (Table 1). The latter two were discrete and were used in the factorial ANOVA together with absence/presence of the predator to determine whether the predator had any significant effect on trout abundance when the substrate or the catchment area was taken into consideration. The abundance of yearlings was significantly different at localities with burbot present as compared with localities without burbot when the substrate was also taken into account (ANOVA, $P=0.018$, Fig. 2). The interaction between burbot and substrate was not significant, however. This was interpreted to mean that both

Table 2. Discriminant analysis of the occurrence of a single fish species with the five abiotic components and the occurrence of four other species. All models were significant at the 99% level. The variables explaining the differences are ordered in decreasing order of significance.

Occurrence of	Variables constituting significant contributory factors	Canonical corr.
Brown trout	= -Climate -N.pike -E.minnow -Burbot -Lake distance;	Can.corr. = 0.36
-yearlings	= -N.pike -Colonis -Stream order -E.minnow;	Can.corr. = 0.29
-older trout	= -Climate -E.minnow -N.pike -Burbot +Depth -Colonis +Bullhead;	Can.corr. = 0.44
Bullhead	= +Colonis -Climate +Stream ord. +Depth +Lake distance;	Can.corr. = 0.63
E. minnow	= +Stream order -Climate -N.pike -B.trout +Lake distance;	Can.corr. = 0.53
Burbot	= +N.pike +Stream order +Depth -B.trout;	Can.corr. = 0.32
Northern pike	= +Climate +Burbot -E.minnow +Depth -B.trout +Colonis -Stream order;	Can.corr. = 0.50

Table 3. Stepwise forward regression of the abundance of each species versus the abundance of other species and the five environmental PCA-components. All regressions were significant at the 99% level.

All localities:		r^2
Brown trout	= -Burbot-Stream order-Northern pike;	0.15
-yearlings	= -Burbot-Stream order;	0.05
-older trout	= -Stream order-N.pike-Burbot;	0.24
Bullhead	= +Colonis-Climate+Depth;	0.14
E. minnow	= +Stream order-Climate;	0.11
Burbot	= +N. pike -Brown trout+Stream order;	0.20
N. pike	= +Burbot+Climate-Brown trout-Stream order;	0.28
Only localities where the species was found:		r^2
Brown trout	= -Stream order+Climate;	0.18
-yearlings	= -Stream order;	0.13
-older trout	= -Stream order+Climate-N.pike;	0.28
Bullhead	= -Stream order-Climate;	0.30
E. minnow	= +Bullhead-Colonis;	0.15
Burbot	= -Stream order+N.pike+Climate;	0.47
N. pike	= -Stream order+Climate;	0.16

substrate and the predator individually influenced the abundance. The same was found for older trout versus northern pike occurrence with substrate (ANOVA, $P < 0.001$, Fig. 3). The catchment area did not have a significant influence as far as yearlings versus burbot were concerned, but was a highly significant factor explaining differences in occur-

rence between older trout and pike (ANOVA, $P < 0.001$). In this latter case the interaction between northern pike and the catchment area was also significant and thus the effect of northern pike on older brown trout could not be assessed in isolation.

European minnow was more frequent at localities where predators were absent (Table 2), but

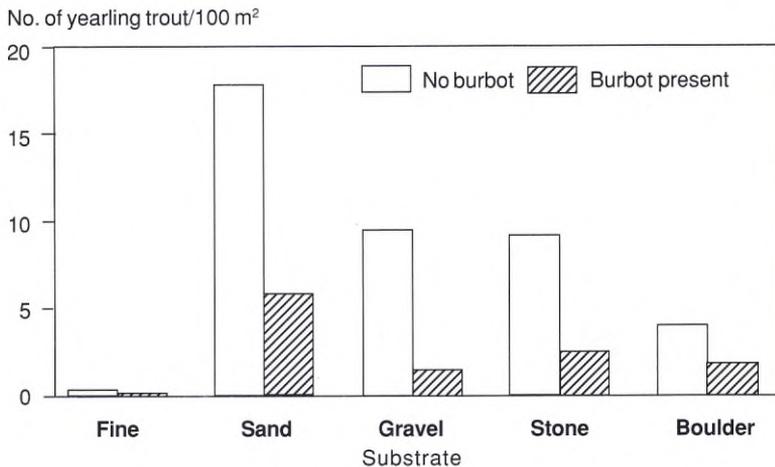


Fig. 2. The abundance of yearlings of brown trout at localities with burbot present and absent, respectively, depending on the predominant bottom substrate.

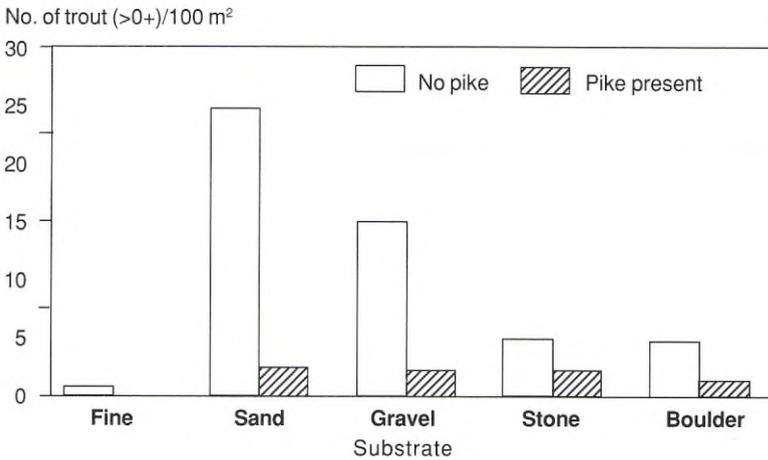


Fig. 3. The abundance of brown trout older than yearlings at localities with or without northern pike depending on the predominant bottom substrate.

did not show any correlation with the abundance of predators. The abundance of bullhead was only correlated to abiotic variables. Abundance decreased with increasing stream order and colder climate.

Discussion

A general view is that abiotic regulation of biota is the predominant factor in the small low-order streams studied (Vannote et al. 1980). Since all localities chosen in this study were within the environmental and dispersal limits for all five species, the PCA-hyperspace, it was suggested that biotic interaction ought to be the major explanation for the abundance and presence of a species at a specific locality. But within the common space, i.e. environmental range, of localities selected abiotic factors were still the predominant factor influencing the presence and the abundance of fish species. For instance, abiotic interactions were the only factors with which there was a correlation to the variation in the occurrence and abundance of bullhead in the material. Studies have shown that the production of brown trout was as great at localities with bullhead as without (Williams and Harcup 1986). This leads to a suspicion that these species did not utilise the same food, but no data is available. In the present material brown trout and bullhead occurred together at several localities, but obviously without

any sign of biotic interaction that could be detected with the crude methods used.

The discriminant analysis performed gave few indications of any biotic induced species exclusion. Certainly this could be interpreted to mean that biotic interactions do not play a role, even in this reduced set of localities, but it is also possible that the sampling units are too small, allowing the effects of chance to assume importance. This is further indicated by the fact that species abundance of the predators (burbot and northern pike) is usually 2 individuals per 100 m² (Sers and Degerman 1992). The localities studied were small (approx. 100-500 m² with an average depth of 0.3 m) and the effect of predation may therefore have been underestimated.

However, the effect of biotic interaction between fish species was more pronounced in this material than in a larger sample where no environmental hyperspace was formed (Degerman and Sers 1992). Sers and Degerman (1992) using a similar, but unreduced, data set found a correlation between brown trout abundance, temperature and the size of the catchment area. In the present reduced data set abiotic parameters were still important, but brown trout also occurred at lower frequency and reached lower abundances in combination with northern pike and burbot. This observation was due to the fact that the data set was reduced using the PCA-hyperspace technique.

Thus, the use of PCA to reduce first the abiotic parameters and then the localities included led to results that seemed biologically sound. For example, it is commonly found that northern pike caught in small streams have brown trout in their stomachs (Degerman et al. 1990). There was a more negative correlation between yearlings of brown trout and burbot, whereas older trout had a closer negative correlation with northern pike. This could be because burbot prey on fry and early stages of brown trout, particularly during the cold season, whereas northern pike prey more on larger trout that have left the shallow spawning grounds. The structuring effect of pike predation has also been found in small Spanish streams where pike have been introduced (Rincon et al. 1990). There was also a negative correlation between the occurrence of European minnow and northern pike. It is suggested that this is due to predation, which may force the prey species to avoid localities with predators (Brown and Moyle 1991, Bugert and Bjornn 1991, Greenberg 1991, 1992, Resetarits 1991). The importance of predation in structuring the fish assemblage of small streams is thus a commonly occurring phenomenon (op.cit.). The positive correlation between northern pike and burbot seems mainly to be explained by a preference for the same type of lentic environment. Northern pike is a daytime predator, whereas burbot feeds at night. In this way niche segregation is achieved and there is a risk of predation for other species throughout the diel cycle.

Competitive interaction seems to have been low at the localities studied. This may very well be a bias caused by the parameters included. If, for instance, a trophic component (comprising total-phosphorus, the numbers of invertebrates serving as food etc) could have been included, it would have been more probable that signs of competition could have been detected. In other words, the present study has focused on the environment as a spatial resource, while the energy resource has not been dealt with to the same extent. This could lead to predation being easier to detect than competition. It is probable that species in the narrow small stream environment ultimately interact. Such interspecific interaction ought rapidly to lead to exclusion of one species, either by increased mor-

tality or because it leaves the locality temporarily or permanently. It is generally more common that species segregate spatially than in terms of food utilisation (Schoener 1974), which would make it hard to find negative correlations between species. Interaction would then mainly manifest itself as absence/presence. Whether and to what extent a certain species is excluded by species interactions must be studied experimentally or by means of sampling several large localities in a certain stream over many years. Competitive exclusion, i.e. loss of a species due to competition, could play a role during stable conditions in summer when water velocity decreases and temperature rises. This accords well with the 'river continuum' concept, i.e. that biotic interaction increases in a more stable habitat.

Studies based on time series have reported on competition between species in these low-order streams (Degerman et al. 1990, Degerman and Appelberg 1992), which is not surprising, since the species in such habitats tend to be omnivorous (Vadas 1990). Competition is ultimately for food (Slaney and Northcote 1974), but is often manifested as a struggle for the best territory (Kalleberg 1958). The larger, more aggressive fish or species are predominant (Kalleberg 1958, Bohlin 1977, 1978). Competitive displacement thus occurs between stream fish species (Kalleberg 1958, Degerman and Appelberg 1992) and within species (Bohlin 1977, 1978).

Abiotic factors are the major mechanisms regulating the fish fauna in low order streams, although predation does play a significant role. However, competition could hardly be studied using the present method. Competition is probable during stable periods and in larger streams. In conclusion, the technique of establishing a common environmental niche, the PCA-hyperspace, could be an advantageous way of eliminating redundant data and not just 'an illusion of technique'. Simplicity is achieved by complex reduction of data. However, the technique used could be further improved. For instance, it is proposed that the environmental limits be set at other points than at each species extreme on the PCA-axes. Using the standard deviation for each species on the axes would probably enable further studies of possible biotic influence.

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Size-Dependent Catchability of Brown Trout and Atlantic Salmon Parr by Electrofishing in a low Conductivity Stream

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Abstract

The catchability of different size-classes of brown trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) parr, by electric fishing with a pulsed DC back packer, was estimated in a low conductivity stream in western Norway. The absolute number of parr in the stream was estimated by mark-recapture (Petersen method). The relationship between fish length (L) and catchability (q) was described by linear regression models. The catchability of both species increased significantly with increasing total length of the parr. For brown trout parr the equations were $q = -0.281 + 0.286 \cdot L$ and $q = -1.017 + 0.326 \cdot L$ by autumn and winter samplings, respectively. The corresponding equation for catchability of Atlantic salmon parr by autumn samplings was $q = -1.094 + 0.278 \cdot L$. This implies that the number of small and young parr will be considerably underestimated relative to larger and older parr in low conductivity streams if catch data are used alone.

Keywords: Electrofishing catchability, low conductivity, brown trout and Atlantic salmon parr.

Introduction

Assessments of salmonid parr numbers and population length frequency distributions in streams are of importance in management considerations. Knowledge of possible size-dependent catchability by the sampling method is therefore important. Electrofishing is a common sampling method for salmonids in streams (e. g. Bohlin et al. 1989, Bohlin 1990), and usually, information about catchability of parr of brown trout, *Salmo trutta*, and Atlantic salmon, *S. salar*, by this sampling method is achieved by estimation of population abundance by successive removal methods (e. g. Bohlin 1982) and, more seldom, by mark-recapture methods (e. g. Heggberget and Hesthagen 1979). Because the efficiency of electric fishing is positively correlated with the specific conductivity of the water (Alabaster and Hartley 1962, Lamarque

1990, Zalewski and Cowx 1990), the catchability is expected to be particularly low in streams which have low conductivities. Furthermore, the catchability may increase with fish size (Junge and Libosvasky 1965, Lelek 1966, Bohlin et al. 1989), and in low conductivity streams this may produce substantial differences in catchabilities between size-classes of parr. Therefore, our objective was to estimate the size-dependent catchability of brown trout and Atlantic salmon parr by electrofishing in a typical low conductivity stream in western Norway, where numbers of parr were estimated by mark-recapture.

Study area

The study was carried out in a 375 m long side-channel to River Øyreselv in western Norway

(60°10'N, 6°17'W), from the branching with the main river about 10 m a. s. l. to the outlet in the fjord. The waterflow is regulated, resulting in relatively stable discharge, with less than 1 m³ sec⁻¹ in the side-channel, except during short periods of flood. Average width of the side-channel is 10.0 m ± SD 2.9 m, with a stream bed dominated by large cobbles and boulders. The stream alternates between short riffles and pools. In the uppermost part of the study site, small waterfalls obstruct upstream migration for small fish. The mean specific conductivity for four sampling occasions was 36.6 µS cm⁻¹ ± SD 2.3. During our samplings, the temperature was in the range 0-2.5 °C in winter and 8.5-12.5 °C in the autumn. Fish species are Atlantic salmon and brown trout, with brown trout being the dominant species by number in samples obtained by electrofishing.

Methods

Fish were collected by a pulsed DC back packer (current output 600 V at 1000 Ω, pulse length 1.8 ms at 70 Hz); the anode was a wand-mounted ring, 15 cm in diameter, covered by fine-meshed net to be used as an extra hand-net, and the copper wire cathode lay on the stream bottom. The batteries had a voltage in the range 12-13 V.

Chapman's adjusted Petersen method (Ricker 1975) was used to estimate numbers of brown trout and Atlantic salmon parr in the population:

$$N = \frac{(M + 1)(C + 1)}{R + 1}$$

where N = estimated number in population, M = number of marked fish in first fishing run, C = number of captured fish controlled for marks in second fishing run, and R = number of recaptured fish in second fishing run. Approximate confidence intervals were obtained using number of recaptures (R) distributed in a Poisson frequency distribution (Ricker 1975). Captured fish were anaesthetized with benzocain, total length measured to the nearest mm, and marked either by cutting the

adipose fin or by injecting Alcian blue at the base of the pelvic, ventral, anal or caudal fin with a Jet inoculator (Hart and Pitcher 1969). To minimize possible negative effects of the electrofishing, the entire stream was only fished once during the marking and recapture run, by wading upstream during day-time. As a consequence, we did not estimate the number of fish by the successive removal method.

The catchability (q) was estimated as the fraction of the number of parr present caught during the first sampling run ($q = C_1/N$), where C_1 = number marked plus number dead. A linear regression model was used to describe the functional relationship between catchability (q) and fish length (in mm) for brown trout by autumn and winter samplings separately, and for salmon parr by autumn samplings.

To be able to sample the whole stream bed effectively, all markings and recaptures were carried out at low and approximately similar discharges. As the whole side-channel was sampled, numerical changes between marking and recapture sampling runs due to emigration were minimized. Marking and recapture sampling runs were carried out in August 25-26 and October 21 1988, August 30-31 and September 5 1989, March 28-29 and April 10 1990, February 27-28 and March 13 1991, August 28-September 1 1991, March 5-8 1992, and September 2-4 1992. Length distributions of brown trout in the winter catches were similar to the distributions in the previous autumn catches. The length frequency distribution of the captured trout parr indicated three peaks, corresponding to the age-classes 0+, 1+, and 2+ and older, with small differences in length frequencies between marking and recapture samplings. Four peaks, corresponding to the age-classes 0+, 1+, 2+, and older parr, were identified in the length-frequency distributions of salmon parr in 1991 and 1992. In August-October 1988, few salmon parr below 100 mm in length were captured and marked. Recaptures of salmon parr during the February-March estimations were limited to a narrow length interval, and no comparison of size-dependent catchability was possible for this species by the winter samplings.

Table 1. Estimated number of brown trout parr in different length-classes, obtained by the mark-recapture method in River Øyreselv (m=marking date, r=recapture date, K=number killed first run, M=number marked, C=number captured, R=number recaptured, N=estimated number).

Year	m	r	Length class, mm	Mean length, mm	K	M	C	R	N	Confidence limits (0.95)
1988	Aug 25	Oct 21	48- 75	60	8	145	94	13	991	596-1,756
			76-109	96	4	93	85	17	449	287- 742
			110-135	123		77	89	28	242	170- 358
			136-165	148	2	86	91	31	250	178- 364
			166-199	177	1	17	20	10	34	19- 66
1989	Aug 30	Sep 5	76-109	99		117	95	14	755	462-1,302
			110-135	119		98	82	16	483	304- 806
			136-165	148		72	56	22	181	122- 281
			166-199	178		14	10	6	24	12- 52
1991	Aug 28	Aug 30	37- 69	56		169	141	23	1,006	682-1,547
			70- 99	83		288	245	57	1,226	950-1,580
			100-129	115		291	295	96	891	731-1,086
			130-159	139		101	92	31	296	211- 431
			160-189	165		8	12	5	20	9- 45
1992	Sep 2	Sep 4	35- 49	46	4	139	161	15	1,418	879-2,413
			50- 69	57	3	155	180	20	1,345	888-2,139
			70- 89	81		160	162	44	583	437- 795
			90-109	100		172	169	51	566	439- 758
			110-129	119		154	166	69	370	296- 475
1990	Mar 28	Apr 10	130-149	138		80	74	20	289	191- 460
			46- 75	58		53	49	2	900	329-2,250
			76-109	101		66	67	11	380	220- 712
			110-135	121		101	101	26	385	267- 578
			136-165	148		68	57	20	191	126- 303
1991	Feb 27	Mar 13	166-199	179		14	15	6	34	17- 75
			38- 75	54	8	62	117	5	1,239	585-2,859
			76-109	91	25	246	275	52	1,286	985-1,677
			110-135	126	9	67	74	19	255	167- 408
			136-165	150	19	84	103	43	201	150- 275
1992	Mar 5	Mar 7	166-199	181		13	10	6	22	11- 48
			37- 69	56		56	49	3	713	291-1,781
			70- 99	85		195	160	29	1,052	741-1,547
			100-129	117		215	200	72	595	474- 746
			130-159	139		83	77	29	218	154- 309
			160-189	170		17	16	7	38	20- 81
			190-219	205		18	22	9	44	24- 87
			220-249	232		19	17	12	28	16- 50
250-279	262		10	6	5	13	6- 30			

Results

Catchability of brown trout

According to the Petersen estimates, trout parr below 100-110 mm in total length dominated by number at all sampling occasions (Table 1). The total number of parr increased from August 1988-89 and March 1990 to February and August 1991,

and March and September 1992, mainly due to an increased number of parr below 100 mm in length (Table 1).

Both during the autumn and the winter samplings the catchability (q) increased considerably with fish length (Fig. 1). By the autumn samplings, parr with mean lengths in the range 46-69 mm had an estimated catchability in the range 0.101-0.168, while parr with mean lengths in the range 165-177

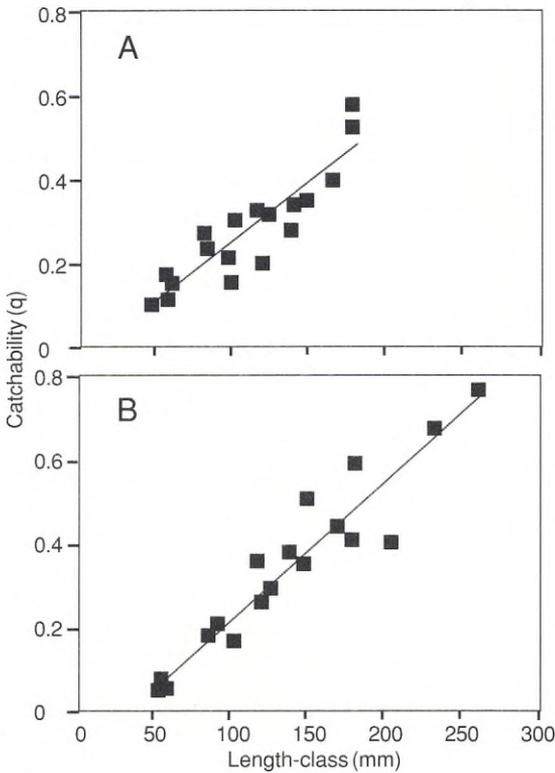


Fig. 3. Estimated catchabilities of brown trout parr in River Øyreselv by electrofishing in A) August-September 1988, 1989, 1991, and 1992, and B) February-March 1990, 1991, and 1992, with corresponding regression lines.

mm had estimated catchabilities in the range 0.400-0.583. The estimated catchabilities of the smallest length-classes were lower by the winter samplings compared to the samplings in August-September (Fig. 1); parr with mean lengths in the range 54-58 mm had estimated catchabilities in the range 0.056-0.079. Parr with mean lengths in the range 170-181 mm had estimated winter catchabilities in the range 0.447-0.591, or practically identical to the autumn values.

The functional relationship between catchability (q) and mean length in mm (L) of each length-class (from Table 1) was fitted by a linear regression model. The relationship is described by the equation $q = -0.281 + 0.286 \cdot L$ ($P < 0.0001$, $r^2 = 0.79$) for the autumn samplings, while for the winter samplings the relationship is described by $q = -1.017 + 0.326 \cdot L$ ($P < 0.0001$, $r^2 = 0.90$).

Catchability of Atlantic salmon parr

The estimated numbers of salmon parr were low compared to numbers of trout parr in corresponding length-classes (Table 2). The 0+ salmon were smaller than 0+ brown trout, and due to the low numbers of 0+ salmon captured and marked, no estimates for salmon parr below 55 mm in length were possible.

Table 2. Estimated number of Atlantic salmon parr in different length-classes, obtained by the mark-recapture method during the autumn in River Øyreselv (m=marking date, r=recapture date, K=number killed first run, M=number marked, C=number captured, R=number recaptured, N=estimated number).

Year	m	r	Length class, mm	Mean length, mm	K	M	C	R	N	Confidence limits (0.95)
1988	Aug 25	Oct 21	90-114	105		52	61	10	299	169- 576
			115-134	124		43	45	11	169	98- 316
			135-159	142		41	55	14	157	96- 270
1991	Aug 28	Aug 31	60- 79	69	1	116	94	10	1,010	573-1,950
			90-109	100		97	80	11	662	383-1,240
			110-139	116	1	38	29	6	167	83- 366
1992	Sep 2	Sep 4	55- 79	71		81	93	7	964	501-2,028
			80- 99	88		71	104	10	687	390-1,326
			100-119	109		62	68	14	290	177- 500
			120-139	128		36	60	12	173	103- 313
			140-149	145		6	9	3	18	7- 44

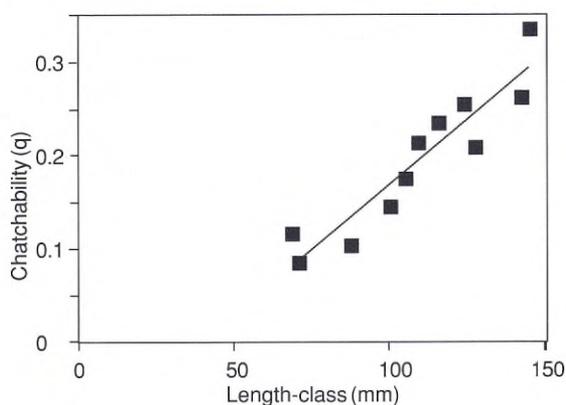


Fig. 2. Estimated catchabilities of Atlantic salmon parr in River Øyreselv by electrofishing in August-September 1988, 1991, and 1992, with corresponding regression line.

Within the length range 55-159 mm, the estimated catchabilities by autumn samplings increased considerably with increasing size of salmon parr (Fig. 2). The q -values for salmon parr by autumn samplings were even lower than for brown trout parr; salmon parr with mean lengths in the range 69-71 mm had estimated catchabilities in the range 0.084 - 0.116, while parr with mean lengths in the range 142-145 mm had values in the range 0.261 - 0.333. The functional relationship between the catchability (q) and the mean length (L) is described by the linear regression equation $q = -1.094 + 0.278 \cdot L$ ($P < 0.0001$, $r^2 = 0.87$).

Discussion

The size-dependent catchability of brown trout and Atlantic salmon parr by electrofishing demonstrated in our study, contrasts with previous results from streams with higher specific conductivities, where much higher catchabilities of 0+, and smaller differences between size or age-classes, have been reported. Bergheim and Hesthagen (1990) estimated the probability of capture to be in the range 0.37-0.56 for 0+ and 0.56-0.65 for older parr of brown trout in the stream Kvasshemsåna. According to Hesthagen (pers. comm.) they used

the same type of back packer as in our study. In 1974-76, this stream had conductivity values in the range 60-392 $\mu\text{S cm}^{-1}$ (Snekvik et al. 1977). In South Swedish streams, Karlström (1977) estimated the catchability of 0+ brown trout to be in the range 0.25 - 0.50, and of 1+ in the range 0.40 - 0.80. Similar results have been obtained for juveniles of salmon (Karlström 1977, Amiro 1990). In several studies it has been concluded that the mark-recapture method will probably give a more accurate estimate of population number than successive removal methods (Heggberget and Hesthagen 1979, Peterson and Cederholm 1984, Bohlin and Cowx 1990). However, the pronounced difference between our results and those estimated by successive removal methods in streams with high conductivities, can hardly be explained solely by differences in estimation methods, or by the type of gear used, i. e. a pulsed DC back packer. A low specific conductivity may give an overall low catchability (Alabaster and Hartley 1962, Cuinat 1967), and it is more likely that the large relative differences in catchabilities between different size-classes in River Øyreselv mainly is an effect of the low conductivity of the stream.

The estimated catchability values are likely to be positively biased, because even within shorter size-classes there is probably a variable catchability. A change in habitat use with size of the parr may also increase differences in size-dependent catchabilities. Due to the tendency of small parr to hide in the substrate during day-time, in particular at low temperatures (Hegggenes et al. 1991), they may attain electrotaxis without rising from the substrate. According to Zalewski and Cowx (1990) fish tend to be less vulnerable to electric fields at temperatures below 4 °C. The winter samplings in River Øyreselv were carried out at temperatures below 3 °C, which may explain the lower catchabilities of the smallest length-classes of brown trout compared with the autumn results. Furthermore, the coarse substrate in the stream may reduce the visibility and catch efficiency of stunned fish. In particular the smallest parr may "disappear" in the interstices of the coarse substrate after having been stunned. The lower catchability values for Atlantic salmon parr than for brown trout

parr probably reflects the difference in habitat use of the two species. Salmon parr frequently use deeper habitats with higher water velocities and a coarser substrate than brown trout (Heggenes 1988, 1990), thereby reducing the catch efficiency by electrofishing.

Because marked fish may have a higher catchability than unmarked, at least when recapture is made shortly after marking (Bohlin and Sundström 1977), population and catchability estimates made by a mark-recapture method can theoretically result in an underestimation of population size, and thereby an overestimation of catchability. In our study, the time elapse between marking and recapture sampling was at least two days, reducing the possibility of differential catchability between marked and unmarked fish.

The large differences in size-dependent catchability may have important implications for the analysis of electrofishing data. We therefore suggest that more mark-recapture experiments be carried out in a variety of low conductivity streams, preferably in combination with removal methods. Because our results indicate that electrofishing catchability in low conductivity streams is exceptionally low, catch per unit effort by DC backpackers will be of little use as an estimator of relative size-class density, i. e. the abundance of age-classes in the catch does not reflect the relative abundance in the stream. Furthermore, since the precision by removal methods depends on high catchabilities (Bohlin et al. 1990), estimates of number of small parr in low conductivity streams by this method will be very uncertain. Even when electrofishing is restricted to estimation of relative population changes, as commonly practiced e. g. in Norway (Saltveit 1990), short length intervals should be treated separately when catch per effort is used as an estimator of fish abundance in low conductivity streams. Although the catchability may be increased by increasing the voltage output and the size of the electrodes (Zalewski and Cowx 1990), an increase in current line density would also increase the mortality of the fish (Bohlin et al. 1989), thus resulting in even more biased population and catchability estimates.

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Modelling Turnover of Cs-137 in Two Subarctic Salmonid Ecosystems

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Abstract

The turnover of cesium-137 was simulated in two categories of subarctic, alpine lake ecosystems - a natural lake with *Gammarus lacustris* as major fish prey and a lake reservoir with introduced *Mysis relicta* as a new fish-food organism. The resulting concentrations of Cs-137 in two salmonid species - Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) - were calculated using a multi-compartment model. Observed data were taken from a major case study evaluating the distribution, pathways and major transport mechanisms of Chernobyl cesium through northern lake ecosystems in 1986-90 (Hammar et al. 1991a). The aim of this study was to design a specific conceptual model for calculation of the levels of Cs-137 in fish from simple lake ecosystems, which could be adopted for other more complex types of lakes.

A multi-compartment model of the ecosystem was designed and the equations were solved with the BIOPATH-code. The uncertainty of the results due to the uncertainty of input values was examined using the PRISM-system. The model gave good correlations (predicted/observed ratios within a factor 2) to measured data for Cs-137 in water, zooplankton, macroinvertebrates and fish in both lakes. The predicted levels in sediments were, however, considerably lower than the observed values. The inflow of Cs-137 from the drainage area to the two lakes was identified as the main contributor to the uncertainty of the long-term prognoses.

Keywords: Multi-compartment model, radionuclides, freshwater, *Salvelinus alpinus*, *Salmo trutta*, *Mysis relicta*, *Gammarus lacustris*, subarctic Sweden.

Introduction

The fallout of cesium-137 from the Chernobyl accident in 1986 reached high levels over a wide geographical area of Sweden (Persson et al. 1987). Several studies of the fallout from the atmospheric bomb tests in the sixties showed that radiocesium in lake ecosystems accumulates in fish muscle (e.g. Davis and Foster 1958, Kolehmainen et al. 1968). This is partly due to the chemical similarity between cesium and potassium. Important factors

affecting the concentration of radiocesium in fish are, among others, the trophic state of the lake, the biological half-life of cesium in the species, and the food habits of the fish (Kolehmainen et al. 1968, Hewett and Jefferies 1978, Evans 1988, Hammar et al. 1991a).

The long physical half-life of Cs-137 ($T_{1/2} = 30$ years) in combination with a high bio-availability may cause long-term accumulation in fish, to levels higher than those acceptable for consumption. After the Chernobyl accident, this became

evident in numerous Swedish lakes, where fish previously were harvested for recreational as well as commercial purposes (Andersson et al. 1991).

The turnover of radioactive nuclides in the environment has been the subject of modelling efforts since the 1960s, primarily due to governmental radiation regulations for the nuclear industry. This is essentially because of health concerns, both in short and long term perspectives. In addition to the assessments of dose prognoses, modelling also serves as a useful tool for increasing our understanding of major pathways and processes of importance for the turnover of radioactive nuclides and other pollutants in the biosphere.

Since models are theoretical simplifications of our perception of reality, their results are affected by an inherent uncertainty. This is affected by the successive phases in the process of modelling and can be divided into the following main components:

- interpretation of the scenario
- model structure
- parameter values

Two joint international studies, VAMP and BIOMOVs II (IAEA 1988, 1989, BIOMOVs 1991), are presently being carried out with the main purpose of testing the accuracy of biosphere radiocology modelling. BIOMOVs I (BIOMOVs) was launched in 1986 by the Swedish Radiation Protection Institute. In the first phase of that study, the turnover of cesium in three lake ecosystems was studied using the "blind test" principle, i.e. the models were designed and executed before the observed values were presented to the modelers (Sundblad 1991). The co-ordinated research program VAMP organized by IAEA/CEC is divided into four main projects, one of which treats the behavior of radiocesium in freshwater systems. One of the aims of that particular group is to use observed data from seven lakes, representing a wide range of conditions, to identify suitable models (IAEA 1990, Nordlinder and Bergström 1992).

The main objective of this case study was to design a specific model for simulating the Cs-137 levels in two sympatric salmonid species - Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) - in two alpine, oligotrophic lake types - a natural and an impounded lake. The constructed model should consider the major transport processes for the uptake of Cs-137 in fish in order to identify the significance of various pathways to fish with different food habits. Another objective is to identify the major contributions to the uncertainty in the predicted levels of Cs-137 in the fish species. The two lakes used in this study have previously been investigated in detail (Hammar et al. 1991a,b), and the long-term prognosis from that study, made with a more empirical approach, is compared with the results from the present model. The model is intended to be so general that it could be used to predict long-term levels of Cs-137 from the Chernobyl fallout in other lakes and fish species, by a simple change in input values. However, such evaluations for other systems have not been included in this study.

Material and Methods

Description of the lakes

The data on the observed levels of Cs-137 in the different components of the two ecosystems originate from Lakes Ankarvattnet and Storsjouten, on River Ångermanälven, northern Sweden. The lakes, which were studied during 1986-1990 (Hammar et al. 1991a,b) represent a series of natural lakes and reservoirs, with or without introduced fish-food organisms. Whereas Lake Ankarvattnet has natural water level fluctuations, Lake Storsjouten is a reservoir with a maximum water level amplitude of 11 m (Table 1). Both lakes are 60-70 m deep and oligotrophic. The fish fauna is dominated by Arctic char and brown trout. Whereas the dominant fish-food organisms are zooplankton and *Gammarus lacustris* in Lake Ankarvattnet, zooplankton and introduced *Mysis relicta* dominate in Lake Storsjouten.

Table 1. Physical information on Lakes Ankarvattnet and Storsjouten.

Unit	L. Ankarvattnet	L. Storsjouten
Altitude, m a.s.l.	448	442-453
Area, km ²	9.4	31
Volume, km ³	0.263	0.773
Catchment area, km ²	430	625
Max depth, m	70	60
Mean depth, m	23	25
Turnover rate, year	0.46	1.12
Latitude	64°50'13"N	64°32'13"N
Longitude	14°14'35"E	15°05'08"E

In the study by Hammar et al. (1991a), which described the distribution, pathways and major transport mechanisms of Cs-137 of Chernobyl origin in a series of natural and impounded lake ecosystems, these were found to be sinks for radiocesium with extensive accumulation in detritus, sediment, invertebrates and salmonids. Whereas the concentration of Cs-137 in water and biota declined from the extreme peak levels of 1986-87, the levels in surface sediment increased extensively until fall of 1988. The concentration in fish populations feeding on benthic invertebrates, i. e. mysids and amphipods, was higher than in planktivorous fish. During each of the three first winters a significant increase in levels of Cs-137 in the winter-active Arctic char was recorded, whereas the levels declined during the succeeding summers. *Mysis relicta* was found to enhance the transport of Cs-137 from zooplankton and settling particles to Arctic char and brown trout. The results seemed to show a successive change in the transport of radiocesium from water via zooplankton to planktivorous fish during the initial phase, to post-depositional mobilization via benthic organisms to benthic fish during the following period.

Mathematical tools

The approach used in this study is based on compartment theory. This implies that the system studied is divided into a number of physically defined areas or volumes, i.e. compartments. Exchange between these compartments is described

by rate constants expressed in turnover per time unit. Mathematically, this is expressed by a set of first order linear differential equations with constant or time varying transfer coefficients (rate constants).

The assumptions are that:

- the outflow from a compartment is solely dependent upon the quantity of the element in that particular compartment
- the compartment is instantaneously well mixed
- all elements have the same probability of leaving the compartment.

In general, compartments can be designed to fulfil the condition of instantaneous and homogeneous mixing with satisfactory precision. In nature, however, such ideal compartments are often connected to media with gradients, or the probability of leaving the compartment may vary substantially within the compartment (e.g. sediment). A more realistic situation is then obtained by further dividing such media into several compartments.

The amount of radioactivity in a given compartment is dependent on:

- the source term for the compartment system, such as the direct release to one or several compartments, or generation within them by decay from the parent nuclide
- the outflow to and inflow from other compartments
- radioactive decay.

The differential equations were solved with the BIOPATH-code (Bergström et al. 1982). This code gives deterministic results. To study the uncertainty of the results due to unknown and/or varied input values, an integrated system of computer programs, PRISM (Gardner et al. 1983), was applied to the BIOPATH-code.

Within the PRISM-code, sets of the parameter values are generated from given distributions of each parameter. The responses of the model are then calculated for each set of values generated and the results are analyzed statistically. The outcome shows the distribution of the responses, in this case, the concentration of cesium in the compartments. In addition, information on the main parameters that contribute to the uncertainty is given for each response.

The PRISM system consists of three main steps. In PRISM 1, random values are generated by using a systematic sampling method, Latin Hyper Cube. As input to PRISM 1, the mean values, type of distributions, standard deviations and the upper and lower limits are given for each parameter. These data are then used to define probability density functions. The Latin Hyper Cube method, used to generate the sets of values from the given distributions, is an efficient Monte Carlo sampling technique which produces random values within the whole desired range. In addition, correlation between the parameters can be taken into account, no matter what type of distributions they are drawn from. Secondly, in PRISM 2 the model is run for each set of values. Finally, PRISM 3 statistically evaluates and summarizes the joint set of parameters and predictions.

The general statistics for the distribution of each parameter and the response of the model to this distribution contain the following: arithmetic mean, standard deviation, coefficient of variation, geometric mean, percentiles (5, 25, 50, 75, and 95 %), and the five highest and five lowest values, respectively.

Correlations between the parameters and the responses as well as between the responses themselves are also obtained from this last part of the analysis. Two correlation coefficients are calculated: the simple Pearson correlation coefficient, and Spearman Rank, which is the correlation of the ranked values of the parameters and model responses. Associated with each correlation coefficient is their percent covariation (COVAR). This represents the percent variance that one variable accounts for in another variable or response. In the cases of correlated parameters and responses, percent COVAR indicates the amount of variability in the model response that is explained by the variability of that particular parameter.

The regression procedures are used to obtain the relationship between model parameters and model uncertainties. The parameters to be entered into the regression analysis are selected from those which give the greatest improvement on the sum of squares of regression. From these analyses the relative contribution to the total uncertainty from each parameter is obtained.

The compartment system for the lakes

According to the model structure the two lake systems to be compared are divided into appropriate compartments. The division into compartments and their connections represent a compromise between:

- a sufficiently differentiated system in order to encompass all major processes
- simplicity of design in order to facilitate the uncertainty analyses and the comparison of model predictions with observations
- available information on dispersal mechanisms.

Ten compartments were designed for the simulation of the Cs-137 turnover in the two systems (Fig. 1). The water component in each lake is described as a single compartment. This is a simplification, especially during periods when the water column is stratified. Furthermore, the drainage area is also treated as a single compartment. It was beyond the scope of this project to model in detail the leakage of Cs-137 from the watersheds.

The sediment component of each lake is represented by three compartments. The surface is divided into two parts, one representing the near shore sediment or transport bottoms, and the other the sediments at greater water depths, where accumulation takes place. Below the latter a third compartment acts as a final sink for the nuclide.

The biotic compartments included in the model are zooplankton, benthos and fish. The benthos is represented by *Gammarus lacustris* in Lake Ankarvattnet and by *Mysis relicta* in Lake Stor-sjouten. The two fish species considered in both lakes are Arctic char and brown trout.

Transport of radioactive cesium

The conceptual model designed for the two lake ecosystems considers all major transfers which are of importance for the estimation of the concentrations of cesium-137 in water and the fish species. The transfer coefficients (TC) or rate constants in these systems symbolize resultant transfers of radiocesium between the compartments (Fig. 1). In reality, they consist of a combination of more or less complicated processes dependent upon physical, chemical and biological conditions. However,

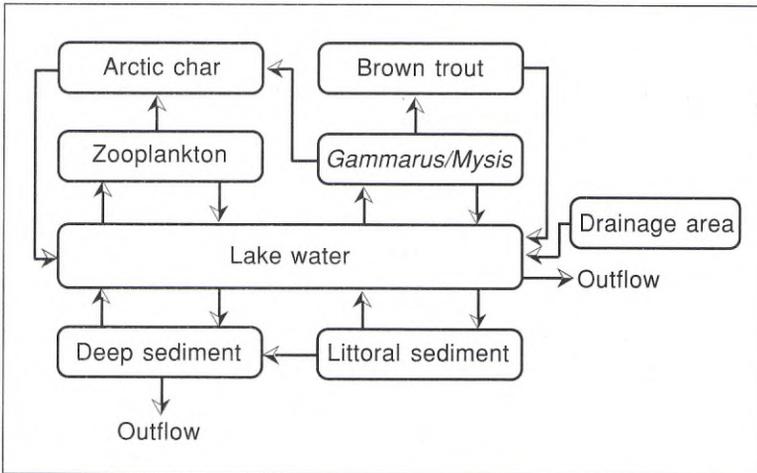


Fig. 1. Structure of the compartment model for the ecosystems of lakes Ankarvatnet and Storsjouten. The arrows indicate the resulting flows of Cs-137 within the system.

in most of the transfers there is one process which dominates the flow needed to be considered between the compartments. The resultant transfers in the model are obtained from expressions based on biological and physical parameters when possible and they are shown below. The advantages are threefold

- the same basic model can be applied to different lake systems with differences in site-specific values of the parameters
- uncertainty analyses can be performed on a rational systematic basis
- important parameters for resultant concentrations in fish and other compartments can be identified.

In some cases no relevant information is available to give an expression for the transfer coefficient. One such process is the leakage of cesium from the drainage area to the lake. This value therefore had to be estimated from experience (Bergman et al. 1991) and previous model calculations (Bergström and Nordlinder 1989, Nordlinder and Bergström 1992). Due to these facts this parameter varies within a wide range.

The initial amount of Cs-137 in the water column decreases via outflow and by transfer to the sediment. In Lake Storsjouten the water flow is well known and the mean monthly transfer coefficient has been calculated from 4 years of data (1986-89) (information from SMHI). The annual turnover of water in Lake Ankarvatnet has

been calculated (see Hammar et al. 1991a). This annual value has been distributed among months with consideration to seasonal variation (e.g. spring-flood).

The transfer of cesium to the sediments depends on interactions with mineral and organic particles. This process is dependent on the chemical form of the element and the environmental conditions. Diffusion may also transfer cesium from the water column to the sediment.

To obtain the transfer coefficient for the transport of radionuclides from water to sediment (TC_{ws}), the following equation was used (Hill and Lawson 1980):

$$TC_{ws} = K_d \cdot S / [h_m \cdot (1 + K_d \cdot SS)]^{-1} \quad (1)$$

where

K_d = distribution coefficient between water and sediment (= concentration in solid/concentration in liquid phase) [m^3/kg]

S = sediment growth rate [kg/m^2 , month]

h_m = mean depth of lake [m]

SS = concentration of suspended matter in the water [kg/m^3]

The processes within the sediment are complex with physical, chemical and biological mechanisms causing redistribution of the radiocesium. Our main emphasis is not to model these processes in detail but instead to estimate the fraction of

cesium that re-enters the water and/or is retained in the deeper sediment, where it is not available for biological processes. One approach which has been successful in other studies is to base the rate constants upon mass-balance, since the major part of the cesium is bound to particles. Diffusion and biological transport seem to have a minor influence on the flow from the sediments for continuous release of nuclides to a lake (Bergström and Nordlinder 1991). The total mass inflow to the sediment is given by sedimentation growth rate (S) which has been calculated from sediment traps (Hammar et al. 1991a). Some of the radiocesium will return to the water phase due to resuspension, a small amount due to mobilization via benthic organisms to benthic fish and subsequent excretion to water (Hammar et al. 1991b), while the remainder settles and is treated in the model as a transfer to deeper sediment layers. Cesium deposited in the littoral zone is primarily transported to the deeper accumulation bottoms.

The complex radioecological mechanisms behind the uptake of Cs-137 by zooplankton and benthos are simplified and described by rate constants based upon bio-accumulation factors (CF) from water, and the biological turnover time of Cs-137 in each specific taxon. This is justified by the fast turnover time in these invertebrates in comparison to the time steps used in the calculations. For compartment models the transfer from water to zooplankton and benthos (TC_{wb}) then becomes

$$TC_{wb} = CF \cdot \ln(2) / T_{1/2bio} \cdot Mb / Mw \quad (2)$$

where

CF = Bio-accumulation factor [(Bq/kg dw)/(Bq/l)]

$T_{1/2bio}$ = Biological half-time [month]

Mb = Total biomass of the species [kg dw]

Mw = Total mass of the water [kg or l]

Values for the bioaccumulation factors for *Mysis* and *Gammarus* were calculated from measured data from two lakes (Hammar et al. 1991a). By definition the factors should be calculated for steady state conditions. However, due to the fast turnover in these species the conditions for steady state could be satisfactorily fulfilled.

In Lake Storsjouten the transfer of Cs-137 to *Mysis* from the sediment is also considered (Hammar et al. 1991b), and the transfer coefficient is calculated in the same manner as for that from water.

Several studies have shown that the main uptake of Cs-137 by fish occurs via food organisms (e.g. Hewett and Jefferies 1976, 1978, Evans 1988a,b, Hammar et al. 1991a). Because of competition for food and habitat, Arctic char and brown trout segregate when coexisting (Nilsson 1967). Depending on individual dominance the brown trout claims the littoral habitat with its abundance of macro invertebrates whereas the Arctic char is forced to rely on zooplankton in the pelagic. In winter time, however, the activity of the brown trout is highly restricted by low temperature which allows the Arctic char to feed actively on littoral invertebrates such as *Gammarus* in Lake Ankarvattnet or *Mysis* in Lake Blåsjön (Hammar 1984, Hammar et al. 1991a,b, Hammar in prep). The model presumes different winter and summer habits, with the brown trout feeding on benthos during the summer and nothing during the winter, while the Arctic char feeds on zooplankton in the summer and benthos in the winter. The transfer coefficient describing the uptake of Cs-137 in fish muscle is thus based upon seasonal consumption data and fractional assimilation (TC_{bf}). The rate constant is obtained by:

$$TC_{bf} = I \cdot Uf \cdot Mf / Mb \quad (3)$$

where

I = Intake of the dominating prey species [kg dw/month/kg ww fish]

Uf = Proportion of ingested to incorporated Cs-137

Mf = Total biomass of fish [kg ww]

Mb = Total biomass of food organism [kg dw]

In the model the turnover of Cs-137 in the biotic compartments are only dependent on the biological half-time of Cs-137 within them. The rate constant (TC_{bw}) is obtained by:

$$TC_{bw} = \ln 2 / T_{1/2bio} \quad (4)$$

Table 2. Values of parameters, best estimate (BE), type of distribution (Dist) and minimum and maximum values of ranges (Min, Max). Data taken from Hammar et al. 1991a and unpublished information.

Parameter	Unit	Dist ¹⁾	Lake Ankarvattnet			Lake Storsjouten		
			BE	Min	Max	BE	Min	Max
Ql	Bq	T	7.0 ¹¹	5 ¹¹	9 ¹¹	1.6 ¹²	1 ¹²	2 ¹²
Qd	Bq	T	1.5 ¹³	1 ¹³	2 ¹³	1.5 ¹³	1 ¹³	2 ¹³
TC _{wo} , spring	1/month	T	1.1	0.9	1.3	0.0	0.0	0.0
TC _{wo} , normal	1/month	T	0.11	0.1	0.12	0.07	0.05	0.09
h _m	m	T	23	22	24	25	22	28
SS	kg/m ³	LT	1.0 ⁻³	5 ⁻⁴	5 ⁻³	1.0 ⁻³	1 ⁻⁴	5 ⁻²
S	kg/m ² .mo.	LT	7.8 ⁻³	3 ⁻³	1.3 ⁻²	9.8 ⁻³	6 ⁻³	1.1 ⁻²
K _d	m ³ /kg	LT	100	10	500	100	10	500
Zooplankton:								
CF	kg/l	LT	2.7 ⁴	1 ⁴	5 ⁴	1.1 ⁴	5 ³	5 ⁴
T _{1/2bio} , win	month	LT	0.23	0.1	0.3	0.23	0.1	0.3
T _{1/2bio} , sum	month	LT	0.066	0.01	0.1	0.066	0.01	0.1
Benthos:								
<i>Gammarus lacustris</i>								
CF	kg/l	T	3.8 ⁴	2 ⁴	6 ⁴	-	-	-
T _{1/2bio} , win	month	LT	0.46	0.2	0.7	-	-	-
T _{1/2bio} , sum	month	LT	0.23	0.1	0.3	-	-	-
<i>Mysis relicta</i>								
CF, water	kg/l	LT	-	-	-	2.0 ⁴	5 ³	5 ⁴
CF, sediment	kg/kg	LT	-	-	-	0.02	0.005	0.05
T _{1/2bio} , win	month	LT	-	-	-	0.46	0.1	1
T _{1/2bio} , sum	month	LT	-	-	-	0.23	0.1	1
Fish:²⁾								
Brown trout								
I, win	g dw/day	C	0.	0.	0.	0.	0.	0.
I, sum:	g dw/day	T	4	2	6	4	2	6
T _{1/2bio} , win	months	C	∞	∞	∞	∞	∞	∞
T _{1/2bio} , sum	months	LT	4	2	8	4	2	8
Uf	-	T	0.6	0.4	0.8	0.6	0.4	0.8
Arctic char								
I, win	g dw/day	T	1	0.5	2	1	0.5	2
I, sum:	g dw/day	T	2	1	3	2	1	3
T _{1/2bio} , win	months	T	16	12	20	16	12	20
T _{1/2bio} , sum	months	LT	5	3	9	5	3	9
Uf	-	T	0.6	0.4	0.8	0.6	0.4	0.6

¹⁾ Distribution types: C = Constant, N = Normal, T = Triangular, LT = Log-Triangular

²⁾ Data for the fish species were extracted from the references given in the table head and from Evans 1988b, 1989, Forseth et al. 1991, Korhonen 1990, and Meili 1991.

Ql = Source-term, deposition on lake
 Qd = Source-term, deposition in drainage area
 TC_{wo} = Transfer coefficient for outflow from the lake
 h_m = Mean depth
 SS = Concentration of suspended material in water
 S = Sedimentation growth rate
 K_d = Distribution coefficient between solid and soluble

CF = Bioaccumulation factor
 T_{1/2bio} = Biological half-time of Cs-137
 I = Intake of food
 Uf = Proportion of ingested to incorporated Cs-137
 win = Winter (December-May)
 sum = Summer (June-November)

Parameters

A short description of the lakes has been given above. For further description of the lakes, physical and biological data (see Hammar et al. 1991a). The values used in the model were estimated based on these observed data (Table 2).

The general source term of the model is the atmospheric deposition of Cs-137, both on the lake surfaces and in the drainage areas. Therefore, the total initial input to each lake corresponded to an area 1.5 times the actual area. This was justified by the assumption that the deposition occurred during the spring flood when there was higher run-off (Nylén and Grip 1989). Using the lower initial source term, the calculated concentrations of Cs-137 in the water could not have reached the observed levels.

Masses of the biota compartments were constants with values taken from Hammar et al. (1991a). Because of the structure of the model they cannot contribute to the variation in the results.

Results and Discussion

The model's performance was assessed by studying the ratios of predicted to observed concentrations (P/O) for each observation. Geometric mean (GM) and geometric standard deviation (GSD) were calculated for these time series and each type of sample. If the value of GSD approaches 1.0, this indicates that the evolution of the model predictions is similar to the observations,

furthermore GM should also approach 1.0 to show good agreement and unbiased results. High values of GSD show discrepancies between the trends of predictions and observations even if the GM value is near 1.0.

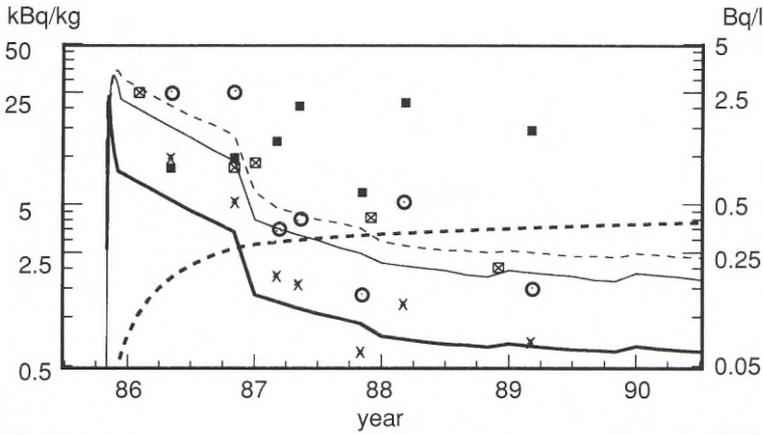
The calculated concentrations of Cs-137 in water, zooplankton, *Mysis*, *Gammarus* and the two fish species are in fairly good agreement with the values observed (Table 3), as the geometric mean of predicted to observed ratios (P/O) is mostly within a factor of 2. The only GSD value above 2 is that recorded for zooplankton in Lake Storsjouten. This is due to the very low observed concentration in April 1987. Omitting this value from the analysis, the GSD decreases to levels comparable to the other responses. However, the predicted levels in sediments are considerably lower than the observed values.

The profile of the decline of radiocesium in water differs between the two lakes (Figs. 2 and 3). This is mainly because of differences in the discharge dynamics. During spring and summer the outflow of Lake Storsjouten is closed, in order to fill the reservoir for the hydro-power plant. In contrast, Lake Ankarvattnet has a natural flow, where the turnover of water is considerably larger during the spring flood. In spite of the poor agreement between values for radiocesium in the sediment, which interacts with cesium in the water, the importance of the different water flow schemes are clearly well illustrated by the models.

The observed levels of Cs-137 in the sediments were far higher than the calculated values. This is

Table 3. The geometric mean (GM) and geometric standard deviation (GSD) of the ratios of predicted to observed concentrations and number of observations (N) for the different samples.

	Lake Ankarvattnet			Lake Storsjouten		
	N	GM	GSD	N	GM	GSD
Water	7	0.76	1.42	8	1.18	1.36
Sediment	7	0.23	1.54	8	0.18	1.82
Zooplankton	7	0.78	1.78	9	1.30	2.37
<i>Gammarus</i>	5	1.01	1.46	-	-	-
<i>Mysis</i>	-	-	-	8	0.92	1.42
Brown trout	8	0.81	1.19	7	0.99	1.28
Arctic char	13	0.62	1.38	8	0.50	1.32



	calc.	obs.
<i>Gammarus</i>	— · —	⊠
<i>Mysis</i>	— · —	⊠
Zooplankton	·····	○
Sediment	- - -	■
Water	————	x

Fig. 2. Lake Ankarvattnet; Results of deterministic model calculations for the concentration of cesium-137 in water (Bq/l), sediment (kBq/kg dw), zooplankton (kBq/kg dw) and *Gammarus* (kBq/kg dw) shown as lines during the years 1986-90. Corresponding observations for respective components are shown as dots.

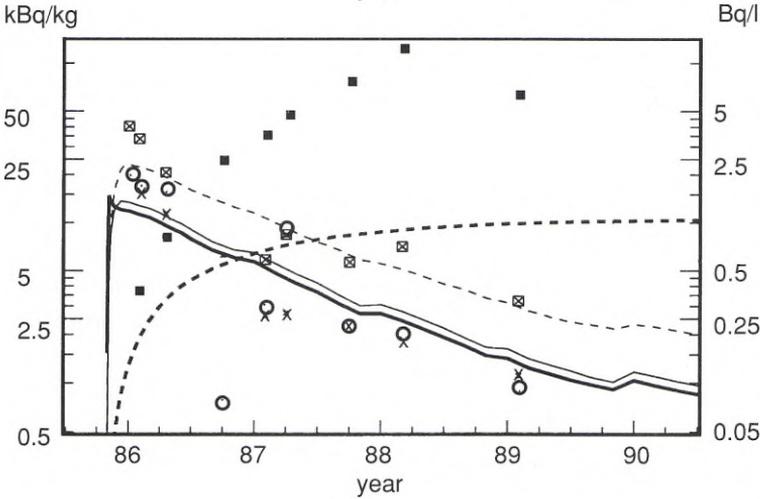


Fig. 3. Lake Storsjouten; Results of deterministic model calculations for the concentration of cesium-137 in water (Bq/l), sediment (kBq/kg dw), zooplankton (kBq/kg dw) and *Mysis* (kBq/kg dw) shown as lines during the years 1986-90. Corresponding observations for respective components are shown as dots.

probably due to processes not considered in the model, e.g. an initially higher load of Cs-137 to the sediments than the average values used in the model. The initially deposited cesium may be chemically and/or physically different and thus cause a higher direct transfer to the sediments. It has been shown that the fall-out of cesium from the Chernobyl accident had mobile and inert fractions (Oughton et al. 1991). These processes were not dealt with due to lack of data from the first days or weeks after the deposition.

The concentrations of Cs-137 in zooplankton and benthos clearly reflect the concentrations in water because of the fast turnover of Cs-137 between these compartments. The good agreement between predicted and observed concentrations results from the use of site-specific data to

obtain the transfer coefficients. According to the assumptions in the model, zooplankton and benthos assimilate Cs-137 from the water column, except for *Mysis* where there is an additional uptake from the sediment. In the model this transfer of cesium to *Mysis* was less significant, which again may reflect the underestimation of the levels in sediment. In the empiric investigation a significant positive correlation between Cs-137 in *Mysis* and detritus from sediment traps was found (Hammar et al. 1991a,b).

The outcome of the model for cesium levels in the Arctic char and the brown trout is presented both in deterministic and probability terms. The P/O ratios of the deterministic results for brown trout are well within acceptable confidence limits in both lakes. The concentration in Arctic char is

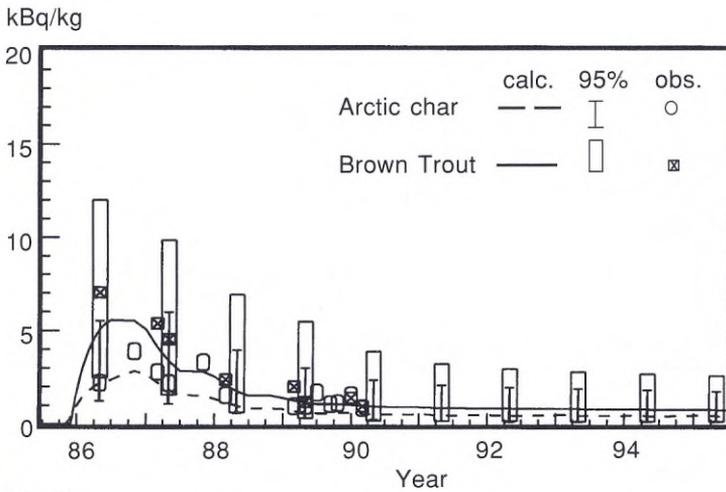


Fig. 4. Lake Ankarvattnet; Results of deterministic and probability model calculations of the concentration of cesium-137 in Arctic char and brown trout (kBq/kg ww) during the years 1986-95. The deterministic results are shown as lines while the probability results are shown as the interval of 95% confidence intervals. Corresponding observations for fish species are shown as dots.

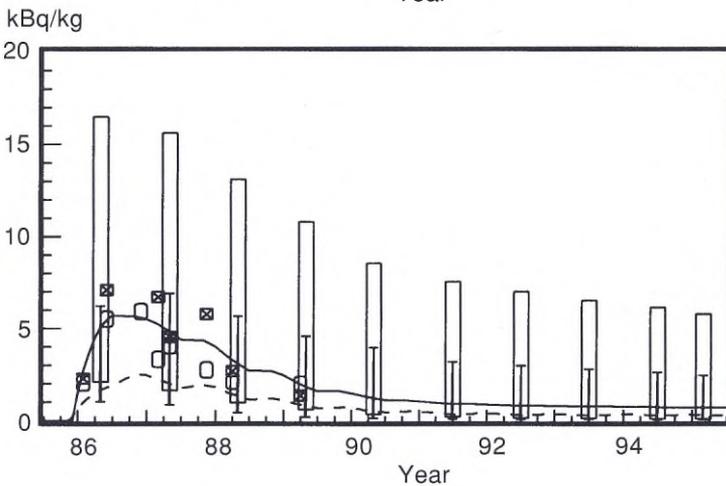


Fig. 5. Lake Storsjouten; Results of deterministic and probability model calculations of the concentration of cesium-137 in Arctic char and brown trout (kBq/kg ww) during the years 1986-95. The deterministic results are shown as lines while the probability results are shown as the interval of 95% confidence intervals. Corresponding observations for fish species are shown as dots.

underestimated by a factor of two. Due to the good agreement between observed and predicted values in zooplankton, benthos and brown trout, it can be assumed that one or several parameters for the uptake and turnover in the Arctic char are biased. However, the 95% confidence interval of the probability results covers the observed levels of Cs-137 in fish (Figs. 4 and 5). The input data used in the deterministic calculations comprise the best estimate from the distributions of values used in the probability calculation. The frequency distributions of the calculated individual levels of cesium in the two salmonids are skewed in a similar manner to the observed distributions (Hammar et al. 1991a). These skewed distributions reflect the skewed

distribution of the input values (Table 2).

For the two salmonids the variation is wider in Lake Storsjouten than in Lake Ankarvattnet. The relative contribution from the parameters to the total uncertainty will change with time (Fig. 6). The parameters that mainly contribute to the uncertainty during the first year are the bioaccumulation factors for the zooplankton and benthos, and those used for calculating uptake and excretion in the fish species. These bioaccumulation factors are obtained from the observed data. The ranges of the observed data were larger in Lake Storsjouten for corresponding species.

In both cases the same values and ranges have been used for the parameters describing the

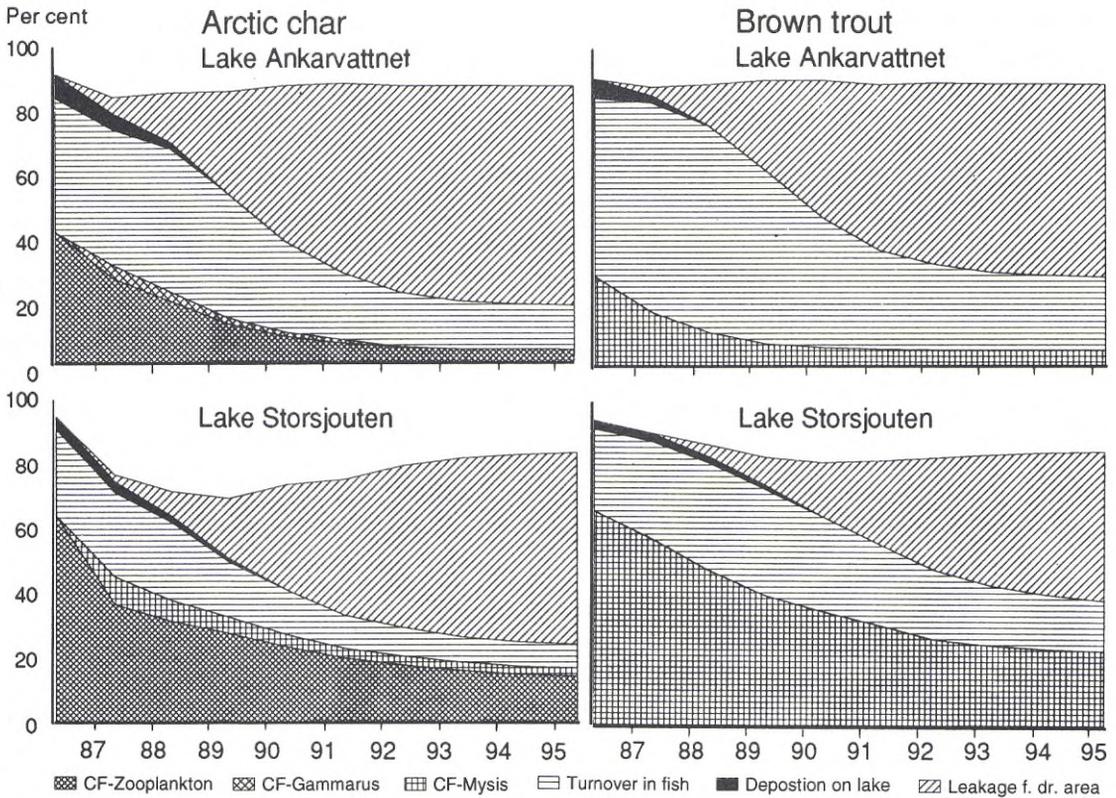


Fig. 6. Percentage contribution of dominant parameters to the uncertainty in the model as a function of time (1986-95) for calculated concentrations of cesium-137 in the fish species in the two lakes. These dominant parameters are the bioaccumulation factors for zooplankton and benthos (CF), those related to the uptake and elimination in fish (Turnover in fish), initial deposition on the lake (Deposition on lake) and leakage from the drainage area to the lake water (Leakage from drainage area).

accumulation of radiocesium in fish muscle (e.g. consumption, uptake fraction and biological half life). The relative contribution to the total uncertainty from these parameters is larger for Lake Ankarvattnet, which is an effect of the smaller range of total uncertainty for this lake (Figs. 4 and 5).

The concentration of cesium-137 in the fish species will of course primarily depend on the amount deposited. Because of the small variation in the deposition ($\pm 25\%$), this parameter makes a small contribution to the uncertainty in the levels in fish muscle. The duration of this low contribution to the uncertainty differs between the two lakes, and is shorter in Lake Ankarvattnet. This

may be due to the impoundment of Lake Storsjouten, where a larger amount of the total deposition of radiocesium still remains within the lake system, especially in the sediment (Hammar et al. 1991a).

The residence time of water in the lake is also important for the recovery of the lakes from elevated radiocesium levels. Such data are fairly well known for these two lakes. With time the secondary leakage of radiocesium due to resuspension from the sediment and inflow from the drainage area will contribute to the concentration in the ecosystem. The contribution to the total uncertainty in fish, of leakage from the drainage area is

negligible during the first few years, but increases with time and will dominate in the future (5 years for Lake Ankarvattnet and about 10 years for Lake Storsjöuten). The dominant contribution of this parameter is of course an effect of the relatively wide range of variation. The model, however, does not indicate any importance of resuspension from the sediment to the water. A probable explanation for this is that the lakes are deep. For shallow lakes in central Sweden it has been shown that the transport of cesium-137 from sediment is of major importance in maintaining the concentration of radiocesium in the water (Bergström and Nordlinder 1989, Broberg and Andersson 1991, Sundblad et al. 1991).

Conclusions

The model developed in this study seems to be useful for modelling the concentrations of radiocesium in different parts of Subarctic lake ecosystems, both for the estimation of peak values as well as for long-term prognoses. The majority of predicted values for water and biota do not differ by more than a factor of 2 from the observed values.

During the period of prediction (10 years from deposition) the mean concentration in Arctic char and brown trout will not fall below 300 Bq/kg. The prediction of Hammar et al. (1991a), based upon observed values, that the ecological half-time of Cs-137 would be 5 to 9 years, is below this limit. However, these latter values used means from several lakes, also including natural systems with estimates of very short ecological half-times of Cs-137. However, the predicted duration of concentrations above the radiological guideline (1,500 Bq/kg), is similar in both studies.

For a lake with a known source term of radiocesium and residence time of water, two main phases can be identified when estimating the concentration in fish muscle. The first phase is the peak concentration of Cs-137 during the first years. In this phase biological parameters, such as the turnover in fish and their prey organisms, are the most important factors for the precision of the estimate. In the second phase, which is the prolonged prognosis, the processes of significance are those maintaining the concentration in the water. One of those

is the inflow from the drainage area. A similar conclusion was also reached in the empirical study by Hammar et al. (1991a).

Another subject for further study is the chemical composition of the deposited Cs-137. If the chemical composition of the cesium fall-out can be taken into account this may increase the precision of the calculations.

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Fish Community Status in Norwegian Lakes in Relation to Acidification: a Comparison between Interviews and Actual Catches by Test-fishing

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Abstract

Inquiries are used to obtain information on fish community status in terms of unchanged, reduced and lost communities, to assess the effects of acidification in lakes. The aim of this paper was to investigate the validity of this method by comparing fish status with actual catches on standard gillnet series (CPUE). Data from 230 test-fishing incidents comprising 357 stocks of 7 different fish species are presented. We found significant differences in CPUE between perceived fish status categories for brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and perch (*Perca fluviatilis*), for which sufficient data were available. A discriminant analysis revealed that for stocks reported as unchanged and lost, the predicted membership ranged between 60.0-72.1%, respectively. However, a dominant fraction (50.0-66.7%) of stocks reported as reduced were assigned as lost. Stocks which have been declining for less than 10 years, had a significantly higher CPUE than stocks which have declined for a longer period of time (versus 10-20 and 20-30 years). Another apparent change in population characteristics was an acidification induced increase in mean weight for fish in affected stocks. It is suggested that interviews tend to overestimate the current fish status. This is discussed in relation to a time-lag between when the damage started and the time when it became apparent to fishermen, and rapid decline in population numbers.

Introduction

Acidification has seriously affected fish populations in Norwegian lakes (Sevaldud and Muniz 1980, Henriksen et al. 1989a, Berger et al. 1992). The damage has mainly been documented through enquiries or interviews concerning the current status of lakes still supporting fish, and those previously known to contain fish. These studies were initiated in the early 1970's when the damage to fish populations due to acidification became strongly evident in southernmost Norway (Jensen and Snekvik 1972, Snekvik 1974, 1977). Earlier results documented good correspondence between status reported by enquiries and actual catches on

standard gillnets for brown trout (*Salmo trutta*) populations (Rosseland et al. 1980, Hesthagen and Jonsson 1986). In this paper we compare reported status and CPUE for brown trout, Arctic char (*Salvelinus alpinus*) and perch (*Perca fluviatilis*). In addition, some data for four other less common species from lakes in southern Norway are given.

Methods

Fish community status and test-fishing data were collected in southern Norway during the period 1980-92, mainly as part of the Norwegian monitoring programme for long-range transported air pollutants (SFT 1991). The majority of the lakes

Table 1. Fish assemblages (still or previously present) in the study lakes. A few lakes inhabited by brown trout, perch and Arctic char also supported brook trout.

Fish community	Number of stocks
Brown trout	119
Brown trout and brook trout	19
Brown trout and perch	32
Brown trout and Arctic char	26
Brown trout, perch and Arctic char	2
Perch	2
Arctic char	9
Others*	21
Total	230

* 17 of these lakes supported brown trout.

are located in the southernmost counties in areas of slowly weathering rock (granite and gneisses) susceptible to acidification. Some of the lakes in this area were test-fished because they originally were sampled during the programme "Acid precipitation - effects on forest and fish" (Overrein et al. 1980, Rosseland et al. 1980). However, we selected lakes in all counties in southern Norway to cover different geographic regions. We also selected the lakes on the basis of their fish communities to obtain data for the three most common fish species, i.e. brown trout, perch and Arctic char (Table 1). Further, we excluded smaller lakes (<20 hectares), and localities which were affected by local activities (industry, agriculture), liming or hydroelectric regulation.

We obtained perceived fish community status from persons with good knowledge about each lake over a longer period of time such as fishery managers, landowners or local fishermen. Standardized questionnaires about fish status have been worked out (Sevaldrud and Muniz 1980), and each person was requested to answer either by mail or by personal interviews. Information on status was obtained from more than one person if there was any uncertainty about evaluating the current fish status. The number of persons from which information was obtained within a certain area varied

considerably, depending upon their individual knowledge and ownership rights.

Five categories of perceived status were defined for every fish species that once had existed or still exists in each lake as (i) unchanged self-sustainable populations which give rise to satisfactory catches, (ii) unchanged, self-sustainable populations which never have been numerous due to natural factors such as limited spawning areas, interspecific competition, etc., (iii) populations which have recently experienced an apparent decline in abundance, (iv) populations which are virtually extinct and (v) no self-sustaining population exists due to the absence of spawning areas (includes brown trout stocks only). Brook trout (*Salvelinus fontinalis*) stocks which were reported as unchanged and naturally sparse, were considered as good and sparse stocks, because natural propagation is unimportant in these stocks.

For populations which were defined as either reduced or lost, we asked when the damage had occurred, expressed in time periods of 0-10, 10-20 and 20-30 years etc. before the date of the enquiry.

We used a standard series of bottomset gillnets to obtain relative abundance of different fish species. Each series consisted of 8 nets of 27 x 1.5 m with mesh sizes between 10-45 mm (Rosseland et al. 1979). In some lakes we used a series of benthic survey nets of 32 x 1.5 m, mainly in addition to the standard series. These survey nets consist of 4-m long panels of the same mesh sizes as the standard gillnet series. A series of survey nets consisted of three nets, i.e. a total length of 96 m. The catch per unit effort (CPUE) of these survey nets was transformed to its standard series equivalent in terms of m² net area. We usually employed one or two series in each lake depending on lake size. Single nets were placed perpendicular to the shore and distributed randomly throughout each lake, covering different depth intervals within the lake. Test-fishing was conducted in the autumn, mainly in August and September, with a few samplings in early October.

Test fishing results are affected by lake surface area and maximum depth of the lake (Nyberg and Degerman 1988, Degerman et al. 1992). However, our study lakes were mainly small (<80 hectare), so any lake-size effect should be relatively small.

All statistical tests were performed with the SPSS/PC computer package. Differences in CPUE between reported unchanged, reduced and lost stocks were tested using the nonparametric Mann-Whitney test. Further, we used a discriminant analysis to obtain a classification table of predicted group membership. To test for differences in mean fish weight among stocks of different status categories, we used an ANOVA with the Scheffé a posteriori test to reveal the sources of variance in cases where significant differences ($P < 0.05$) were found.

Results

A total of 230 test-fishings (196 lakes) and 7 fish species comprising 357 populations were included in this study (Table 2). Brown trout exhibited a significant difference in CPUE between stocks reported as unchanged and reduced as well as between stocks reported as reduced and lost (Mann-Whitney test, $Z = -8.15$ and -8.42 , respectively, $P < 0.0001$). Similar differences were found for

Arctic char, $Z = -3.97$ ($P < 0.0001$) and -2.75 ($P < 0.01$) and perch, $Z = -3.21$ ($P < 0.005$) and -3.76 ($P < 0.0005$). For the stocks which were classified as naturally sparse, the catches were low compared to those for unchanged stocks of the same species.

We also present some data on reported status of 43 stocks of whitefish (*Coregonus lavaretus*), roach (*Rutilus rutilus*), brook trout and Northern pike (*Esox lucius*), Table 2. However, no statistical analysis was carried out for these stocks due to low sample numbers.

Considerable variation in CPUE was found within each category (Fig. 1). There were indications of an over-optimistic evaluation of reported status, as test-fishing yielded no fish in 12% of brown trout and 30% of Arctic char stocks classified as reduced.

Stocks reported as affected were in various stages of reduction as indicated for brown trout (Fig. 2). Stocks which have been declining for less than 10 years, had a significantly higher CPUE than stocks which have declined for a period

Table 2. Mean number and standard deviation ($\bar{x} \pm SD$) of fish caught per standard gillnet series in each status category with number of stocks (N_s) and total number of fish (N_F).

Reported status	Brown trout			Arctic char			Perch			Whitefish		
	$\bar{x} \pm SD$	N_s	N_F									
Unchanged	58.8 ± 34.2	61	5,251	53.1 ± 43.4	20	1,378	150.3 ± 97.9	30	5,575	-	-	-
Reduced	15.7 ± 18.8	74	1,481	4.2 ± 8.7	9	50	17.9 ± 18.1	4	106	6.2 ± 7.6	12	143
Extinct	0.6 ± 1.8	63	50	0.1 ± 0.1	13	2	0.1 ± 0.3	14	1	0	1	0
Naturally sparse	8.1 ± 5.2	12	122	1.2 ± 0.7	5	11	40.1 ± 74.4	6	311	-	-	-
Stocked fish only	22.5 ± 27.1	3	60	-	-	-	-	-	-	-	-	-
Total		213	7,052		47	1,441		54	5,993		13	143

Reported status	Roach			Brook trout			Northern pike		
	$\bar{x} \pm SD$	N_s	N_F	$\bar{x} \pm SD$	N_s	N_F	$\bar{x} \pm SD$	N_s	N_F
Unchanged				55.1 ± 30.3	7	386			
Reduced							1.5 ± 2.1	2	3
Extinct	0	1	0				0	1	0
Naturally sparse	30 ± 0	1	30	6.1 ± 7.9	17	104	0	1	0
Stocked fish only									
Total		2	30		24	490		4	3

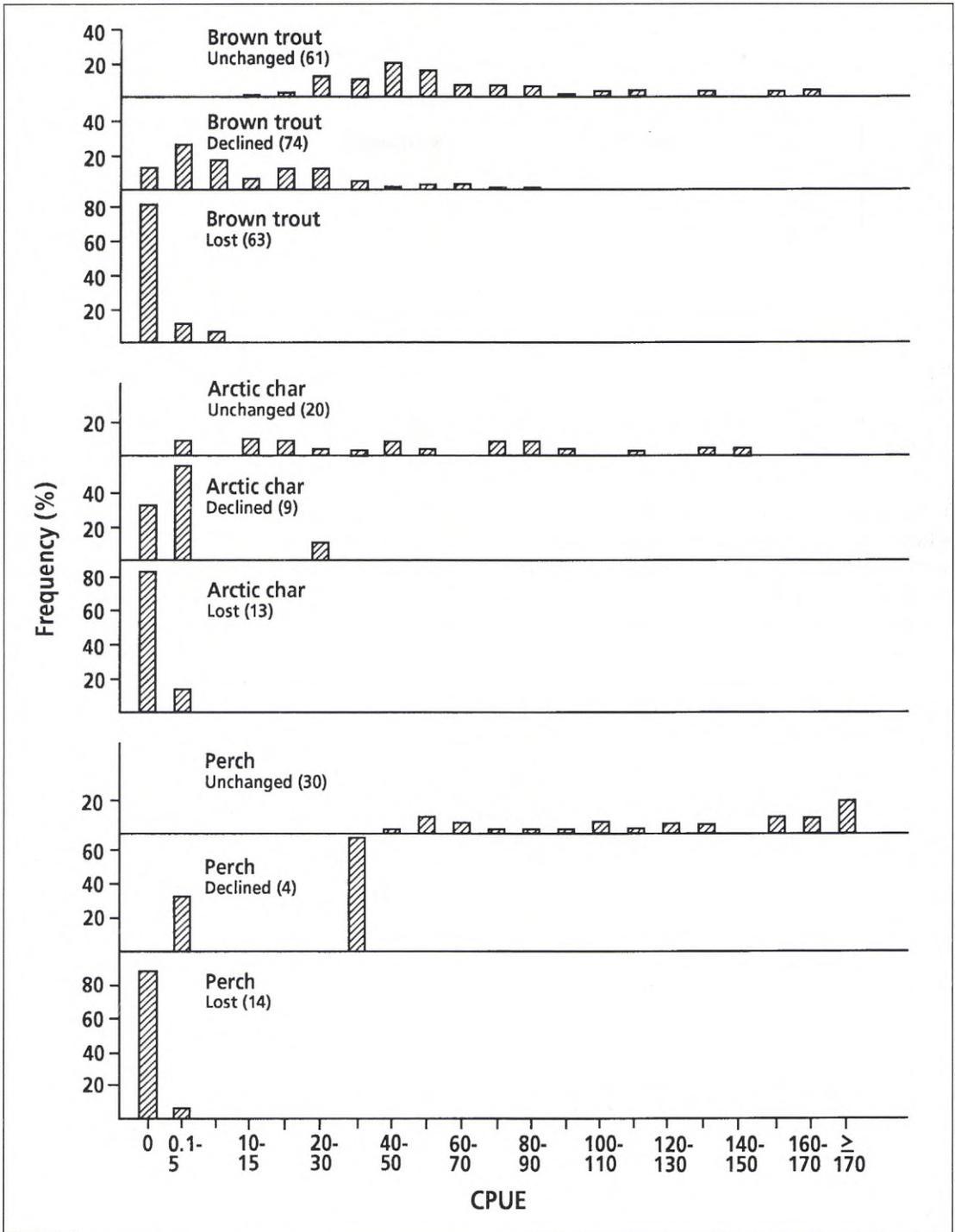


Fig. 1. Distribution (%) of CPUE for brown trout, Arctic char and perch for unchanged, declined and lost stocks. Number of stocks in parenthesis.

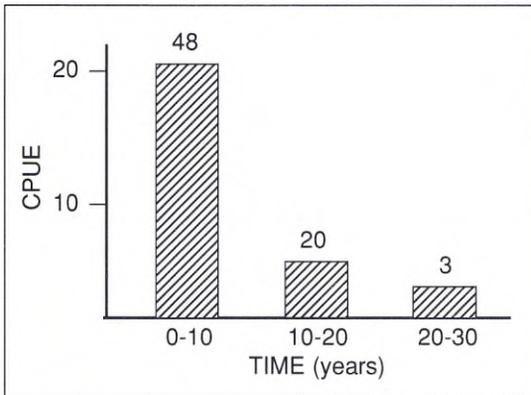


Fig. 2. CPUE of brown trout stocks reported to have declined between 0-10, 10-20 and 20-30 years. Number of stocks in each category are indicated above each column.

between 10-20 years ($Z=-4.24, P<0.0001$). A significant difference was not found for stocks which have declined for 10-20 years versus 20-30 years ($Z=-0.19, P>0.05$). Most populations in decline for 20-30 years were effectively extinct. In most stocks of brown trout, Arctic char and perch,

which were classified as lost, the test-fishing yielded no fish (83-93%). In four lakes which had lost their fish stocks, no data on time of disappearance were available.

A discriminant analysis showed that the predicted status membership was good for stocks reported as unchanged (60.0 to 76.9%) and very high for stocks reported as lost (98.4 to 100.0%), Table 3. However, a relatively small fraction of stocks reported as reduced were assigned correctly (33.3 to 50.0%), and most of these stocks were identified as lost.

The mean weight of brown trout from stocks reported as unchanged was significantly lower than that from stocks in decline ($P<0.05$, Table 4). A corresponding difference was found between fish in declining stocks and those in stocks reported to be extinct, but where fish were found during the test fishing (ANOVA, $P<0.05$). For Arctic char, a similar and significant difference in mean weight was found between stocks reported as unchanged and reduced only ($P<0.05$). Among perch, no such statistical analysis could be done because the sample size was insufficient.

Table 3. Predicted group membership of different fish status categories of brown trout, Arctic char and perch based on a discriminant analysis. N = number of stocks.

Species	N	Group	Correctly classified	Predicted group membership (%)		
				Unchanged	Reduced	Lost
Brown trout	61	Unchanged	68.2	72.1	27.9	0.0
	74	Reduced		9.5	39.2	51.4
	63	Lost		0.0	1.6	98.4
Arctic char	20	Unchanged	66.7	60.0	35.0	5.0
	9	Reduced		0.0	33.3	66.7
	13	Lost		0.0	0.0	100.0
Perch	30	Unchanged	81.3	76.9	23.3	0.0
	4	Reduced		0.0	50.0	50.0
	14	Lost		0.0	0.0	100.0

Table 4. Mean weight (g) and standard deviation ($\bar{x} \pm SD$) for different fish species and status categories. N = number of stocks.

Reported status	Brown trout		Arctic char		Perch		Whitefish		Brook trout	
	$\bar{x} \pm SD$	N								
Unchanged	91 ± 36	61	61 ± 35	20	53 ± 30	27			153 ± 44	6
Reduced	191 ± 198	61	289 ± 132	2	222 ± 169	4	357 ± 129	12		
Extinct	345 ± 288	11	148 ± 0	1	230 ± 0	1				
Naturally sparse	227 ± 137	10	148 ± 168	4	50 ± 13	5			186 ± 121	17
Stocked fish only	82 ± 46	3								

Discussion

There was a generally good agreement between reported fish status and CPUE. The interview method also provided historical data about fish stocks which had disappeared or were not obtained in the catches. Reliable data on fish status in lakes in southern Norway is available for at least two reasons. Firstly, a large number of Norwegian lakes are privately owned, and thus well protected. In spite of this, Norwegian citizens are allowed to fish at many of these localities. The rest of the land area is owned by the state or rural communities, where all citizens are allowed to fish. Secondly, there is a long tradition and keen interest in exploiting inland fish stocks in Norway. However, it is more difficult to obtain information about fish stocks in areas such as in Finnmark county in Northern Norway (Henriksen et al. 1989b), where a large number of lakes are rarely exploited.

There was considerable variation in CPUE within each status category. Affected stocks are in various stages of reduction and local extinction, and CPUE varies according to the stage reached. Apart from actual status-related variation in CPUE, there may also be some catch variability due to the sampling method. Firstly, most lakes included in this study were mainly test-fished once. It is well known that biotic and abiotic factors can cause temporal variation in the fishing success of passive fishing gear like gillnets (Lagler 1971). Secondly, variation in CPUE can be related to morphoedaphic factors in the lake (Ryder 1982) or numbers of coexisting species (Nyberg et al. 1986, Degerman et al. 1992).

There may also be other shortcomings of using gillnets to evaluate population responses to acidification. This is illustrated by the connection between CPUE and the time elapsed from the onset of decline to the date of the inquiry; a population may decline for 20-30 years before it becomes effectively extinct (Fig. 2). In cases of rapid population decline, there may be large discrepancies between reported fish status and CPUE. In most cases, a rapid change in population abundance is related to episodes of massive fish kills, mainly of adult, pre- and postspawners. There are examples that it took less than 10 years from the first noticed fish kill until the lake was completely barren. This was the case for brown trout in Lake Tveitvatn in southernmost Norway, where the first major fish kill was observed during the snowmelt in 1975 (Muniz et al. 1975, Leivestad and Muniz 1976). The first population response was juvenilization, and later recruitment failure, resulting in a barren lake by 1982 (Rosseland et al. 1980, SFT 1984).

In a population which is originally short-lived with rapid growth and access to good spawning areas, new recruits might within a few years compensate for a single episode of fish kill. Hence, the resultant juvenilization of the population should only be temporary. If no population data other than CPUE from gillnets are available, such episodes would rarely be detected. Also, if the primary population response is reproductive failure caused by mortality of embryos in spawning areas, the time-lag between the juvenile stage and catchable size will always delay information on population decline obtained through gillnetting. In cases where

fish experience slower growth and reach catchable size at an older age, such as in mountain lakes, there might be a considerable delay before any damage becomes evident.

We suggest therefore that fish status information obtained through interviews is biased because of a time-lag between when the damage actually starts and the time it becomes evident to local fishermen. Hence, the reported fish status for damaged stocks tends to be too optimistic. This was evident for stocks reported as declining, as indicated by the discriminant analysis which classified a high fraction of these stocks as lost. Another difficulty of reported status exists for stocks which are in an early phase of decline because there might be an increase in size and condition of the fish. This may result in higher catches in gillnet mesh sizes which are commonly used by anglers, and thus status may be evaluated over-optimistically. Fish stockings might to some extent also be carried out in affected lakes, masking some changes in population abundance. However, many of these stockings are difficult to trace.

In our test fishing study, changes in population characteristics during acidification became evident not only through a reduction in abundance, but also through a higher mean weight compared to unaffected stocks. This is probably because the main population response to acidification is ageing; the failure of recruitment of new age-classes into the population (Rosseland et al. 1980, Harvey 1982). The decline in population size may also cause increased growth and improvement of condition of survivors (Beamish and Harvey 1972). Larger body size of brown trout in affected stocks is consistent with an increase in weight of this species from the acidified Loch Doon in Scotland, which coincided with a decrease in CPUE (Maitland et al. 1991). During the same period, the mean size of adult Arctic char in this lake has also increased significantly. Typically, Arctic char populations in some acidic lakes in southwestern Norway were characterized by a predominance of old fish (Andersen et al. 1984).

Natural fluctuations in abundance and age class strength, which are typical for perch stocks (Thorpe 1977), might also cause discrepancies between reported fish status and CPUE. In a regional study

of population characteristics of perch in some Norwegian lakes, we obtained a high CPUE in a naturally sparse stock due to a high number of recruits (Hesthagen et al. 1992). Such changes in population structure are rarely detected by local fishermen.

Some lakes which were reported as empty still supported fish. However, the number of fish left in these lakes was too low for practical sport-fishing purposes (Rosseland et al. 1980). Because we use gillnets of different mesh sizes in our test-fishing programme, we have a higher probability of catching fish belonging to size-groups that ordinary fishermen never would have caught.

We suggest that interviews is a useful tool to assess the preceiving fish status in Norwegian lakes. However, the discriminant analysis showed that the accuracy with which actual status can be predicted from interviews were not satisfactory compared to test fishing results for stocks reported as reduced. Because a dominant fraction of these stocks were assigned as lost, fish status based on the interview method actually implies an underestimation of the damages caused by acidification. Despite certain shortcomings of our test fishing studies, the method seems generally to give reliable data on fish status.

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Liming of a Swedish River: Effects on Atlantic Salmon (*Salmo salar*)

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Abstract

This investigation describes the long-term effects of wetland liming of catchment areas in Mörrumsån, a river in southeast Sweden. Feral parr of Atlantic salmon were collected from three localities in the River Mörrumsån and in two tributary brooks. Aluminium concentrations in the gills and liver, plasma electrolytes and gill morphology were analysed before and after liming. Liming resulted in long-term increases in pH, alkalinity and hardness in tributary brooks, and in reduced concentrations of different aluminium fractions. Atlantic salmon restocked in these still relatively acidic, aluminium-rich brooks were characterized by gill lesions and plasma electrolyte depletion, reflecting acid/aluminium stress. In the River Mörrumsån, an increased density of 0+ was recorded, indicating that living conditions had improved. Furthermore, the Atlantic salmon there were characterized by nearly normal gill morphology and decreasing hepatic aluminium level.

Keywords: liming, Atlantic salmon, acidification, Al accumulation, gill morphology.

Introduction

About 20% (16,000) of all lakes in Sweden, are severely acidified (Bernes and Thörnelöf 1990). Liming has been conducted over the last few decades in thousands of Swedish lakes and rivers. The various types of liming treatments made have all aimed at restoring water parameters such as pH, alkalinity and hardness (Nyberg and Thörnelöf 1988).

The River Mörrumsån, one of the most important salmon rivers in Sweden, has been exposed to acid rain for many years (Miljödepartementet 1990). Many small tributary brooks that had pre-

viously been important habitats for spawning and early development of different fish species have been abandoned. In addition to the direct effects on these habitats caused by the infiltration of acidic, metal-rich water, the water quality in the main stream is also affected since it receives water from the large number of acidic brooks. There have been numerous reports that elevated concentrations of metals in acidic fresh waters, leached out from sediments and soils, may contribute to ill health and mortality in fish (Leivestad and Muniz 1976, Karlsson-Norrgren et al. 1986a, Ingersoll et al. 1990). Metals such as Al, Cd, Mn and Zn can be mobilized from surface sediments of aquatic sys-

tems, and elevated concentrations can readily be attained in acidified waters (LaZerte 1986). Acidic waters in Europe and North America, besides having high metal concentrations, are also characterized by low concentrations of calcium. The liming of acidic waters is often accomplished by adding mineral lime (CaCO_3), which increases both alkalinity and hardness (Raddum et al. 1986). However, a rapid change in water quality owing directly to liming activities or to the mixing of limed streams with unlimed acidic ones can result in extremely toxic conditions (Rosseland et al. 1992).

In the lower part of River Mörrumsån is a fish farm producing Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) located. During the early 1980s high mortality was recorded in the fish farm. This loss of fish interfered partly with the salmon compensatory programme for the Baltic Sea. As a result liming operations were suggested and an investigation of water quality and fish health was conducted in the River Mörrumsån area before and after the liming of wetland catchment areas. This paper focuses mainly on the post-

liming period, considering aspects such as water quality, fish population density and the long-term impact of liming on wild and farmed Atlantic salmon.

Materials and methods

Investigated area and liming operations

The area of the River Mörrumsån under investigation is located in Blekinge, in the southeast part of Sweden. Fig. 1 shows the general outline of the river, the location of the fish farm and the areas where water and fish were sampled. Liming was started in February 1988, and a total of 6,500 tons of mineral lime (CaCO_3 , MgCO_3) was spread by helicopter over the catchment areas of the tributaries.

Study sites

Wild Atlantic salmon from the River Mörrumsån were caught by electrofishing upstream at Hovmansbygd, in the central part at Åkeholm and downstream at Mörrum. Fish were also collected in Gängelbäcken and Bjällerbäcken. These two small brooks, severely affected by acidification, were restocked with Atlantic salmon fry. Farmed Atlantic salmon were collected at the fish farm, which is located at Mörrum approximately 5 km upstream from the river mouth in the Baltic Sea (Fig. 1).

Water analysis

Water samples from Paradiset, Mörrum, Gängelbäcken and Bjällerbäcken (Fig. 1) were analysed according to Swedish Standards Institution (SSI). Temperature, alkalinity (SS028139), calcium and magnesium (SS028121-2), colour (SS028124-2), conductivity (SS028123), Fe (SS028152), Mn (SS028157), Zn and Cd (SS028183) and pH (SS028122-2) were determined every month during the study period from 1987-90. In addition, total Al, filterable Al and non-labile Al were determined (SS028141). The filterable Al fraction was determined after passing the water through a 0.45- μm Millipore filter. The non-labile Al frac-

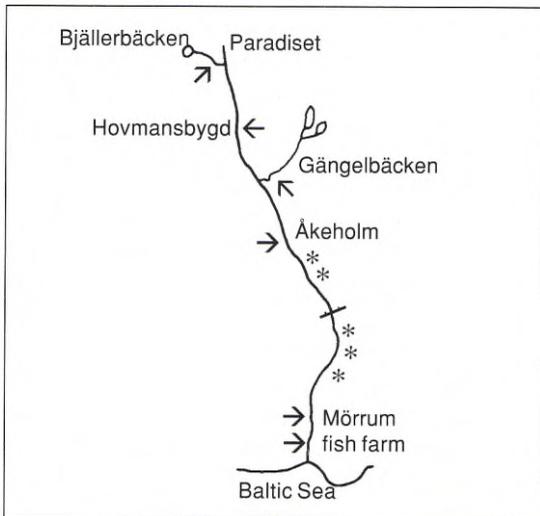


Fig. 1. Map of the River Mörrumsån showing sites at which water and wild fish were sampled. Arrows indicate areas where feral Atlantic salmon were caught. Asterisks show areas where population density was estimated. The location of the hydropower station is indicated by a bar.

tion was analysed after passing the filterable Al fraction through a cation-exchange column (prepared with Na^+). The reactive Al fraction, which is trapped in the column, was calculated as the difference between the filterable and the non-labile Al fractions. Al was assayed by the catechol-violet method (Dougan and Wilson 1974).

Fish studies

Sampling

Atlantic salmon were caught in September 1987, in April and September of 1988, 1989 and 1990. The fish were transported live, in oxygenated water from the sampling area, to a regional laboratory. Within 2 h after capture all fish were sampled and dissected.

Blood and plasma analyses

Blood samples were taken in a heparinized syringe (ammonium heparin, SIGMA) by blind puncture of the caudal vein, to determine hematocrit (Ht) and plasma levels of Na^+ , Cl^- and Ca^{2+} . Na^+ was measured photometrically (Corning), Ca^{2+} concentrations by atomic absorption spectrophotometry (Perkin-Elmer 460) and Cl^- by titration (Radiometer CMT10).

Tissue Al analysis

To measure the Al content of the tissues, gill and liver were dissolved in concentrated HNO_3 followed by H_2O_2 at 110 °C. The analysis was performed using plasma emission spectrophotometry (SpectraSpan IIIA).

Morphological studies

Gills were dissected from freshly killed fish. The specimens were fixed in either phosphate-buffered formalin, for light microscopy (LM), or in a mixture of 1.5% glutaraldehyde and 1.5% paraformaldehyde in 0.1M phosphate buffer (pH 7.4) for transmission and scanning electron microscopy (TEM and SEM). Tissues for LM were processed and embedded in paraffin. The sections were stained with eosin-haematoxylin for structural studies. Al precipitates were disclosed histochemically, by exposing paraffin sections to 1% aqueous solu-

chrome azurine solution (Denton et al. 1984) at pH 5.2 for 4 h. Specimens for TEM were postfixed in phosphate-buffered, 1% OsO_4 , dehydrated in a graded series of ethanol, passed through propylene oxide and embedded in Epon. Ultrathin sections were cut, double-stained with uranyl acetate and lead citrate and examined in a Philips TEM 420.

Tissues for SEM were treated in the same way as for TEM up to the absolute ethanol stage. They were then passed through Freon TF, which served as an intermediate fluid, and critical point dried using liquid CO_2 as the transitional fluid. After drying, the specimens were mounted on stubs with colloidal graphite paste (Leit-C), coated with gold-palladium in a sputter coater and examined in a JEOL SEM 840.

Population density of juvenile Atlantic salmon

Both Atlantic salmon and brown trout spawn in the river. However, the Atlantic salmon predominates among the juvenile fish. Electrofishing was performed at five sites along the River Mörrumsån to estimate the population density of juvenile Atlantic salmon. Two of the sites were located upstream from a hydropower station and the other three downstream, as shown in Fig. 1. All localities are known to be high productive areas where natural spawning takes place. Each site encompasses an area of 160 to 350 m^2 . The density of juvenile Atlantic salmon in each site was estimated by making three removals and applying calculations from a maximum-likelihood method. Separate estimates were made for 0+ and $\geq 1+$. Each site was investigated yearly in September from 1984 to 1991, except in 1987 and 1988 when population density estimates were impossible because the river flooded. In this paper results from the 1984-86 are compared with those from 1989-91, i.e. a three-year period before liming and a corresponding period after liming.

Results

Water analysis

The results of the water analysis are presented in Tables 1 and 2, and in Fig. 2.

Pre-liming period

The pH in the River Mörrumsån, both upstream at Paradiset and downstream at Mörrum, has been nearly constant throughout the years. The lowest levels, around pH 6, were registered during spring, while higher levels, around pH 7, occurred during the autumn. The hardness of the water was approximately 0.5 meqv/l, the mean alkalinity 0.11 meqv/l and the mean conductivity 11.0 mS/m³. The mean pH in Gängelbäcken and Bjällerbäcken before liming was 5.6 and 5.5, respectively.

Post-liming period

Liming was started in February 1988. Over the following year, the mean filterable Al concentra-

tion increased from 38±17 to 86±44 µg/l at Paradiset and from 54±31 to 95±45 µg/l at Mörrum. However, the reactive Al concentration did not change. During 1989 and 1990, the filterable Al concentrations were in the range observed before liming. No change in hardness was recorded.

The pH in Gängelbäcken and Bjällerbäcken ranged from 7 to 8 and from 6 to 6.5, respectively, during 1988-90. The mean filterable and reactive Al concentrations in Gängelbäcken were reduced from 349±54 to 239±89 µg/l (32% reduction) and from 61±52 to 24±9 µg/l (60% reduction), respectively, the first year after liming. During the following years both mean filterable and reactive Al concentrations decreased, with the mean values for 1990 being 141±62 and 11±10 µgAl/l, respectively. The mean filterable Al concentration in Bjällerbäcken did not change during the first year after liming. However, the mean reactive Al concentration decreased from 55±39 µg/l to 22±14 µg/l (40% reduction). During 1989 and 1990, there were also reductions in filterable Al concentrations.

Table 1. Water parameters measured before and after liming. Mean values and standard deviation. NS=not significant from the preliming period, * $P<0.05$, ** $P<0.01$, *** $P<0.001$, $N=10-12$.

		pH	Alkalinity meqv/l	Colour mgPt/l	Mg meqv/l	Ca meqv/l	Conductivity mS/m ³
Paradiset							
before liming	1987	6.6±0.22	0.11±0.01	35±6.2	0.17±0.01	0.36±0.03	11.0±0.7
after liming	1988	6.6±0.14NS	0.10±0.02*	59±14***	0.17±0.03NS	0.33±0.02*	9.5±0.2***
after liming	1989	6.7±0.10*	0.12±0.03*	49±18NS	0.17±0.02NS	0.35±0.03NS	9.5±0.4***
after liming	1990	6.7±0.09NS	0.12±0.02NS	33±10NS	0.17±0.04NS	0.36±0.03NS	10.2±0.3**
Mörrum							
before liming	1987	6.8±0.18	0.11±0.01	39±8	0.17±0.02	0.37±0.02	11.0±0.6
after liming	1988	6.8±0.19NS	0.10±0.02NS	66±13***	0.17±0.02NS	0.34±0.02*	9.5±0.2***
after liming	1989	6.9±0.20**	0.13±0.02***	51±20NS	0.16±0.02NS	0.36±0.03NS	9.7±0.5***
after liming	1990	6.9±0.12**	0.12±0.02*	34±7NS	0.16±0.02NS	0.37±0.02NS	10.4±0.3**
Gängelbäcken							
before liming	1987	5.6±0.39	0.02±0.02	169±49	0.15±0.02	0.25±0.04	7.8±0.7
after liming	1988	7.1±0.58***	0.54±0.47**	233±99*	0.22±0.06***	0.74±0.42**	11.7±4.0**
after liming	1989	6.8±0.21***	0.25±0.16***	133±46NS	0.18±0.03*	0.43±0.09***	9.1±1.1**
after liming	1990	6.8±0.22***	0.24±0.16**	86±15**	0.18±0.02***	0.46±0.08***	10.0±0.8***
Bjällerbäcken							
before liming	1987	5.5±0.36	0.03±0.02	197±57	0.16±0.02	0.27±0.04	8.6±1.1
after liming	1988	6.1±0.22***	0.09±0.05***	282±131**	0.18±0.03*	0.31±0.05**	7.9±0.7**
after liming	1989	6.2±0.23***	0.10±0.05***	179±42NS	0.17±0.04NS	0.34±0.06*	9.5±1.9NS
after liming	1990	6.0±0.35***	0.09±0.08**	125±27**	0.19±0.03**	0.36±0.05**	10.5±1.3**

Table 2. Metal concentrations in water measured before and after liming. Mean values and standard deviation. NS=not significant from the preliming period. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $N = 10-12$.

	Total Al µg/l	Filterable Al µg/l	Reactive Al µg/l	Al Fe mg/l	Mn mg/l	Zn µg/l	Cd µg/l
Paradiset							
before liming 1987	53±28	38±17	8±4	184±62	71±34	2.5±1.9	0.0098±0.0041
after liming 1988	106±47*	86±44**	12±12NS	353±111**	89±64NS	3.8±2.3*	0.0168±0.0081**
after liming 1989	71±34NS	48±33NS	8±7NS	262±148NS	79±66NS	2.5±1.3NS	0.0135±0.0061NS
after liming 1990	75±28NS	36±15NS	7±4NS	219±55NS	98±71NS	2.0±0.7NS	0.0130±0.0049*
Mörtrum							
before liming 1987	84±25	54±31	7±7	250±92	82±41	3.4±1.7	0.0108±0.0024
after liming 1988	131±52NS	95±45*	5±5NS	376±104*	70±32NS	3.6±2.2NS	0.0173±0.0070*
after liming 1989	89±33NS	57±29NS	4±2NS	280±155NS	53±20NS	2.5±1.2NS	0.0133±0.0039NS
after liming 1990	80±29NS	45±18NS	7±6NS	183±60*	61±24NS	2.5±1.0NS	0.0138±0.0064NS
Gängelbäcken							
before liming 1987	402±53	349±54	61±52	1440±544	105±63	7.2±3.3	0.0300±0.0197
after liming 1988	281±111NS	239±89**	24±9*	1310±1310NS	77±50NS	4.7±2.8*	0.0225±0.0057NS
after liming 1989	218±108***	190±84***	13±8**	818±404**	44±27*	4.1±2.8***	0.0153±0.0042NS
after liming 1990	176±60**	141±62***	11±10**	540±91***	24±17**	3.8±1.5**	0.0137±0.0035NS
Bjällerbäcken							
before liming 1987	754±138	474±128	55±39	2060±830	105±29	16.6±8.3	0.0437±0.0146
after liming 1988	592±185NS	454±115NS	22±14*	2350±1770NS	102±43NS	10.9±5.9**	0.0384±0.0081NS
after liming 1989	375±73***	259±104***	22±12*	2190±805NS	97±34NS	12.9±4.5NS	0.0400±0.0082NS
after liming 1990	388±120***	280±141**	39±35NS	1610±875NS	111±37NS	15.8±9.8NS	0.0493±0.0176NS

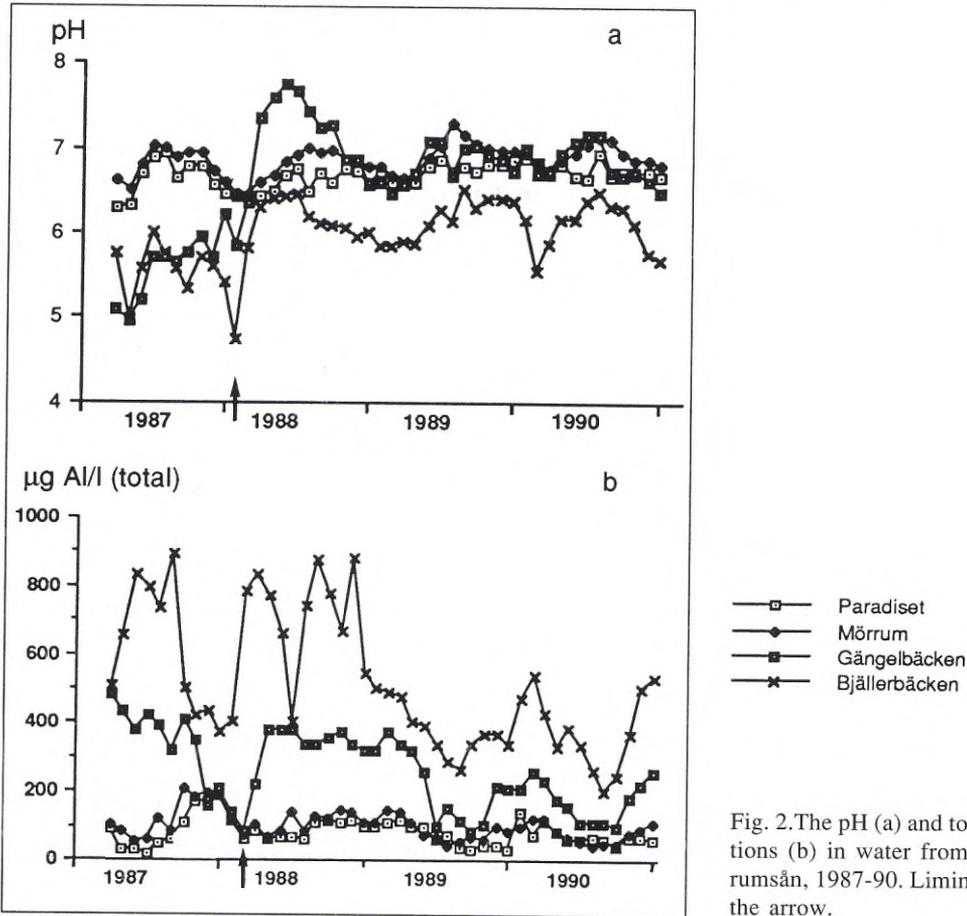


Fig. 2. The pH (a) and total Al concentrations (b) in water from the River Mörrumsån, 1987-90. Liming is indicated by the arrow.

Population density

The population density of young Atlantic salmon was found to be high in all five investigated areas, i.e. 75 and 300 individuals per 100 m². The density of 0+ fish increased over the three-year period after liming, reaching levels higher than those observed during the three years before liming. The increase, which was statistically significant, was found in all five sites. No significant change in the density of Atlantic salmon $\geq 1+$ was noted (Table 3).

Al concentrations in tissues

Pre-liming period

The mean Al concentrations in gill and liver of Atlantic salmon before liming are presented in

Fig. 3a and b. Mean Al concentrations in liver were generally higher than in gill. No fish were caught in Gängelbäcken or Bjällerbäcken before liming.

Post-liming period

Mean Al concentrations in tissues from farmed Atlantic salmon were not affected by liming, with values ranging from 3 to 10 $\mu\text{g/g}$ in gill (Fig. 3a) and 0.4 to 6 $\mu\text{g/g}$ in liver (Fig. 3b).

After liming, mean Al concentrations in gill increased in fish caught in the River Mörrumsån. This increase was especially pronounced at Mörrum, where salmon contained mean concentrations of between 15 and 75 $\mu\text{gAl/g}$. Corresponding values upstream at Hovmansbygd were 9-28 $\mu\text{g Al/g}$. The concentration of Al in liver tended to

Table 3. Mean population densities during 3 year periods of Atlantic salmon before and after liming.

Site	Period	Population density of Atlantic salmon				
		Area(m ²)	0+	SD	≥1+ SD	
Upstream power station	1984-86	510	14	20	7	6
Upstream power station	1989-91	510	72	40 *	9	3
Downstream power station	1984-86	615	88	32	36	14
Downstream power station	1989-91	615	191	55 *	36	15

decrease after liming, with mean levels at Hovmansbygd, Åkeholm and Mörrum ranging from 5-12, 4-21 and 2-16 $\mu\text{g Al/g}$, respectively.

Tissues from fish caught in Gängelbäcken and Bjällerbäcken contained relatively high concentrations of Al. Mean concentrations in gill were 21-60 $\mu\text{g Al/g}$ and 45-119 $\mu\text{g Al/g}$, respectively, while concentrations in liver were 14-42 $\mu\text{g Al/g}$ and 20-41 $\mu\text{g Al/g}$.

Blood and plasma analyses

Pre-liming period

Before liming, blood analyses were conducted only on fish from the River Mörrumsån. The mean concentrations of electrolytes in plasma from farmed Atlantic salmon were 155 mmol Na⁺/l (Fig. 4a), 131 mmol Cl⁻/l (Fig. 4b) and 2.8 mmol Ca²⁺/l, and the mean hematocrit was 40%. Corresponding values for feral fish from the River Mörrumsån were not significantly different from values recorded for the farmed salmon.

Post-liming period

The mean concentration of sodium and chloride in plasma from farmed salmon was similar to that measured during the pre-liming period. In September 1988, the mean concentration of sodium in plasma from fish caught in Gängelbäcken and Bjällerbäcken was 149 mM/l and 142 mM/l, respectively. Corresponding values for chloride were 114 mM/l, at both localities. In September 1988, values for feral Atlantic salmon caught at Åkeholm and Mörrum differed significantly from those of the farmed fish (Figs. 4a and 4b). In April 1989,

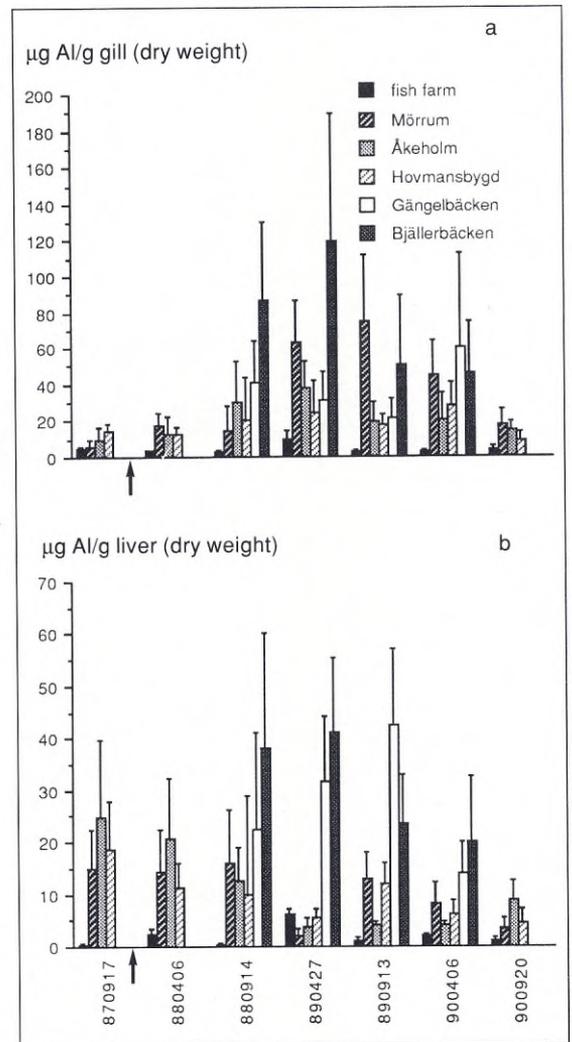


Fig. 3. The Al concentrations in gill (a) and liver (b) of Atlantic salmon. Liming is indicated by the arrow.

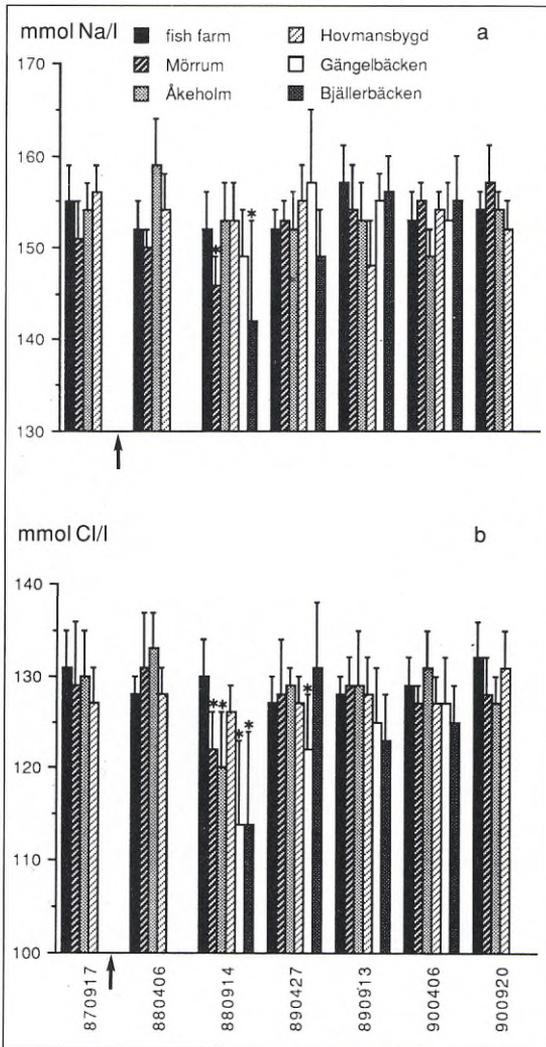


Fig. 4. Sodium (a) and chloride (b) levels in plasma from Atlantic salmon. Liming is indicated by the arrow, and significant differences between Atlantic salmon in the fish farm and feral Atlantic salmon are indicated by an asterisk ($P < 0.05$).

the chloride concentration in plasma from fish in Gängelbäcken was significantly lower compared with the level in farmed Atlantic salmon. Later during the investigation, no significant differences were recorded over time or between sampling points.

Morphological studies

Pre-liming period

In morphological studies of gills from wild Atlantic salmon caught before liming various types of lesions were found. Gills from salmon caught at Åkeholm and Mörrum exhibited different kinds of pathological alterations, the most dramatic being a total collapse of the pillar cell system (Fig. 5). Intensive mucus accumulation on the gill surface and fusion between neighbouring secondary lamellae were frequently observed (Fig. 6). Farmed Atlantic salmon were infected with encysted, tennis-racket-shaped parasites. Some wild fish were heavily infected with protozoan parasites, classified as *Trichophyra* spp, and monogean trematodes.

Post-liming period

In April 1988, Atlantic salmon caught at Hovmansbygd had normal gills, which were characterized by well separated secondary lamellae (Fig. 7). The apical plasma membrane of the epithelial cells was folded so as to form a micro-ridge pattern and was free from excess mucus. Atlantic salmon caught at Åkeholm and Mörrum showed pathological alterations, including fused secondary lamellae (Fig. 8) and chloride cell hyperplasia. Chloride cells were present not only in the primary epithelium but also in the secondary lamellar epithelium where the respiratory cells had been replaced by chloride cells (Fig. 9).

In September 1988, Atlantic salmon restocked in Gängelbäcken had gills characterized by chloride cell hyperplasia, with the electron-dense precipitates in close association with the plasma membrane. In contrast to gills from fish caught in the River Mörrumsån, the gills of Atlantic salmon caught in Bjällerbäcken were heterogeneous in structure; some were nearly normal whereas others showed severe lesions characterized by necrotic epithelial cells and numerous mitotic figures in the primary lamellar epithelium (Fig. 10). The epithelial plasma membrane was often coated with mucus droplets. Electron-dense precipitates within the epithelial cells and/or on the surface of the plasma membrane (Fig. 11), identical to the precipitates

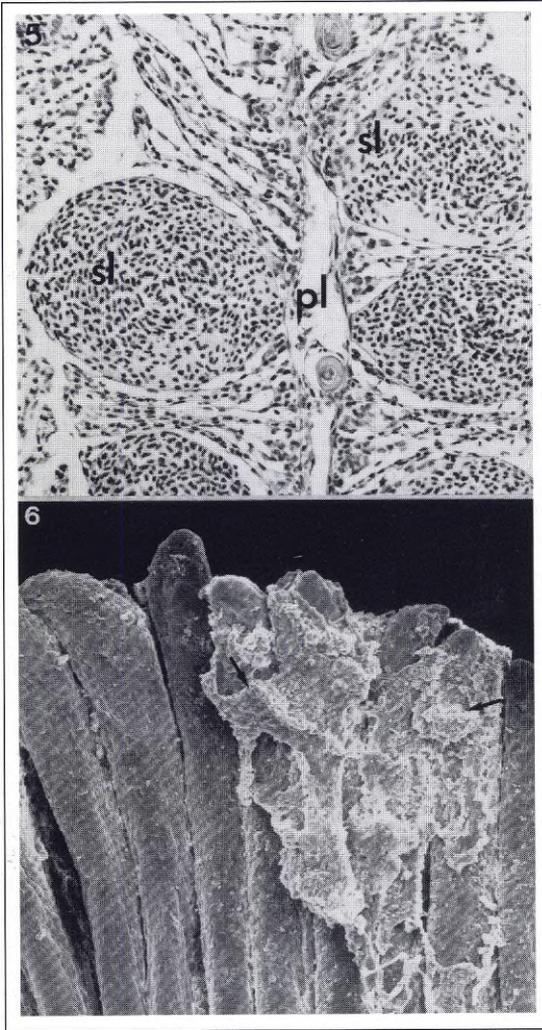


Fig. 5. Light micrograph (LM) of a gill from an Atlantic salmon caught at Åkeholm before liming. The secondary lamellae have collapsed (sl). (900x)

Fig. 6. Scanning electron microscopy (SEM) micrograph of a gill from an Atlantic salmon caught at Åkeholm before liming. Note fused secondary lamellae and intensive mucus secretion (arrow). (200x, pl=primary lamella)

observed on the gills of Atlantic salmon caught in Gängelbäcken, were also observed on the gills of fish caught in Bjällerbäcken.

Fish caught in Mörrumsån, Gängelbäcken and Bjällerbäcken differed in terms of the structure of the secondary lamellar epithelium. The Mörrumsån salmon exhibited secondary lamellae with a thin epithelial sheet and with a short diffusion distance between water and blood (Fig. 12). The secondary lamellar epithelium in the gills of fish caught in Gängelbäcken were characterized by a large number of chloride cells interposed within the secondary lamellar epithelium (Fig. 13). Gills

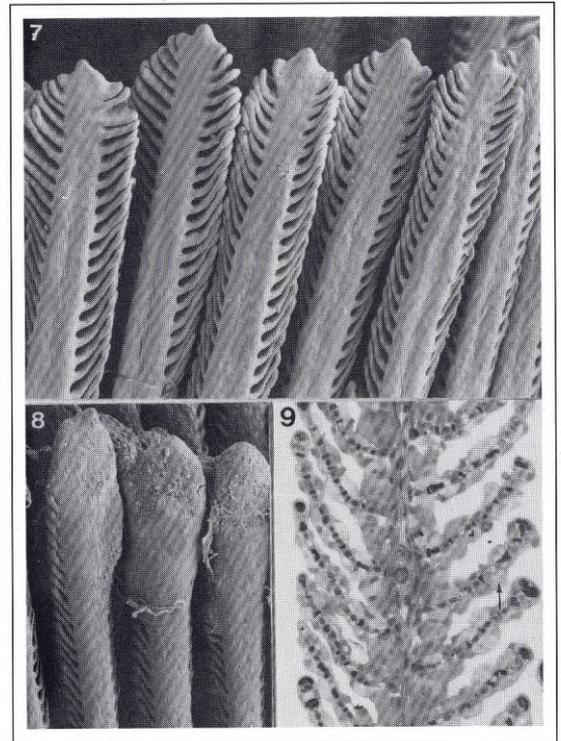


Fig. 7. SEM micrograph of a gill from an Atlantic salmon caught at Hovmansbygd after liming. (200x)

Fig. 8. SEM micrograph of a gill from an Atlantic salmon caught at Åkeholm after liming. Neighbouring secondary lamellae fused together (arrow). (200x)

Fig. 9. LM photograph of chloride cell hyperplasia (arrow) in a gill from an Atlantic salmon caught at Åkeholm after liming. Note the frequent number of chloride cells in the secondary lamellar epithelium. (400x)

from fish caught in Bjällerbäcken were dominated by large lymphatic spaces within the secondary lamellar epithelium and degenerating cells (Fig. 14).

Gills from Atlantic salmon caught in Gängelbäcken and Bjällerbäcken gave a positive staining reaction with solochrome azurine, indicating the

presence of Al precipitates. Electron-dense precipitates in close association with the plasma membranes of epithelial cells (Fig. 11) of the gills and intracellular precipitates in the same area were analysed using an X-ray microanalytical technique (EDXA, LINK QX 200). The analysis showed that Al was the dominant element in such precipitates.

During 1989 and 1990, Atlantic salmon caught in the River Mörrumsån had a nearly normal gill structure, at all sampling points. On the other hand, the gills of some of the fish caught in Gängelbäcken and Bjällerbäcken were characterized by fused secondary lamellae and chloride cell hyperplasia.

The gills from farmed Atlantic salmon had well separated secondary lamellae and a plasma membrane with a normal mucus sheet and did not show any chloride cell proliferation. No differences in gill structure were found between farmed fish sampled before liming and those sampled afterwards.

Discussion

Salmonids are relatively sensitive to low pH and metal exposure, and in many rivers salmon populations have declined or disappeared owing to acidification (Rosseland and Henriksen 1990). Causes of extinctions and reductions in population densities due to acidification are complex. Direct effects on physiological functions (MacDonald et al. 1991, Wilson and Wood 1992) as well as effects on recruitment can be involved (Rask et al. 1990, Vuorinen and Vuorinen 1991). Before liming, Atlantic salmon were caught only in the Mörrumsån, since fish were unable to survive in Gängelbäcken or Bjällerbäcken. However, after liming, restocked Atlantic salmon were caught in both Gängelbäcken and Bjällerbäcken. This shows that liming improved the habitat enough to allowing Atlantic salmon to survive. The improvement was also reflected in the increased population densities of 0+ salmon in the Mörrumsån. This increase, which varied between 2- and 5-fold, was recorded at each of the five stations. However, the number of $\geq 1+$ was not affected, which suggest that living conditions were improved most for early life stages.

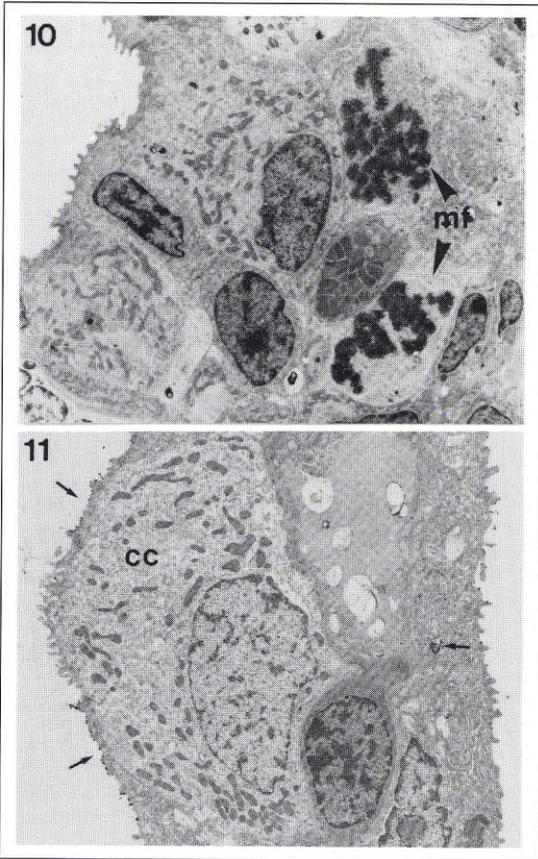


Fig. 10. Transmission electron microscopy (TEM) picture of the interlamellar space in a gill from an Atlantic salmon caught in Bjällerbäcken. Two mitotic figures (mf) can be seen. (5000x)

Fig. 11. TEM picture of a chloride cell (cc) in the secondary lamellar epithelium of a gill from a fish caught in Gängelbäcken. Note electron-dense precipitates (arrow) coating the apical plasma membrane of neighbouring epithelial cells. (5000x)

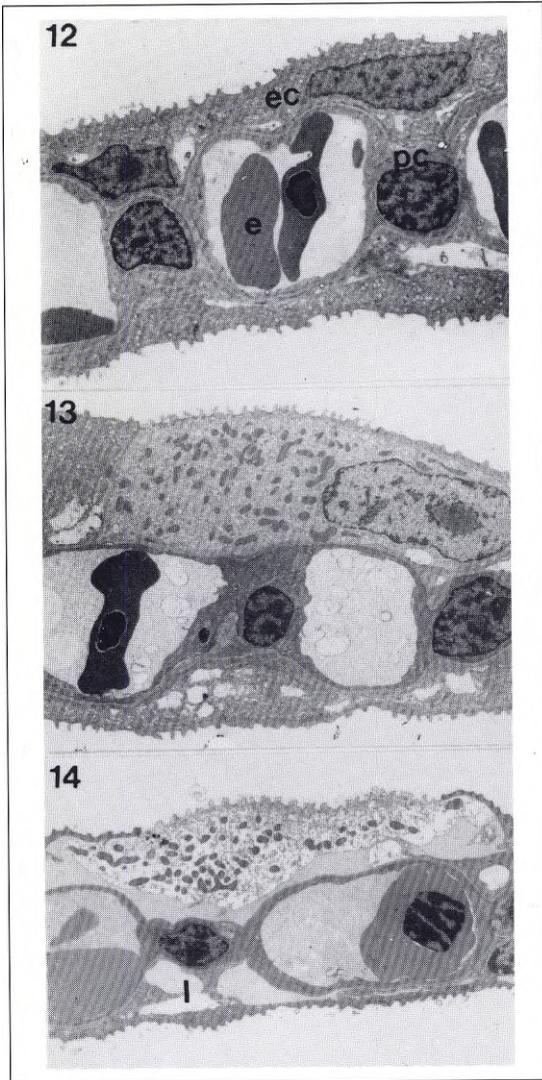


Fig. 12. TEM picture of a secondary lamella from a farmed Atlantic salmon. The epithelial cells (ec) are separated by the pillarcell (pc) system. (5000x)

Fig. 13. TEM picture of the central part of a secondary lamella in a gill from an Atlantic salmon caught in Gängelbäcken. The oedemic secondary lamellar epithelium is invaded by chloride cells. (5000x)

Fig. 14. TEM picture of the central part of a secondary lamella in a gill from an Atlantic salmon caught in Bjällerbäcken. Observe degenerating chloride cell and large lymphatic space (l). (5000x)

Populations of young salmonids vary in density between years owing to natural variation in biotic and abiotic factors. Although weather conditions and water flow may have had a positive influence on the Atlantic salmon density in the River Mörrumsån during the post-liming period, the observed increase in density cannot only be ascribed solely to this natural variation. Nor was there any change in the number of migrating adults in the area during the period. Therefore, it seems probable that the liming induced improvement in water quality, which was the most important factor explaining the observed increase in density of young Atlantic salmon. This interpretation is supported by reports that the liming of acidic waters resulted in normalized spawning behaviour in Atlantic salmon as well as increase fry survival and adult population density (Lacroix 1992, Norrgren and Degerman 1993).

Before liming, mean Al concentrations in the gills were higher in fish caught upstream in the River Mörrumsån at Hovmansbygd than in fish caught at downstream sites, whereas concentrations in the liver were similar irrespective sampling point. The filterable Al concentration in the Mörrumsån increased during the first year after liming. This was reflected in an increased mean Al concentration in the gills, especially from fish caught downstream at Mörrum. Before liming, 13-21% of the filterable Al in Mörrumsån water was present as reactive Al. By contrast, during the first year after liming, only 2-14% of the filterable Al was in reactive form. The range in the proportion of reactive Al in Bjällerbäcken and Gängelbäcken was 12-18% before liming and 5-10% afterwards. However, the mean concentrations of reactive Al in Gängelbäcken and Bjällerbäcken were still relatively high (11-39 $\mu\text{g/l}$ compared with mean levels (4-12 $\mu\text{g/l}$) in the River Mörrumsån.

Both before and after liming, the gills of wild Atlantic salmon caught in the lower part of the River Mörrumsån were occasionally characterized by chloride cell hyperplasia, an alteration described in fish experimentally exposed to acidic, Al-rich water (Leino and McCormick 1984, Karlsson-Norrgren et al. 1986a). Numerous studies have concluded that low pH in combination

with Al results in plasma electrolyte depletion owing to reduced uptake and increased leakage gill epithelia (Wood and McDonald 1987, Witters et al. 1992). In an acidic water with sublethal Al concentrations this effect may be compensated for by the increased secretion of cortisol causing chloride cell proliferation, which in turn enhances the uptake of ions from ambient water (Wendelaar Bonga and Dederen 1986). The ion-regulating chloride cell is an important target for Al (Karlsson-Norrgren et al. 1986a, Youson and Neville 1987), consequently Al may interfere with chloride-cells functioning and thereby disturb ion regulation over branchial epithelia.

Atlantic salmon from Bjällerbäcken showed individual variation in gill structure, Al concentration and plasma sodium and chloride levels. The most common types of gill lesions were areas of degenerating epithelial cells, mitotic figures and enlarged lymphatic spaces. These kinds of lesions have been reported earlier in fish characterized as showing an acute toxic response to episodic acid stress (Karlsson-Norrgren et al. 1986b, Mueller et al. 1991) and metal exposure (Tuurala and Soivio 1982, Stromberg et al. 1983). Reintroduced Atlantic salmon in Bjällerbäcken were subjected to low pH and high Al concentrations as well as synergistic/additive effects attributed to other metals, i.e. Fe, Zn and Cd, which may explain the loss of plasma electrolytes and acute gill lesions.

During the 1980s, before any liming treatments had been made occasional periods of high mortality among young Atlantic salmon in the fish farm were attributed to the acidification of the River Mörrumsån. However, in the present study, the pH of the fish farm water was between 6.5 and 7 and the mean filterable Al concentration was relatively low. In addition, the Al contents of gill and liver from farmed Atlantic salmon were low compared to those of wild fish, and the general gill structure in farmed fish was normal. Consequently, the relatively high mortality in the fish farm cannot be explained by acid stress. On the other hand, there was a high frequency of encysted parasites in the gills of farmed Atlantic salmon which should be considered. These parasites have been described as the agent causing epitheliocystis and were

isolated from rainbow trout in a hatchery where high mortality was recorded (Rourke et al. 1984).

In summary, the long-term effects of liming resulted in increased pH, alkalinity and hardness in tributary brooks, as well as to reductions in concentrations of different Al fractions. The Atlantic salmon restocked in these still relatively acidic, aluminium-rich brooks survived, but suffered from gill lesions and plasma electrolyte depletion reflecting acid/aluminium stress. In the River Mörrumsån, the population density of 0+ increased after liming, indicating improved living conditions, especially for young life stages. Furthermore, post-liming analyses of the Atlantic salmon in the Mörrumsån showed that gill morphology was nearly normal again and that hepatic Al levels had decreased.

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Predator Detection and Perception of Predation Risk in the Crayfish *Astacus astacus* L.

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Abstract

The responses of young-of-the-year crayfish *Astacus astacus* L. to chemical and visual stimuli from various predaceous fish species, from a non-predatory fish, and from adult conspecifics were examined in laboratory experiments. Chemical stimuli from the four predatory fish tested increased crayfish refuge use, while the crayfish did not respond to chemical stimuli from either the non-predatory fish or from the adult crayfish. The crayfish showed a stronger response to a starved predator than to a non-starved. Given only visual stimuli, the crayfish did not increase refuge use in response to any of the tested fish species. The results suggest that the ability of *A. astacus* to detect co-occurring predatory fish by their odour is a genetically based adaptation which enables the crayfish to minimize predation risk from fish.

Keywords: Freshwater crayfish, *Astacus astacus*, predator fish, behaviour, odour.

Introduction

Freshwater crayfish are usually the largest invertebrates in their natural environment and they often constitute a major component of the benthic biomass in lakes (Momot et al. 1978). Accordingly, crayfish are a valuable food resource for many inshore predatory fish species (Stein 1977, Gowling and Momot 1979, Dehli 1981, Quinn and Janssen 1989). While little is known about the impact of fish predation on crayfish mortality in natural populations, the behavioural responses of crayfish to avoid encounters with their predators are more well-documented. Experimental studies have demonstrated that crayfish reduce activity, and change microhabitat use by choosing the substrates affording most protection, in the presence of predatory fish (Stein and Magnuson 1976, Appelberg and Odelström 1988, Resetarits 1991, Söderbäck 1992, Blake and Hart 1993). Stein and Magnuson (1976) also showed that predatory fish reduce feeding rates of juvenile crayfish and they suggested that predators may depress crayfish

growth rates by reducing daily ration. Field observations in Swedish lakes varying in predatory fish abundance further suggest that predatory fish may negatively affect crayfish growth rate by decreasing foraging activity (Appelberg 1986).

A prerequisite for a prey organism to avoid a predator is an ability to detect the predator and gauge the predation risk before being attacked. Blake and Hart (1993) reported that juvenile *Pacifastacus leniusculus* showed a marked antipredator behaviour when exposed to visual and/or chemical stimuli from two predatory fish species. However, they did not examine the effect of stimuli from non-predatory fish species on the behaviour of the crayfish.

The purpose of the present study was to determine if the crayfish *Astacus astacus* (L.) can detect and avoid co-occurring predatory fish, and also, to examine if *A. astacus*, given only chemical cues, can gauge predation risk and adjust its behaviour in adaptive ways with varying risk. As predators, we used European eel (*Anguilla anguilla* L.) and European perch (*Perca fluviatilis* L.), known to be

important predators on crayfish in Swedish lakes (Vallin 1942, Svärdson 1972, Dehli 1981). We also tested the response to two other potential crayfish predators; northern pike (*Esox lucius* L.) and burbot (*Lota lota* L.). Adult crayfish were included as a potential predator because cannibalism has been proposed to be an important source of mortality among juvenile crayfish (Mason 1977). The responses to varying degree of predation risk were examined by including a non-predatory fish species, roach (*Rutilus rutilus* L.). Earlier field studies indicate that roach do not prey upon crayfish under natural conditions (Appelberg and Odelström 1984) and, although large roach might be able to consume juvenile crayfish, we assume that roach can be regarded mainly as a non-predator. Additionally, we also studied crayfish responses to chemical stimuli from satiated perch and from starved perch at an increased density.

Since increased refuge use is an important antipredator behaviour, we examined the changes in refuge use of young-of-the-year (YOY) *A. astacus* to chemical and visual stimuli from these predators, including adult crayfish, and from the non-predatory roach, to answer the following questions:

- 1) Do *A. astacus* use chemical and/or visual cues to detect predators?
- 2) Can *A. astacus*, given only chemical cues, gauge predation risk by distinguishing between predatory and non-predatory fish and between satiated and starved predators?

Materials and methods

The responses of YOY *A. astacus* to chemical and visual stimuli from various potential predators, and from a non-predatory fish, were studied in laboratory experiments at the Lake Erken laboratory of Uppsala University between October and March in the winters 1987/88 and 1988/89. *A. astacus* originating from two commercial hatcheries were hatched in May and were artificially reared during the summer both years. The hatchlings originated from wild-caught parents and had not been in contact with lake water or natural predators before the experiments. Crayfish, with

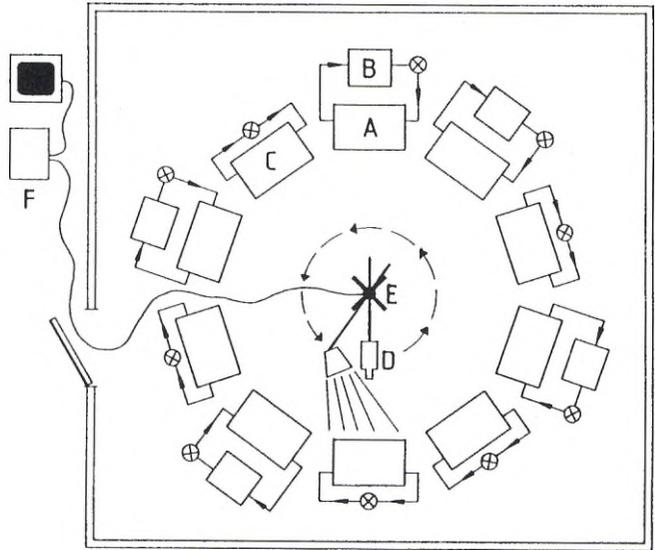
mean carapace length 12.3 mm (range 10.8-13.9 mm), were kept in tanks with recirculating water at 15 °C and fed potatoes and frozen zooplankton between experiments. Lighting regime was constantly 16 h light : 8 h dark, with light switched off at 22:00. No crayfish were used in two sequential experiments.

Perch, pike, burbot and roach (total length 150-200 mm) were collected from Lake Erken 2-3 weeks before they were used in the experiments. The eels (300-400 mm) used, originated from a commercial farm. Fish were kept in tanks with recirculating water at 15 °C and were fed commercial fish pellets. One week prior to the experiments feeding were stopped. In the experiment where the YOY crayfish response to a satiated predator was tested, five perch were fed fish pellets until the day before the start of the experiment.

The effects of chemical and visual stimuli on the YOY crayfish were tested in ten 60 l aquaria placed in a circle of 2.3 m radius. In each trial, five randomly chosen aquaria were used for treatment and the remaining five aquaria served as controls. An IR-sensitive video camera and an IR lamp, mounted on a circulating frame, were placed in the centre of the circle (Fig. 1). The bottom of each aquarium was covered with a black rubber sheet in order to increase the contrast between the crayfish and the bottom, and each aquarium was provided with 20 PVC-shelters (diameter 20 mm). Before each trial the aquaria were carefully cleaned and new water consisting of an aerated mixture of tap water and deionized water (1:1) was added. The water was recirculated separately in each aquarium.

When crayfish response to chemical cues was tested, water from each treatment aquarium was recirculated through a secondary, 30 l, aquarium containing the potential predator. The secondary aquarium was placed beside the treatment aquarium and screened off from the latter in order to exclude visual stimuli from the potential predator. When crayfish response to visual stimuli was tested, the secondary aquarium was placed in the water, about 15 cm above the bottom, in the treatment aquarium. Thereby, the potential predator was always located above the crayfish. Water was recirculated through separate systems in both

Fig. 1. Experimental setup in trials examining the response of *A. astacus* to chemical stimuli from a potential predator. Water in each treatment aquarium (A) was recirculated through a secondary aquarium (B) containing the potential predator. Water in each control aquarium (C) was recirculated in a separate system. A video camera and an IR-lamp (D), fixed on a rotating rack (E), was connected to a video recorder and a monitor (F) outside the experimental room. See text for further details.



aquaria. In all trials, temperature was kept at 16 ± 1 °C with a lighting regime of 16 h light : 8 h dark. During day, light was supplied from a 100 W bulb at the ceiling above the centre of the circle of aquaria.

Ten YOY *A. astacus* per aquarium were acclimatized to the experimental conditions for 48 h before each trial. During the acclimatization they were supplied with an excess of food (potatoes). One hour before the trial started, fish were added to the secondary aquaria and remaining food in the crayfish aquaria was removed. Each trial started at 12:00 and lasted for 24 h. To minimize the influence of behavioural differences between crayfish individuals, the trial was repeated for another 24 h. Before the start of the second 24 h period, the YOY crayfish were exchanged between treatment and control aquaria; the crayfish exposed to the tested stimuli were moved to the control aquaria, and the non-exposed crayfish were moved to the treatment aquaria. Thereafter, the experiment was run for another 24 h. Occasionally, one or two crayfish in an aquarium died during trials. These crayfish were not replaced.

Crayfish activity was monitored by video-recording the aquaria every full hour. When recording, the camera and IR-lamp were automatically

swept around the circle of the ten aquaria for about 2 minutes. After each sweep, the camera and lamp were automatically stopped for one hour, then a new sweep was done. This pattern was repeated over the two 24 h periods and, accordingly, each trial consisted of 48 separate recordings for each aquarium. After a trial, the recorded video tape was analyzed and on each recording occasion the number of exposed crayfish in each aquarium was counted. A crayfish was judged to be exposed when no part of the animal was inside a shelter.

As the results from the first and the second 24 h period within each aquarium were obtained with different groups of crayfish, the two 24 h periods were treated as independent. Thus, each trial consisted of 10 replicates of treatment and 10 control, respectively. Significant differences in crayfish exposure between the two 24 h periods were observed in 4 of the 6 trials testing crayfish response to visual stimuli, and in 2 out of the 8 trials testing the response to chemical stimuli ($P < 0.05$, Mann-Whitney U-tests performed separately for treatments and controls in light and in darkness). In all six cases where differences were obtained, the activity was slightly higher during the second 24 h period. This may possibly be attributed to an increased food search activity during the second 24 h period.

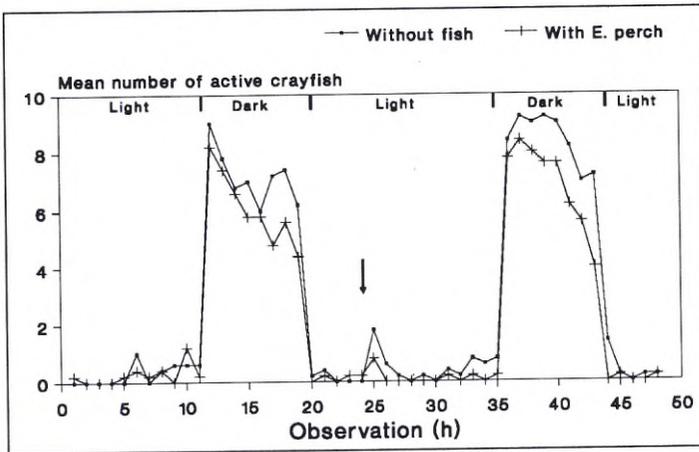


Fig. 2. Refuge use of 10 YOY *A. astacus*, during 48 h in a trial examining crayfish responses to chemical stimuli from one starved European perch. Exposed crayfish and control crayfish were shifted after 24 h (arrow). Each point represents the mean value of 5 replicates.

We calculated the mean number of exposed crayfish during the 16 h light and during the 8 h dark for each replicate. In all trials, the mean values of exposed crayfish during darkness were almost normally distributed, while the distribution of means during light conditions was strongly skewed towards zero. To test for treatment effects, we performed Mann-Whitney U-tests separately for the two light conditions in each trial testing for differences between number of exposed crayfish in treatments and controls. No correction for dead crayfish was done since it was impossible to determine when the crayfish died.

Results

Diel activity pattern

Generally, crayfish activity during the light period was low and in light the number of exposed crayfish was often independent of treatment (Fig. 2). After the initial low activity during the first light period, there was a strong activity peak just after darkness. Activity level then slowly decreased during darkness although a slight increase also could be noted before light was turned on. This pattern was repeated during the second 24 h period. The mean percentage of exposed crayfish in the control aquaria in all trials was $7\% \pm 5$ (SD) during light and $61\% \pm 11$ (SD) during darkness.

Chemical stimuli from various potential predators

We predicted that, if crayfish can detect and avoid predators by chemical stimuli, crayfish refuge use should increase when they are exposed to water conditioned by a predatory fish. A significant increase in crayfish refuge use during darkness occurred in the presence of all four predatory fish species tested (perch, pike, burbot and eel) (Table 1). During the light period, when crayfish activity was low, the mean numbers of exposed crayfish appeared lower in water conditioned by the four predatory fish species than in controls, but only the response to eel was significant.

In contrast to the experiments with predatory fish, no crayfish response was observed during darkness to water conditioned by the non-predatory roach, and in light the number of exposed crayfish was even higher in the treatment aquaria (Table 1). Neither did the crayfish respond to water conditioned by an adult conspecific. The results indicate that YOY *A. astacus*, without previous experiences of predators, can detect predatory fish, and also distinguish between predatory and non-predatory fish species, given only chemical stimuli.

Table 1. Effects of chemical and visual exposure to various potential predators on refuge use of YOY *Astacus astacus*. Mean values of number of exposed crayfish in control aquaria (n=10) and in treatment aquaria (n=10). Observations during light period (16) and dark period (8) were pooled for each aquaria.

Potential predator	Stimuli	Light				Dark			
		Control	Treatm.	Diff.	Sign.	Control	Treatm	Diff.	Sign.
E. perch	Chemo	0.23	0.21	-0.02	NS	7.30	6.14	-1.16	$P<0.001$
N. pike	Chemo	0.26	0.23	-0.03	NS	7.34	6.29	-1.05	$P<0.001$
Burbot	Chemo	1.01	0.69	-0.32	NS	5.89	5.14	-1.40	$P<0.001$
E. eel	Chemo	1.13	0.87	-0.26	$P<0.05$	5.89	4.44	-1.45	$P<0.01$
Roach	Chemo	0.42	0.82	0.40	$P<0.001$	6.81	7.01	0.20	NS
Crayfish	Chemo	0.76	0.85	0.90	NS	5.91	6.11	0.20	NS
E. perch	Visual	0.92	1.36	0.44	$P<0.001$	6.70	7.11	0.41	NS
N. pike	Visual	0.07	0.85	0.15	NS	6.10	6.69	0.59	$P<0.05$
Burbot	Visual	2.17	2.16	-0.01	NS	3.78	3.24	-0.59	NS
E. eel	Visual	0.38	0.86	0.48	$P<0.001$	5.63	6.71	1.04	$P<0.001$
Roach	Visual	0.23	0.60	0.37	$P<0.001$	6.64	6.24	-0.40	NS
Crayfish	Visual	0.55	0.96	0.41	$P<0.001$	4.35	4.71	0.36	NS
E. perch,									
1 satiated	Chemo	0.79	0.50	-0.29	$P<0.05$	8.15	8.00	-0.15	NS
1 starved	Chemo	0.23	0.21	-0.02	NS	7.30	6.14	-1.16	$P<0.001$
3 starved	Chemo	0.36	0.16	-0.20	$P<0.01$	7.79	6.49	-1.30	$P<0.001$

Chemical stimuli from starved and non-starved predators

These trials were performed to determine if crayfish are able to adjust their behaviour in adaptive ways with varying predation risk. We predicted that a starved perch should constitute a greater risk for the crayfish than a satiated perch, and that three starved perch should constitute an even greater risk. *Astacus astacus* exposed to water conditioned by a non-starved perch showed a slight, non-significant increase in refuge use during darkness. When exposed to the odour of one or three starved perch, crayfish refuge use during darkness was significantly increased (Table 1). In light there was a slight increase in refuge use in response to one non-starved and to three starved perch (Table 1).

The three trials were performed during three sequential weeks and there were no significant differences in control activity between the trials,

neither in light nor in darkness ($P>0.05$, Mann-Whitney U-tests). Therefore, comparisons of the strength of crayfish response between these trials can be justified. During darkness, the responses in the two trials with starved perch were considerably stronger than in the trial with a non-starved perch ($P<0.05$, Mann-Whitney U-test, Table 1). The responses to one and to three starved perch did not differ significantly. The results suggest that *A. astacus* are not only able to detect a predator by chemical cues, but also to gauge to what extent a given predator constitutes a predation risk.

Visual stimuli from various potential predators

In these trials, the crayfish could see the potential predator and vice versa, but, since the water from the two aquaria was recirculated through separate systems, the crayfish were not exposed to chemical stimuli. We predicted that, if crayfish can

detect and avoid predators by visual stimuli, crayfish refuge use should increase when a predatory fish was placed in the secondary aquarium. However, given visual cues alone, crayfish did not increase refuge use in response to any of the tested fish species, nor to adult crayfish. Instead, crayfish exposure increased in response to all tested species except pike and burbot during the light period (Table 1). Apparently, crayfish did not recognize predators by visual cues, and the observed increase in crayfish activity was probably a response to visual stimuli caused by movements from the tested organisms. In darkness, differences between treatments and controls were small and non-significant in most trials, however, crayfish exposure increased significantly in response to pike and eel (Table 1).

It cannot be excluded that the lack of crayfish response in increased refuge use to visual stimuli from predatory fish was an experimental artefact. The predator was always situated at least 15 cm above the crayfish and we do not know what the reactive distances of *A. astacus* to the tested predators are. No fish was observed to attack the crayfish, and it is possible that the behaviour of the fish was not adequate to cause an avoidance reaction of the crayfish.

Discussion

In this study, we have experimentally shown that YOY *A. astacus*, naive of fish predators, are able to detect co-occurring predatory fish given only chemical stimuli, and also to gauge the predation risk and adjust its antipredator behaviour according to the risk. Chemically-mediated detection of predators has been documented in a variety of aquatic invertebrates, e.g., mayflies (Peckarsky 1980), mosquito larvae (Sih 1986), caddisflies (Malmqvist 1992), amphipods (Williams and Moore 1985), isopods (Holomuzki and Short 1988) and lobsters (Wahle 1992), freshwater crayfish *Pacifastacus leniusculus* (Blake and Hart 1993). The ability of a prey to chemically detect predators is advantageous in that it enables detection of a predator while remaining in refuges or, when the prey is exposed, before predator encounter and

attack. When a predator is detected, the prey can adjust its behaviour and thereby reduce the risk of mortality.

Although there is little field evidence for a strong impact of fish predation on crayfish mortality, the crayfish are probably exposed to an important mortality risk from predatory fish, especially during their juvenile stages when they are most vulnerable to fish predation (Stein and Magnuson 1976). Therefore, it seems likely that predatory fish have been an important selective force in the development of crayfish antipredator behaviour. Similar to *A. astacus* in the present study, most crayfish species show a nocturnal activity pattern, regardless whether predators are present (Webb 1983). This antipredator behaviour is assumed to be fixed, and the evolutionary result of long-term predation pressure (Stein 1979). Crayfish also show strong reactive antipredator responses to the presence of predatory fish (Stein and Magnuson 1976, Appelberg and Odelström 1988, Resetarits 1991, Söderbäck 1992, Blake and Hart 1993).

The obvious direct benefit of an ability to detect and avoid a predator before an attack is increased probability of survival. However, antipredator responses are often associated with a cost for the prey in reduced feeding or growth rates (e.g. Stein and Magnuson 1976, Sih 1982, Appelberg and Odelström 1988, Holomuzki and Short 1988). Optimality theory suggests that natural selection should produce individuals that maximize their inclusive fitness by optimal behaviour (MacArthur and Pianka 1966). Thus, natural selection should favour prey that show "precise antipredator responses" (sensu Sih 1986), i.e. prey that can make appropriate trade-offs between mortality risk and energy gain. Because of the costs involved in the antipredator responses, there should be an adaptive value for the prey in avoiding unnecessary responses to non-predators or predators that pose little risk. In the present study, YOY *A. astacus*, given only chemical stimuli, responded to predatory fish species but not to a non-predatory fish, and the crayfish showed a stronger response to a starved predator than to a non-starved. An ability of prey organisms to differentiate between predatory and similar non-predatory species, and also between active and non-active predators, has been

documented in experimental studies with several other prey species (e.g., Phillips 1978, Peckarsky 1980, Heads 1985).

Factors responsible for the origin and evolution of antipredator responses can never be identified with certainty. Because the YOY *A. astacus* used in this study were naive to fish prior to the experiments, the observed antipredator responses should be genetically based. We therefore suggest that the ability of *A. astacus* to detect predators chemically is a result of natural selection during long-term coexistence with the tested fish species. Similarly, Kats et al. (1988) showed that larvae of several amphibian species, without previous experiences of fish, detected a predatory fish chemically.

Crustaceans possess sensitive chemoreceptors, which function in the sense of olfaction, on their first pair of antennae (Schmitt 1971). Many studies have shown that crustaceans are able to detect highly diluted concentrations of feeding attractants, and that the active components can vary widely in molecular mass (e.g., Zimmer-Faust 1989). The importance of chemical reception in predator detection has received less attention, and the active components involved in crustacean predator detection are not known. Williams and Moore (1985) suggested that fish mucus (either from the skin or from the intestine) was the most likely substance involved in detection of predatory fish by the amphipod *Gammarus pseudolimnaeus*. The substance detected by *A. astacus* was not a metabolic product from eaten and digested conspecifics since the fish used in this study were not fed crayfish prior to the experiments. Nevertheless, the ability of *A. astacus* to distinguish between fed and starved predators indicates that some kind of metabolic product, excreted from the predator, is involved in chemical detection of predators.

In the present study, crayfish responses were weak relative to the dramatic reduction in exposure in response to free-swimming predatory fish, documented for several crayfish species (Stein and Magnuson 1976, Appelberg and Odelström 1988, Söderbäck 1992, Blake and Hart 1993). The relatively weak crayfish responses to chemical stimuli alone, documented in the present study, suggest that chemoreception is not the only senso-

ry mechanism responsible for crayfish antipredator behaviour. Crayfish have well-developed visual sensory mechanisms (Shaw and Stone 1982), and Blake and Hart (1993) found that the combined effects of visual and chemical stimuli from a predator increased the refuge use in *P. leniusculus*. Crayfish also possess a variety of mechanoreceptors sensitive to waterborne vibrations and changes in hydrodynamic pressure (Bush and Laverack 1982). Although no crayfish response to visual stimuli from predatory fish was observed in the present study, both vision and mechanoreception may be important in close-range predator detection.

The strength of crayfish antipredator responses will probably be influenced also by previous experiences of predators. A capacity for learning has been demonstrated in aquatic insects (Feltmate and Williams 1991) and it seems reasonable that also crayfish have evolved this capacity. Crayfish surviving initial attacks from a non-restricted predator may modify their behaviour and show stronger antipredator responses. Furthermore, the aquaria used in the present study constituted a simplified, artificial environment. Exposed crayfish were often observed in the corners and along the walls of the aquaria. This behaviour may have counteracted antipredator responses to the tested predators and contributed to the relatively weak responses observed.

In summary, we suggest that the ability of crayfish to chemically detect co-occurring predators, documented in this study, is a genetically based antipredator adaptation, enabling crayfish to roughly estimate predation risk. Chemoreception in combination with other sensory mechanisms, and also in combination with earlier experiences, will probably determine the realized crayfish antipredator response to a given predator.

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Predator Training Improves the Anti-predator Behaviour of Hatchery Reared Atlantic Salmon (*Salmo salar*) Smolt

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Abstract

When migrating from freshwater to sea-water habitats, hatchery reared Atlantic salmon, *Salmo salar*, smolts encounter heavy predation. We tested whether smolts, after predator-training in iso-osmotic water, behaved more appropriately when encountering predators in sea-water. Two different training methods were used. The non-contact-trained smolts experienced the predator (cod, *Gadus morhua*) only from behind a transparent partition of netting, while the contact-trained smolts experienced free hunting predators. After the training procedure, groups of smolts were exposed to a single predator. Two types of behavioural response were recorded, viz. that associated with physiological stress and that with anti-predator behaviour. The general results were that the predator-naive smolts and the non-contact-trained smolts displayed stress-behaviour more frequently in sea-water than in iso-osmotic water, whereas the contact-trained smolts did not. In iso-osmotic water, the predator-naive smolts reacted earlier than both the non-contact-trained and the contact-trained smolts did. The predator-naive smolts behaved less appropriately to predation when in sea-water than when in iso-osmotic water than either the non-contact-trained or the contact-trained smolts did, and the non-contact-trained smolts behaved less appropriately than the contact-trained smolts. The results showed that predator-training improved the anti-predator behaviour by the smolt, although the two training methods showed different effects. We suggest that the trained smolts, when subjected to a learning regime in iso-osmotic water, acquired an increased 'self confidence', with the result that they still displayed the requisite behaviour when transferred to sea-water.

Keywords: Predator training, anti-predator behaviour, Atlantic salmon smolt, physiological stress, self confidence.

Introduction

During their large-scale movements from fresh water to the sea, salmon experience heavy mortality, due to predation from both birds and fish assembled in the estuary of the home river and adjacent areas. Many salmon species are involved: pink salmon, *Oncorhynchus gorbuscha*, fry (Parker 1965, 1968), sockeye salmon, *O. nerka*, smolt (Hartman and Burgner 1972, Meacham and Clark 1979), coho salmon, *O. kisutch*, smolt (Larkin 1977, Mace 1983, Fiscus 1980), Atlantic salmon, *Salmo salar*, smolt (Piggins 1959, Mills 1962,

Lindroth 1965, Larsson 1985, Hvidsten and Møkkelgjerd 1987, Kennedy and Greer 1988). In general, the mortality rate is assumed to be significantly higher for hatchery reared smolts than for wild smolts from the same river systems (Piggins 1979, Ísaksson 1979). In fact, it has been shown that a predator may switch from wild to reared prey of the same species as soon as the reared fish have been released in nature (Thompson and Tufts 1967). It has been postulated that the higher mortality experienced by the hatchery reared smolts is due to the fact that they have had no previous experience of predators, which entails that they do

not behave adequately and, hence, are easy victims for predators (e.g. Larsson 1977, Olla and Davis 1989). In order to enhance predator avoidance, hatchery fish have been exposed to predators, or other stimuli, as exemplified by the studies of Thompson (1966) on chinook salmon, *O. tshawytscha*, and on coho salmon; on chum salmon, *O. keta*, by Kanayama (1968) and Kanayama and Tuge (1968); on brook trout, *Salvelinus fontinalis*, by Fraser (1974); on Atlantic salmon by Larsson (1977). However, the effects of these training experiments were not clear cut, since some of them demonstrated an increase in predator avoidance while others did not.

During the seaward migration, at least two main factors may contribute to the high rate of predation, viz., a response to osmotic stress and a response to the physiological stress due to fright from the assemblage of predators, as well as a cumulative effect of both factors (Järvi 1989a, 1990). It has been suggested that such a combined, acute, physiological, stress response inhibits the normal, requisite and adaptive response by smolts to predators to such an extent that their chances of escaping predators are significantly reduced (Järvi 1989b, 1990). Järvi (1990) showed that predator-trained Atlantic salmon smolts were physiologically less stressed when confronted with predators than were predator-naïve smolts. The mechanism underlying the reduction in stress response was supposed to be a habituation process towards predators, which, physiologically, was shown by declines in the levels of plasma chloride, blood glucose and blood lactate by as much as 40% (Järvi 1990). With reference to the previously reported studies, the higher level of survival of wild smolts during their seaward migration is probably due to the fact that, as fry and parr, they experience predators in freshwater, to which they habituate and adapt their anti-predator behaviour, a mechanism which is still functional when they reach to the sea.

The aim of this study was to establish whether predator training in iso-osmotic water would habituate hatchery reared Atlantic salmon smolts towards a piscine predator (cod, *Gadus morhua*), as revealed by an improvement in anti-predator behaviour and a reduction in stress-related behaviour patterns. Two types of predator-training

methods were used, viz., 'non-contact' training, during which the smolts experienced the predator only from behind a transparent partition of netting, and 'contact' training, during which the smolts experienced free hunting predators.

Material and methods

General procedure

The experiment comprised two parts. A training procedure was initiated, during the course of which the smolt either gained direct experience of a hunting predator, or only experienced them from behind a transparent partition of netting. A study was then made in which the 'stress-response behaviour' and the 'anti-predator behaviour' of these two groups in either iso-osmotic or sea-water towards a live predator was observed. The experiment was carried out at NINA's Research Station at Ims, near Stavanger, in southwestern Norway, during the period from the 15th of April to the 10th of June, 1989.

Experimental fish

The fish used were two-year old Atlantic salmon smolts, which had been spawned by wild stock in the River Imsa but had been reared at the Research Station. The average overall length of the smolts was 171.5 mm (SD = 12.3) at the beginning of the experimental period. The sex ratio was 0.49 males to 0.51 females. When smolts are transferred from freshwater to sea-water containing predators, they are liable to a high mortality rate, caused by a synergetic effect of the osmotic stress and the stress caused by the presence of predators (Järvi, 1989a). In order to avoid this effect, the initial anti-predator training was carried out in iso-osmotic water (12‰). The smolts were individually marked and acclimated to iso-osmotic water (salinity 12‰; temperature 6-12.5 °C) for a period of more than four weeks prior to the training procedure.

The predatory cod used were bought from local fishermen. They weighted 1 to 2 kg. One week prior to the training procedure, 12 cod were placed in iso-osmotic water (12‰) and 8 cod in sea-water (32‰).

Training procedure

The training arena was a 12 m² rearing tank with a water depth of 0.6 m. The tank was divided into two parts by a netting. The smolts were kept in one part (4 m²) and the predators were kept in the other during one of the training procedures. The net mesh was 13 x 13 mm, i.e. large enough for the smolt to be able to recognize the cod on the other side of the netting.

The smolts were trained in two different ways. The first group of smolts only experienced the cod through the netting, partitioning the tank (non-contact smolts). The second group of smolts was placed together with the cod on the same side of the partition (contact smolts). A third and a fourth group of smolts were put in the arena without any predator being present. The third group of smolts were then used as the 'predator naive' group during the subsequent observation study (naive smolts). The fourth group were used as a control group and thus never experienced any exposure to predators throughout the observation study.

Two days before the observation study was started, one group of 100 smolts was taken from the storage tank by hand-net and placed in the training arena. Before the non-contact smolts were put in the training tank, five cod were placed behind the partition. Before the contact smolts were put in the training tank, two cod were placed on the same side of the partition as the smolts. The order of training, as well as of the observation procedures, was non-contact smolts, predator-naive smolts, contact smolts, and the control group of predator-naive smolts in the absence of a predator.

Observation procedure

The observations were conducted from an observation tower, which provided a view of the entire observation arena. The arena was an ordinary rearing tank (12 m²) with a grid (0.1 x 0.1 m) painted on the bottom. The grid made it possible to measure the relative positions of the smolts and the cod to the nearest 0.1 m. The water depth was 0.6 m. In one corner of the tank, an elevatable plastic partition (1 m²) was constructed. Six smolts from either the non-contact, the contact or the predator-

naive groups were sampled from the training tank and placed behind the partition for acclimation before each trial started, with a single cod on the other side of the partition.

The smolts were allowed to acclimate to the experimental situation for 90 minutes. After that time the partition was raised and the observation period started. Each observation period lasted for 60 minutes.

Six replicate trials, in iso-osmotic water (12‰) and in sea-water (32‰), were made with each category of smolt, using six smolts in each replicate, i.e. a total of 72 smolts were tested from each category, 36 in iso-osmotic water and 36 in sea-water.

When smolts are exposed to predators, they may display two types of behaviour, viz., that due to the reaction to physiological stress and that with anti-predator behaviour (Järvi 1989b). The stress response of the smolt is considered to be similar in nature to the General Adaptation Syndrome (GAS), which can be subdivided into the three stages of alarm, resistance and exhaustion (Schreck 1981, Pickering 1981). Rapid change in the ambient salinity, together with the presence of predators, may produce a physiological stress response, entailing exhaustion that affects the normal behaviour pattern of the smolt (Järvi 1989a,b, 1990).

Two different types of 'stress-response behaviour' were noted:

Wobbling: A response to physiological stress can be seen in a change in the swimming behaviour of the smolt, characterized by the smolt 'wobbling about' at the water surface (Järvi 1989b). The frequency of 'wobbling' was measured by counting the number of smolts seen behaving in this way at 5, 10, 15, 30, 45 and 60 minutes after the start of each the trial.

Non-response: When a predator approaches a smolt or the smolt approaches a predator, the smolt sometimes shows no reaction or change in behaviour. Such lack of response is probably due to a physical stress reaction (Järvi 1989a). When a smolt showed no change in its behaviour when the cod was closer than 0.1 m, its behaviour was characterized as 'no-response' throughout the observation period.

Four different kinds of anti-predator behaviour were noted:

Reaction-distance: When a predator is in the vicinity of a smolt, the smolt tries to keep a certain distance away from the predator. This is so both when the predator approaches the smolt and when the smolt approaches the predator (Jakobsson and Järvi 1977, Järvi 1989b). The reaction-distance was assessed during every confrontation throughout the observation period.

Escape-distance: If a predator attacks a smolt, then the smolt possesses the ability to exhibit one of three different kinds of escape behaviour (Jakobsson and Järvi 1977, Järvi 1989b): 1) it may suddenly swim away, in apparent panic; 2) such a panic-like swimming may change into 'surfing', which is panic-like swimming at the surface; 3) the smolt may quickly swim down to the bottom and stay there absolutely immobile (freezing). The distance away from the predator at which a smolt reacts by showing a type of escape behaviour, was defined as the 'escape distance' (Jakobsson and Järvi 1977, Järvi 1989b). The escape-distance was assessed during every confrontation throughout the observation period.

Freezing: When a predator approaches, the smolt will sometimes quickly swim to the bottom and stay there immobile for some time (Jakobsson and Järvi 1977, Järvi 1989b). Such 'freezing' behaviour of the smolts was noted during every confrontation throughout the observation period.

Shoaling: When several smolts are present within a limited area, the smolts may form a shoal, in order to reduce the risk of being killed by an approaching predator (Pitcher 1983, Järvi 1989b). Our definition of shoaling was that two or more individuals should be observed to swim in the same direction, or stay put with their heads pointing in the same direction, without touching the bottom. The distance between each individual should be less than two fish-lengths. The number of shoaling smolts were counted at 5, 10, 15, 30, 45 and 60 minutes after the start of each trial.

To reduce the possible effect of repeated samples on the same individual, the median values for each trial, or for each observation period within each trial, were used in the subsequent statistical

analyses. Evaluation of the alternatives to the null hypothesis was made using non-parametric statistics (Mann-Witney U-test and Wilcoxon Matched Pair Sign test).

Results

Overall, there was a striking difference between the predator-naive smolts and the predator-experienced smolts, which makes it reasonable to suggest that a training effect had been achieved by preparatory exposure of the smolts to predatory cod. Since a significant difference was also noted between the non-contact smolts and the contact smolts, the two training procedures would seem to have affected the smolts differently.

With regard to the type of 'stress behaviour' shown, the predator-naive smolts 'wobbled' more frequently in sea-water than in iso-osmotic water, and the predator-naive smolts 'wobbled' even more frequently in sea-water when they were exposed to the predator than the control group of predator-naive smolts did (Fig. 1). The latter group were those put in the arena without any predator being present. When exposed to a predator, both the predator-naive smolts and non-contact smolts

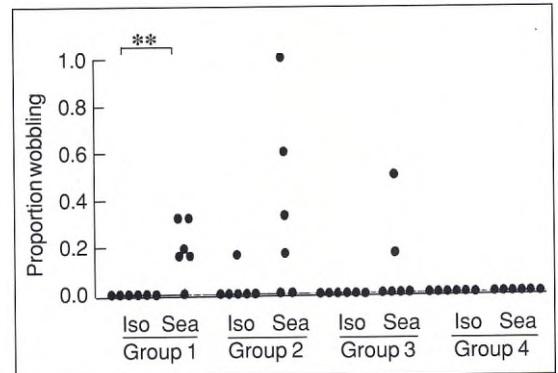


Fig. 1. The median proportion of smolts showing 'wobbling' behaviour in each trial with each training procedure, in iso-osmotic (iso) and in sea-water (sea), respectively. Group 1 is predator-naive smolts, group 2 is non-contact smolts, group 3 is contact smolts and group 4 is predator-naive smolts, which were not exposed to any predator. Significant differences shown by asterisks (** is $P < 0.01$).

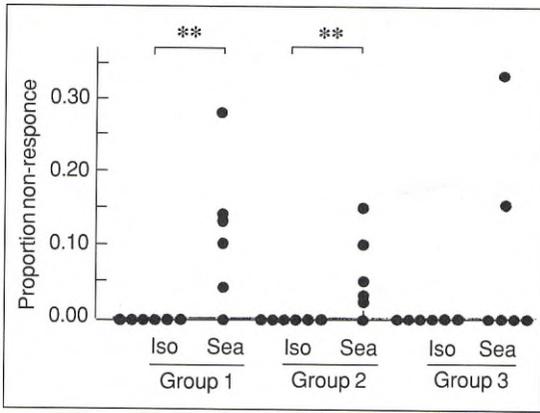


Fig. 2. The median proportion of smolts showing a 'no-reaction' response in each trial with each training procedure, in iso-osmotic and in sea-water, respectively. Group 1 is naive smolts, group 2 is non-contact smolts and group 3 is contact smolts. Significant differences shown by asterisks (** is $P < 0.01$).

showed a significantly higher frequency of 'no-response' towards the predators in sea-water than in iso-osmotic water (Fig. 2). These results imply that both the predator-naive smolts and the non-contact smolts became more stressed in sea-water

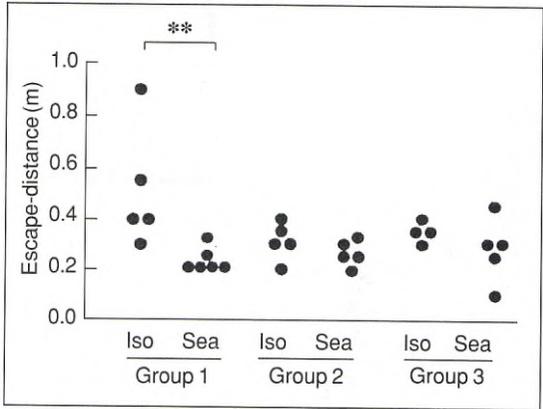


Fig. 4. The median 'escape-distance' of a smolt to a predator in each trial with each training procedure, in iso-osmotic and in sea-water, respectively. Group 1 is naive smolts, group 2 is non-contact smolts and group 3 is contact smolts. Significant difference shown by asterisks (** is $P < 0.01$).

than in iso-osmotic water when confronted with a predator. Because the predator-naive smolts 'wobbled' more frequently in sea-water than the control group of predator-naive smolts did, which the non-contact smolts did not, it seems evident that the predator-naive-smolts were even more stressed in sea-water than the non-contact-smolts were. Because the contact-smolts did not show any significant difference in their stress response in sea-water compared to that in iso-osmotic water, it is evident that they became less stressed when confronted with a predator in sea-water than either the non-contact smolts or the predator-naive smolts did.

Considering the anti-predator behaviour, the predator-naive smolts reacted more rapidly to the presence of a predator when in iso-osmotic water than either group of the predator-trained smolts did (Fig. 3). Furthermore, the predator-naive smolts escaped from approaching predators more rapidly in iso-osmotic water than in sea-water, which neither the non-contact smolts nor the contact smolts did (Fig. 4). Both the predator-naive smolts and the non-contact smolts shoaled less frequently in sea-water than in iso-osmotic water, whereas no such difference was noted for the group of contact smolts (Fig. 5). These differences in the frequency

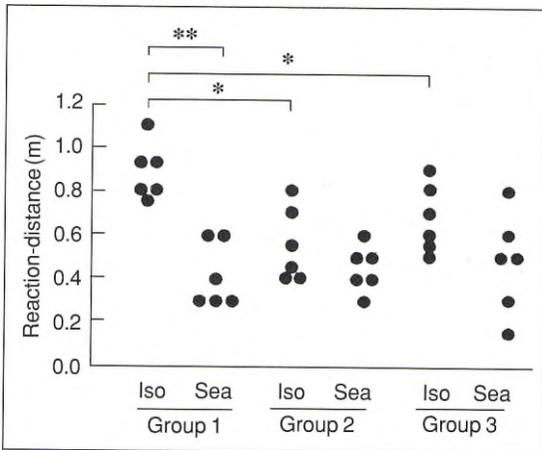


Fig. 3. The median 'reaction-distance' of a smolt to a predator in each trial with each training procedure, in iso-osmotic and in sea-water, respectively. Group 1 is naive smolts, group 2 is non-contact smolts and group 3 is contact smolts. Significant difference shown by asterisks (* is $P < 0.05$, ** is $P < 0.01$).

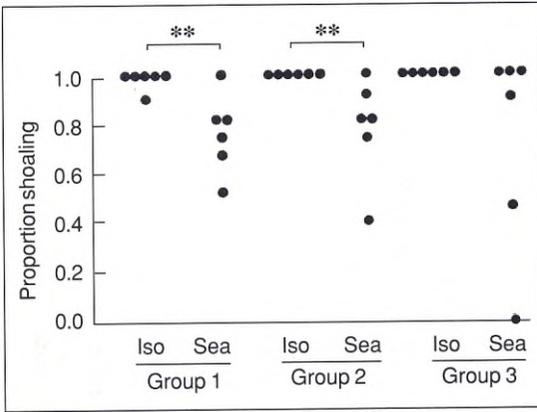


Fig. 5. The median proportion of 'shoaling' smolts in each trial with each training procedure, in iso-osmotic and in sea-water, respectively. Group 1 naive smolts, group 2 is non-contact smolts and group 3 is contact smolts. Significant difference shown by asterisks (**is $P < 0.01$).

of shoaling in iso-osmotic water, compared to sea-water, between the three categories of smolts was very marked. In iso-osmotic water, the tendency of the predator-naive smolts to shoal increased during the first 20 minutes, after which time almost all the predator-naive smolts had shoaled. Such an increase was not obvious in sea-water (Fig. 6). Almost all non-contact smolts had shoaled in iso-osmotic water within the first 10 minutes of the observation period, whereas, in sea-water, the non-contact smolts tended to shoal less frequently at the beginning of the observation period. After 30 minutes, however, the difference was much less obvious (Fig. 6). The contact smolts showed a great tendency to shoal throughout the observation period, both in iso-osmotic water and in sea-water (Fig 6). The number of smolts that exhibited a 'freezing' behaviour was too small for any statis-

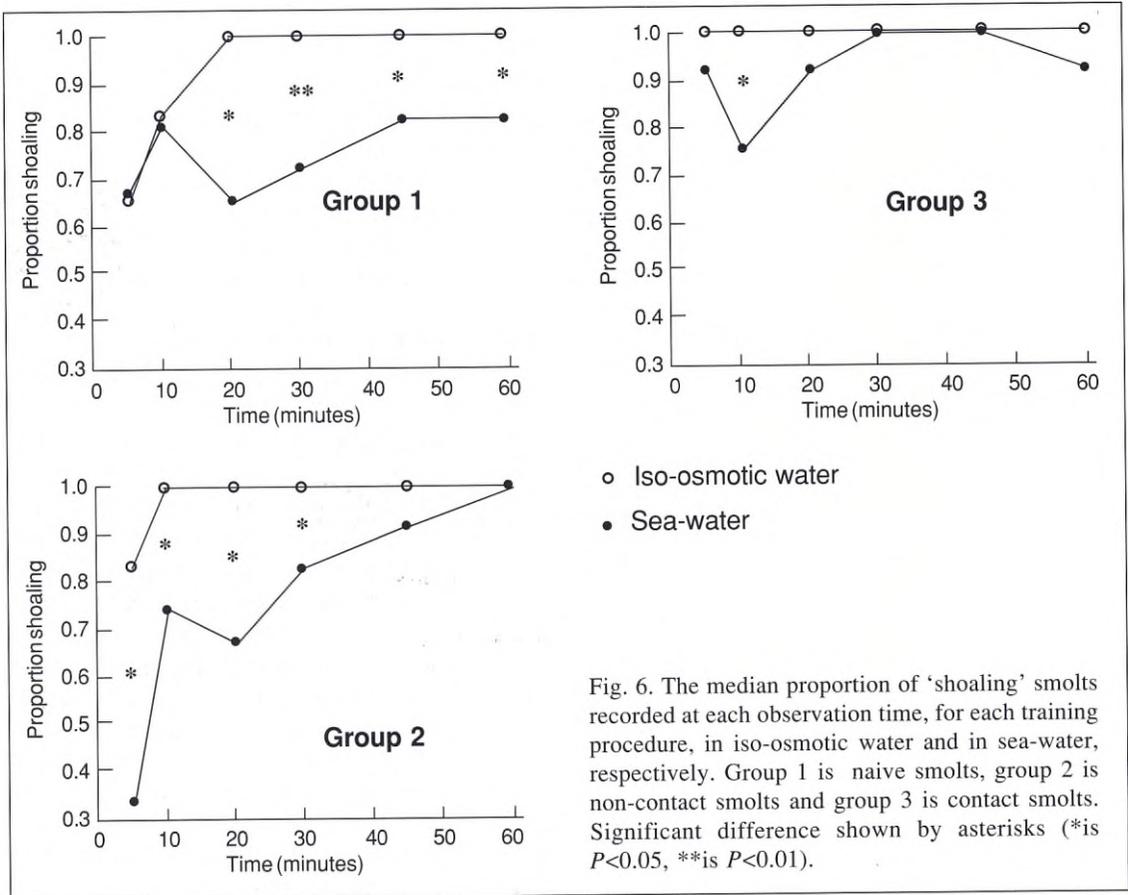


Fig. 6. The median proportion of 'shoaling' smolts recorded at each observation time, for each training procedure, in iso-osmotic water and in sea-water, respectively. Group 1 is naive smolts, group 2 is non-contact smolts and group 3 is contact smolts. Significant difference shown by asterisks (*is $P < 0.05$, **is $P < 0.01$).

Table 1. Number of predator confrontations during which the smolt showed a 'freezing' response, and the number of smolt killed during the observation period (see text for details).

Training procedure	Water quality	Froze	Killed
Naive-smolts	Iso	4	0
	Sea	2	1
Non-contact smolts	Iso	0	0
	Sea	1	2
Contact smolts	Iso	0	0
	Sea	1	0

tical analyses to be made (Table 1). Only three of all the smolts used were taken by the cod during the course of the experiments (Table 1).

Discussion

Novel stimuli, such as the presence of the cod used in this study, may signify danger. Hence, a 'predator naive' smolt should react to such stimuli by showing appropriate defensive behaviour. The theory of habituation predicts that a novel stimulus which results in no negative consequences after its first few occurrences will probably continue to be safe and hence the response made will, eventually, become vague or unnoticeable (Hinde 1970, Mackintosh 1983). Thus, the function of habituation is to discriminate between dangerous and harmless objects in an optimal fashion. In fact, predator-model experiments have shown that prey became most obviously habituated when the less realistic predator models are employed (Magurran and Girling 1986), and when the site of the predator-dummy remained unchanged (Schleidt et al. 1983). Because the cod could not attack any of the non-contact smolts during the training procedure, the prediction was that those smolts should have become habituated and, accordingly, subsequently should have avoided predators less rapidly, than the predator-naive smolts. This was in fact the case in iso-osmotic water. The non-contact smolts were

not initially exposed to hunting predators, which the contact smolts were, and therefore only the non-contact smolts should have become habituated. In spite of that, in sea-water, the contact smolts were less affected by the presence of predators than either the predator-naive smolts or the non-contact smolts. It would thus, seem as though no habituation was involved. Alternatively, the contact smolts, during the training procedure, may learn to adapt their anti-predator behaviour by an associative learning process. However, associative learning in relation to predators has normally been shown to be associated with avoidance learning (Shettleworth 1984). For example, predator-experienced sticklebacks (*Gasterosteus aculeatus*) reacted more rapidly when a greater distance away from a predator than predator-naive ones did (Benzie 1965). After training involving the use of dummy predators, zebra danios (*Brachydanio reiro*) reacted sooner to an approaching dummy predator than the naive ones did (Dill 1974). It would therefore seem inappropriate to invoke associative learning, in that sense, in order to explain the improved anti-predator behaviour shown by the contact-smolts.

A reasonable explanation for our results would be to widen the associative learning theory to include the concept of 'self confidence'. This concept has been invoked to account for how winning and losing in an agonistic interaction may per se influence the probability of an individual winning or to losing in any subsequent confrontation (e.g. Barnard and Burke 1979). This so-called 'confidence' effect has been demonstrated to be effective for many groups of animals, such as crayfish (Rubenstein and Hazlett 1974) crickets (Alexander 1961, Simmons 1986), fish (Franck and Ribowski 1987, Beacham 1988), reptiles (Edsman 1990) and birds (Macbride 1958, van de Poll et al. 1982). The positive outcomes from threatening and dangerous situations, such as intraspecific fighting, can probably be regarded as forming a parallel to confrontations during which the prey successfully escapes from the predator. The experience gained by the, 'predator-trained' contact smolts, is assumed to have aided them in acquiring, or developing, a 'self confidence' that

reduced the effect of physiological stress when they were attacked by the predator in sea-water. Such a reduction in stress response has previously indeed been found by Järvi (1990), who showed that 'predator-experienced' smolts were less physiologically stressed than 'naive' ones when confronted by predators in a changed osmotic milieu. In this study, the 'predator-naive' smolts displayed 'stress-behaviour' in sea-water more frequently when the predator was present in the tank. However, no such change in 'stress behaviour' was noted when the contact smolts were transferred from iso-osmotic water to sea-water.

Acknowledgments

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Patterns of Movement and Migration of Pike (*Esox lucius* L.) in the Baltic Sea

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Abstract

Patterns of movement of pike (*Esox lucius* L.) in the Baltic Sea were analyzed, based on 23 tagging experiments carried out in four areas of Finnish and Swedish coastal waters. To study the strength of sedentary behaviour and homing, pike were moved to various distances before release. The pike remained sedentary; most of the recaptures appeared within 4-6 km from the point of release, although the dispersal was somewhat wider than normal. The homing towards spawning areas was very pronounced in relocation experiments at distances less than 10 km. At distances of 60 km and more, pike did not orient back to their original area. During a warm summer the dispersal expanded somewhat more offshore than during cold summers.

Introduction

Pike (*Esox lucius* L.) commonly appear in shallow coastal waters of the Baltic Sea, but are restricted to areas with salinities below 12-15‰ (Schlumberger 1966). In the upper salinity range of the southwestern as well as in the coldest waters of the northernmost Baltic Sea, reproduction predominantly takes place in fresh water or in estuaries (Johnson and Müller 1978). Pike were one of the first fish species to be individually tagged in northern Europe and hence their movements have been studied intensively since the beginning of this century. Baltic populations of pike were first tagged by Ekman (1915) and Gottberg (1922). Many such studies have since been performed in Finnish and Swedish coastal waters (e.g. Järvi 1931, Hessle 1934, Halme 1957, Halme and Korhonen 1960, Sumari 1965, Kaukoranta and Lind 1975, Lehtonen et al. 1983, Hudd et al. 1984, 1992, Müller 1986). In general, these studies demonstrated sedentary behavior and strong homing toward spawning areas.

The sedentary life of pike may be caused by, e.g., reduced swimming capacity or perhaps by more active behaviour. Homing could also be considered as active behaviour, or merely an effect of the spawning grounds preferred being the only one possible within reasonable distance. In this paper, relocation experiments with tagged pike were used to approach these questions. If relocated pike did not differ in dispersal areas from those released in their original area, we cannot exclude the possibility sedentary behavior originates from a weak swimming capacity. If they largely returned to their original spawning area, through several other potential sites, actual homing toward spawning grounds may be considered to have occurred. Four different areas in the Baltic Sea were studied. Both juveniles and adults were tagged. In addition we analyze and discuss the patterns of movement and migrations on a more general basis in relation to environmental factors in various areas of the Baltic Sea.

Material and methods

Altogether 23 taggings of pike were performed in both Finnish and Swedish coastal areas at Espoo, Helsinki, Marviken and Forsmark in the Gulf of Finland, southwestern Bothnian Sea and the Baltic proper (Table 1, Figs. 1-5). At Forsmark, tagging was performed with Lea tags and in the other areas with Carlin tags. At Forsmark and Marviken a total of about 2,200 pike were caught with fyke nets and tagged during spawning migrations in a brook (at Forsmark) and at the mouth of two bays (at Marviken) (Table 1 and Figs. 4 and 5). Shortly after capture they were released at distances up to 8 km from the spawning area. Fish tagged and released within the Helsinki area (998 ind.) were caught with fyke nets and moved from capture areas in the western Gulf of Finland at distances of about 60 km (Inkoo) and 250 km (Åland). In most cases these fish were anesthetized with MS 222 when tagged. We have found no information on differences in dispersal area due to the different tagging and handling techniques used in this study. Thus, we consider such effects to be negligible. In the Espoo area (493 ind.), and in one tagging at Helsinki (56 ind.), cultured one-summer-old pike originating from an inland population were also used. The fish were caught and released into areas unaffected by pollution, except in the eutrophicated inlets of Helsinki. Recaptures were mainly

Table 1. Number of pike tagged and recaptures (%) in different experiments within Finnish and Swedish coastal waters. Taggings at Espoo and Helsinki VI were carried out with one-summer-old fingerlings. At Marviken and Forsmark pike were relocated from distances <10 km, at Helsinki I-II from 60 km and at Helsinki III-V from 250 km.

Area	Year and season of tagging	Numbers tagged	Percent of recaptures
Espoo	I 1978 autumn	196	11
	II 1978 "	297	5
Forsmark	1971 spring	100	55
	" 1972 "	100	7
	" 1973 "	98	23
	" 1974 "	100	32
	" 1975 "	100	23
	" 1976 "	100	34
	" 1977 "	100	32
	" 1978 "	100	8
Marviken	1979 "	101	21
	" 1984 "	100	27
	1965 spring	257	18
	" 1966 "	255	11
	" 1967 "	258	16
Helsinki	" 1968 "	200	27
	" 1969 "	250	25
	I 1970 spring	250	14
	II 1970 summer	129	16
	III 1971 "	196	4
	IV 1971 "	250	6
V 1971 "	173	4	
VI 1971 autumn	56	25	

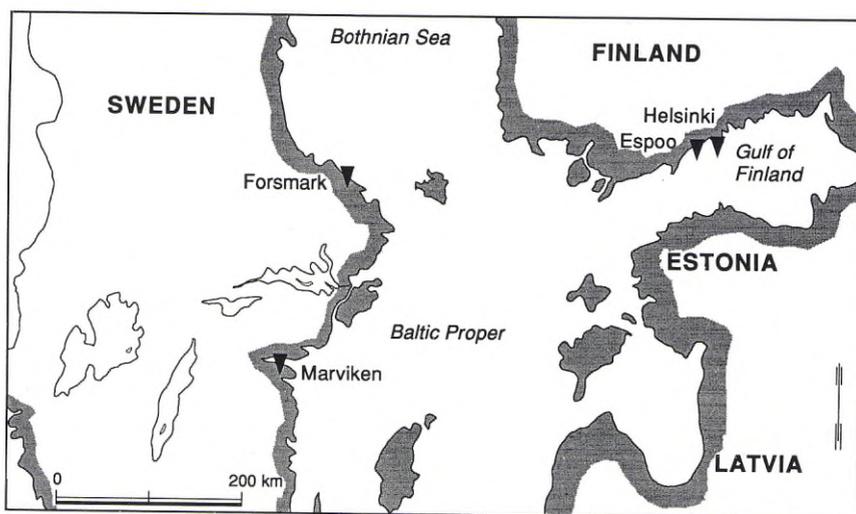


Fig. 1. Study areas (▼).

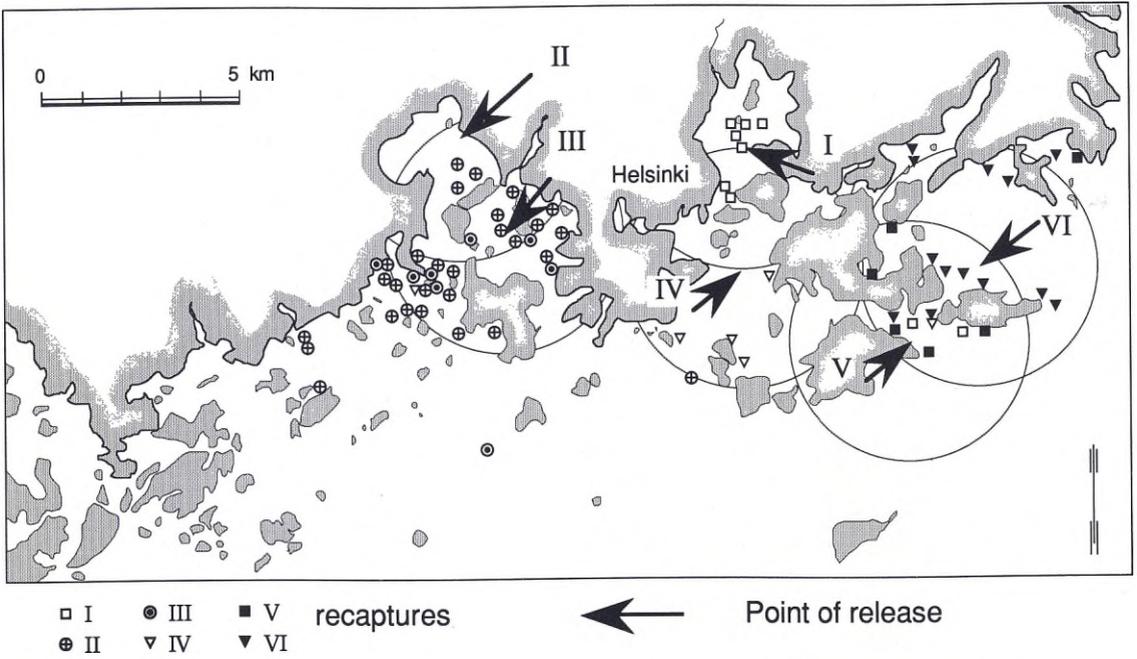


Fig. 2. Distribution of recaptures at Helsinki. A distance of 3 km from the point of release is indicated by a circle. I-VI: different experiments (see Table 1).

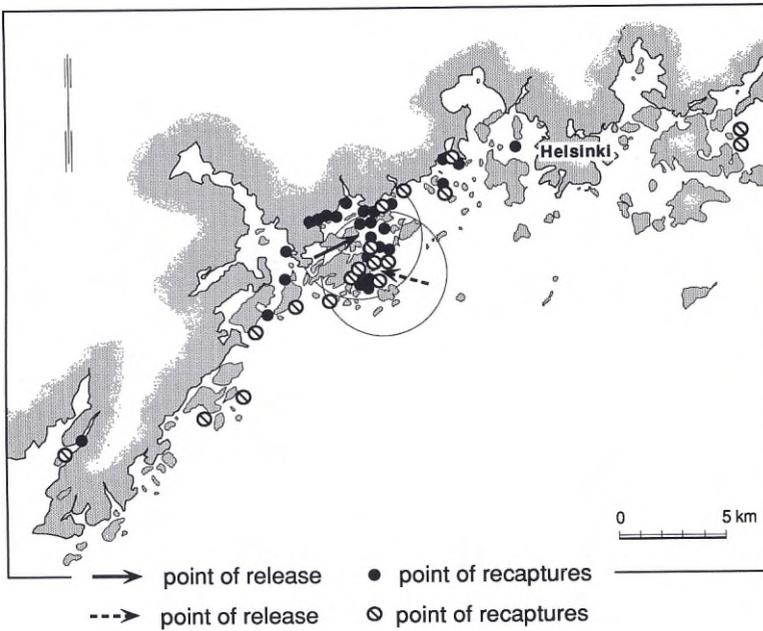


Fig. 3. Distribution of recaptures in two tagging experiments (I and II) of stocked pike at Espoo. A distance of 3 km from the point of release is indicated by a circle.

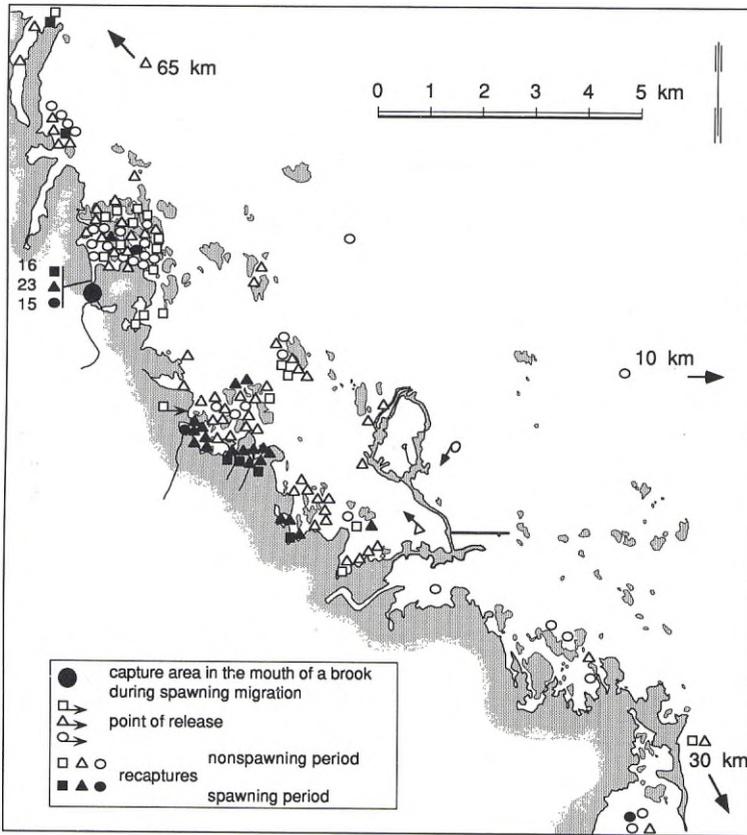


Fig. 4. Distribution of recaptures in translocation experiments at Forsmark.

done by local fishermen. The results were analyzed on the basis of season and geographical distribution. Differences between groups of tagged fish relating to distances of release and recapture sites were analyzed with the Pearson correlation analysis (Sokal and Rohlf 1981). In this analysis, different taggings of the same character were assembled into various groups: the stocked fingerlings in Helsinki (VI) and Espoo, the Helsinki I-V taggings, recaptures outside and during the spawning season at both Forsmark and Marviken, and finally the summer of 1969 at Marviken (Table 2). All figures relating to distances from the point of release to the point of recapture are given as possible swimming distances. The wide variation of recapture percentages (Table 1) has not been considered to influence interpretation of the recapture distances.

Results

During the spawning period, recaptures were concentrated in inlets, estuaries and freshwaters at Forsmark and Marviken (Figs. 4 and 5). Outside the spawning period, recaptures of pike appeared over wider areas. At Marviken this area was typically larger in one of the years (1969) studied ($r=0.75$, $P<0.05$).

As much as 80-95% of the recaptures of the tagged pike appeared within 8-10 km from the point of release in our experiments (Table 2, Figs. 2-5). At Forsmark and Marviken, with translocation <10 km, most individuals were recaptured within their original area and between this and the point of release (Figs. 4 and 5). Furthermore, during the spawning season 60-80% of these recaptures were made within the original area

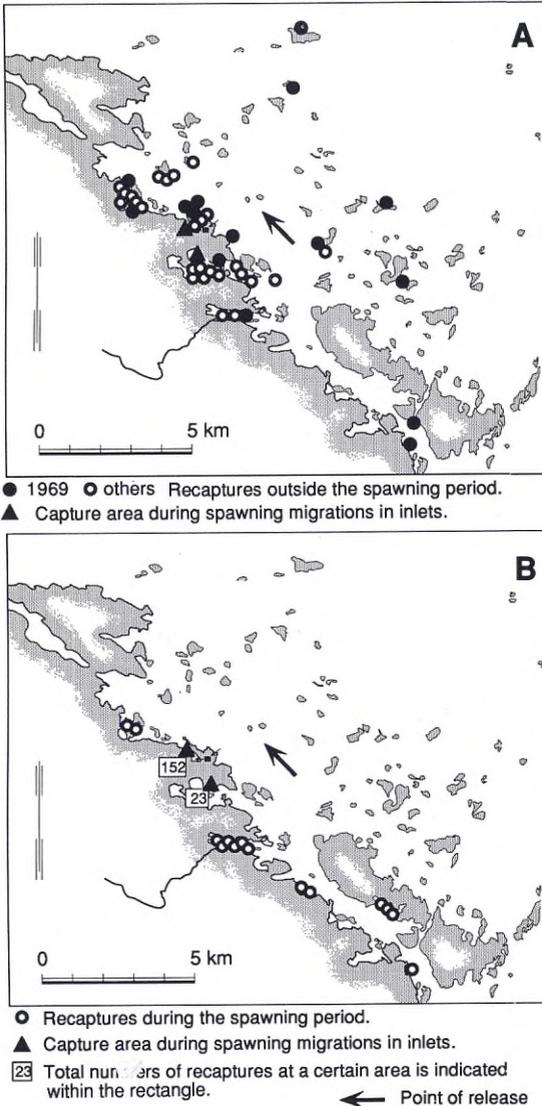


Fig. 5. Distribution of recaptures in translocation experiments at Marviken. A. Recaptures outside the spawning period. B. Recaptures during the spawning period.

(Figs. 4 and 5). In taggings at Helsinki, where pike were transported 60 and 250 km from the Inkoo and Åland archipelagoes, no recaptures were reported from the original home areas. These pikes were generally caught within 4–6 km from the point of release (Figs. 2 and 3, Table 2). The

cultured one-summer-old fingerlings at Espoo and Helsinki (VI) were not so widely dispersed as the adult Helsinki pikes ($p < 0.05$, Figs. 2 and 3, Table 2).

Discussion

Areas of distribution

The distribution of pike in the Baltic Sea is limited to nearshore coastal areas and archipelagoes (Ojaveer et al. 1981). This is clearly reflected in the distributions of our recaptures (Figs. 2–5), although the fishing intensity, and thus possibilities of recapture, may also be anticipated to decrease toward the sea. The highest abundances of pike appear in the innermost habitats. These populations are also the most stable ones, probably due to the relatively rich access to high quality recruitment areas (Lehtonen 1986). According to previous investigations within Swedish and Finnish coastal waters, pike are very sedentary (Ekman 1915, Gottberg 1922, Järvi 1931, Hessle 1934, Halme 1957, Halme and Korhonen 1960, Sumari 1965, Kaukoranta and Lind 1975, Lehtonen et al. 1983, Hudd et al. 1984, 1992, Müller 1986), about 90% of the recaptures being made within 3 km from the tagging site (Fig. 6).

A clear exception to the normal dispersal pattern is a population with its distribution area in the estuary of the Malax River (Fig. 6), in which about 40% of the recaptures were obtained more than 5 km from the tagging site (Hudd et al. 1992). This population is, however, influenced by acidification of its spawning grounds due to drainage of sulphuric soils in the tributary areas. Pike avoid acid waters and therefore dispersed further than they would have done under more normal conditions (Hudd et al. 1992).

The dispersal area of pike varies between seasons, mainly due to aggregations on the spawning grounds in spring and a subsequent dispersal into feeding areas (Figs. 4 and 5). There was, however, also a tendency for differences in this dispersal area between years in our study; a wider dispersal than normal could be established in the summer of 1969 (Fig. 5). The surface water was 4–5 °C warmer in this year than in the other years studied (Neuman 1974), which might have caused an

Table 2. Number of recaptures within different distances (km) from the point of release. Cumulative percentages (c. %) are given in bold figures.

	0-2	2-4	4-6	6-8	8-10	10-15	15-20	>20	mean	SD
Espoo I and II	20	8	8	2	2	3	1	3	6.0	6.18
c. %	43	60	77	81	85	91	93			
Forsmark I	12	29	23	12	20	20	2	3	7.4	8.90
c. %	10	34	53	63	80	97	98			
Forsmark II	4	12	27	2	41	4	-	-	6.7	2.89
c. %	4	17	47	49	95					
Marviken I	3	23	-	-	-	-	-	-	2.8	0.97
c. %	12	100								
Marviken (1969)	3	5	4	1	2	-	-	-	3.5	2.75
c. %	20	53	80	87						
Marviken II	-	175	10	3	1	-	-	-	3.4	0.99
c. %	93	98	99							
Helsinki I-V	17	13	24	1	4	4	2	1	4.0	4.05
c. %	26	50	86	88	94	98	99			
Helsinki VI	6	6	1	-	-	-	-	-	2.1	1.21
c. %	46	92								

increased area of preferred temperatures in the epilimnion in this year. The same observation was also made by Segerstråle (1948) in the Gulf of Finland during the warm summer of 1937.

The patterns of dispersal may differ between populations due to distances between the spawning and feeding grounds. This is clearly illustrated within the Baltic. Thus, both in the Marviken population in the Baltic proper, and within the large and shallow archipelagoes of SW Finland and the Gulf of Finland, the spawning and feeding areas are both situated in the sea very close to each other (Halme and Korhonen 1960, Sumari 1965, Lehtonen et al. 1983). In the northern Gulf of Bothnia, however, warming of the coastal areas takes place later and spawning at sea is not as common (Müller 1986, Lehtonen and Hudd 1990). Instead, pike mainly move up small rivers and brooks from the coastal feeding areas to spawn in freshwater, where suitable temperatures for optimal embryonal and larval development appear earlier in the spring (Müller 1986).

When pike were translocated <10 km in the rather shallow coastal areas of Forsmark and Marviken in our study many of those recaptured were able to return to their original area or were found between it and the point of release (Figs. 4 and 5).

Under these conditions, the area of dispersal was larger than in the longer transport distances of relocation experiments at Espoo and Helsinki (Table 2, Figs. 4 and 5). In the latter taggings, no pike returned to the original area. When compared to earlier studies, where fish were released in their original area, the proportion of those captured within 8-10 km were similar (about 90%) at Espoo and Helsinki (Table 2, Fig. 6). The former populations were, however, more sedentary since among the adult fish 90% were caught within 3-5 km as compared with 50% in the latter (Table 2, Fig. 6). The translocated juveniles of Espoo and Helsinki were more sedentary than the adults (Table 2, Fig. 3). These circumstances may be interpreted to suggest that pikes in the studied populations actively increase their normal area of distribution when moved to a place within close reach of the original area (Forsmark and Marviken), and in some cases even when they were not close to these areas (Espoo and Helsinki). The swimming capacity of pike must also be considered sufficient for adults to have a wider dispersal than normally found since some tagging results have demonstrated a rate of dispersal of at least 2 km/day (Sundbäck 1970). The smaller distribution area of juveniles in this study may, however, possibly be

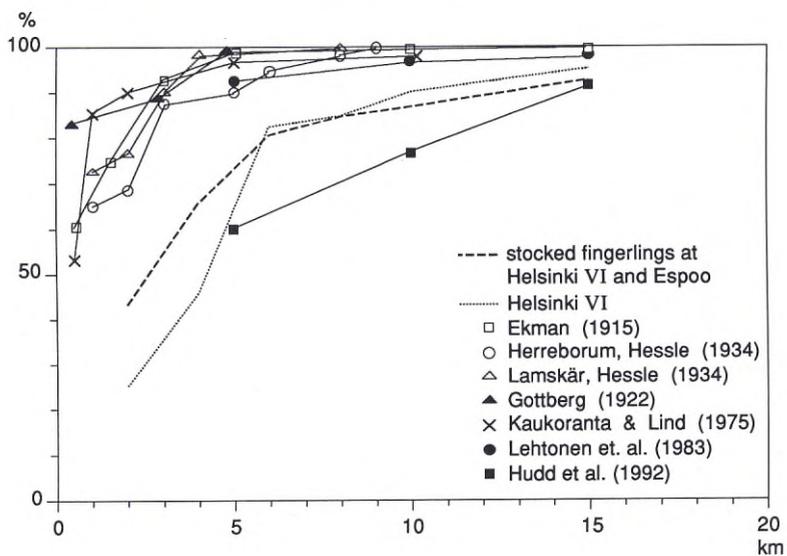


Fig. 6. Cumulative frequency of recaptures in tagging experiments with increasing distance from the point of release. The translocation experiments in the Gulf of Finland of the present study (dashed lines) are compared with similar experiments where translocations were insignificant.

attributed to their lower swimming capacity in comparison to adults.

A larger dispersal area of the pike at Espoo and Helsinki in our study than in the normal situation might, however, have been influenced by the change of environment between the original area and the point of release. If so, it might have caused an increase in swimming activity, and thus swimming distances. It might be argued that pikes in our experiments had wider dispersal areas than normal because most suitable areas in the new environment were already occupied. We do not, however, believe that original abundances were particularly high. Indeed, pike abundances were so low in the Helsinki area at the time of the experiments that stockings were seriously considered.

Homing

Our translocation experiments demonstrated a strong homing behavior towards the spawning grounds when pike were moved within and close to their natural area of dispersal, even if several other potential spawning areas were passed on the way home (Figs. 4 and 5). The same observation was made by Halme and Korhonen (1960) in a similar experiment. The homing behavior of pike in the Baltic thus must be considered to be active in this respect.

Homing towards specific feeding areas was difficult to evaluate on the basis of the taggings available since most of them were made during the spawning period for practical reasons. Halme and Korhonen (1960), however, observed that specimens tagged outside the spawning season were repeatedly recaptured at the original site when relocated at distances of 0.5-2.6 km, thereby demonstrating homing towards feeding areas.

To conclude, although pike were moved to various distances before release they remained almost as sedentary as normal; most of the recaptures were made within 4-6 km from the point of release. However, the pike that were moved the longest distances (>60 km) had significantly larger dispersal areas than the ones that were not translocated. This implies that these fish had the capacity to increase their area of distribution and that sedentary behaviour may normally be considered as active. The homing towards spawning areas was pronounced. Thus, in the relocation experiments at distances up to 10 km, most pike reappeared within their original spawning area although passing several other potential ones on their way home. For this reason, homing must also be considered as an active behaviour in these populations. At very long distances (>60 km), homing did not appear.

Acknowledgments

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Sex Dimorphism in Cultured Eels (*Anguilla anguilla* L.)

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Abstract

In an experimental eel culture, males usually ceased to grow when between 350-450 mm in total length. By continuously removing the largest eels, females were prevented from growing to the silver eel stage. A range of morphological characteristics were related to gonadal sex. Discriminant function analysis (DFA) classified at least 95% of all sexed eels to correct sex. Although the misclassification rate was higher in smaller eels, it was still less than 15% in eels of 300-350 mm length. The single variable "lower jaw" was almost as good as the discriminant function in predicting sex. In dorsal view of the head, the lower jaw was visible (from the tip of the snout to at least just in front of the eyes) in 87% of the females but in only 1% of the males. On the contrary, 98% of the males and only 23% of the females had "protruding eyes". Females had on average longer heads than the males at comparable size. Maturity dependent variables, as water content and eye index, improved the discrimination between sexes. At a certain size males were more close to the silver eel stage than were the females.

Keywords: *Anguilla anguilla*, eel culture, sex dimorphism, silver eel, head shape.

Introduction

In a specified population male and female silver eels can usually be distinguished by their size (Tesch 1991). Males reach the migratory silver eel stage at a smaller mean size than the females, and there is almost no overlap in length between the two sexes. Therefore, yellow eels longer than 450 mm normally can be considered females. A critical point in practical use of the size dimorphism, is to recognize early indices of maturation. The sum of fat and water content is fairly constant, approximately 80% of total weight, during the development from elver to silver eel (Boëtius and Boëtius 1985). By exchange with water the fat content gradually increases from 20 to 80% of the total energy reserve in silver males and females. Therefore, water content can be used as an indirect measurement of fat content, which in turn is an index of stage of maturity. The size of the eyes increases during early maturation, and Pankhurst (1982) used a ratio between eye area and total length as an index. Females with eye indices

greater than 6.5 were considered 'sexually maturing adults'. Pankhurst's (op. cit.) reevaluation of data by Boëtius and Boëtius (1967) revealed that silver males also had eye indices greater than 6.5.

As two phenotypes, broad and narrow headed eels, exist among females, these types were early suggested as two species or subspecies of the European eel (cf. Walter 1910). Nordquist (1917) found a continuous variation in relative head size. In later studies, phenotype was related to feeding habits (Törlitz 1922, Sivertsen 1938, Thurov 1958). Nordquist (1917) also showed that, within the size interval 350-450 mm, male eels had on average longer pectoral fins, longer distance between the eyes and shorter head length than females. Knights (1982) measured width of mouth, head and trunk, as well as length of the jaws, without finding differences between the sexes. On the other hand, Appelbaum and Kugler (1990) visually determined the sex correctly in 95% of cultured eels above 100 g in total weight. He found that females had on average a longer head and a lower condition factor than males.

The European eel (*Anguilla anguilla* L.) has no morphologically differentiated sex chromosomes (Wiberg 1983, Sola et al. 1984). Their gonads are undifferentiated until the eels reach 150-250 mm in total length (Kuhlmann 1975). In addition, the testis-like organ of yellow eels is possibly a reversible gonad which differentiates completely first during the metamorphosis to the silver eel stage (Colombo et al. 1984), i.e. the male sex of yellow eels is not supposed to be definite. The present study is based on eels from a long term experiment, aimed at testing whether the sex differentiation is influenced by water temperature. The special aim of this study was to test the possibility of using the degree of maturity and the external shape of individual eels to identify the determination of gonadal sex.

Material and methods

Experimental eel culture

Glass eels, caught in the English river Severn (Bristol Channel Fisheries Ltd) in April 1988, were imported by a Swedish eelfarm (Lyckeby Fiskodlingar AB), where they were cultured at about 25 °C during 13 weeks. In July 1988 about 7,000 as yet ungraded elvers (70-210 mm in total length, mean 117 mm) were delivered to the Institute of Freshwater Research, Drottningholm. The elvers were randomly and equally distributed to 9 tanks. In sets of three tanks per temperature, the eels were cultured at 17, 20 and 26 °C, as described by Holmgren et al. (1993). Eels were fed only on commercial dry feed (Lactamin). The culture was completely terminated in October 1990.

Sources of eels for the morphological study

All sexable eels from the culture were included. It was assumed that most of the individuals could be sexed by gonadal inspection when at least 250 mm in total length. Eels with folded ribbon-like gonads were considered females. When histologically examined, the germinal area of these gonads contained continuous rows of growing oocytes. Eels with regularly lobed Syrski organs (Freud 1877) were considered males. Such organs were domi-

nated by germ cell nests separated by connective tissue, although single oocytes sometimes occurred. Gonads from the remaining eels appeared as uniform threads or they were more or less irregularly lobed. These eels (523 specimens, 21% of 2,445 dissected eels) were excluded from the analysis of data.

The sexable eels may be divided in 4 categories, 410 selectively removed, 195 sampled and 576 dying specimens as well as 741 eels remaining alive until the end of the experiment (Table 1). The first category refers to the largest eels, which were continuously removed from the experiment. Eels in the second category were sampled, on two occasions, for histological examination of gonads. Firstly, samples of 20 eels (250-349 mm) per tank were taken when the median length was around 300 mm. Secondly, 20 eels (370-429 mm) per tank were sampled in the final phase of the experiment. The categories were not homogeneous, comparable samples. As described in the following section, the final treatment of the eels somewhat differed.

Morphological measurements

When removed alive, the eels were anaesthetized using 0.12 g benzocaine/l of culturing water. Total length was measured to the nearest mm. Excess water was shaken off, and total weight recorded with the accuracy of 0.1 g. Every removed eel was dissected for macroscopical inspection of gonads.

Table 1. Absolute numbers (N) and relative frequencies (%) of dissected males and females in different categories and cultured at different water temperatures.

	Males		Females	
	N	%	N	%
Category				
Selectively removed	298	17	112	55
Sampled (around 30 or 40 cm)	173	10	22	11
Dying	537	31	39	19
Remaining alive until the end	711	41	30	15
Total number	1719		203	
Temperature				
17°C	634	37	78	38
20°C	540	31	52	26
26°C	545	32	73	36
Total number	1719		203	

Most often the gonads were weighed and fixed in 5% glutaraldehyde in cacodylate buffer (pH 7.4). Later on, at least gonads from eels with uncertain sex were studied histologically. The tissue was embedded in HistoResinR (LKB, Sweden), and 2 μm thick cross-sections were cut on a Histo-rangeR (LKB) microtome and stained with Mayers haematoxylin, eosin and floxin. The diameter of each eye was measured both horizontally and vertically using digital calipers. A range of head dimensions was registered (see below), before cutting the skull longitudinally and collecting the sagittal otoliths. The body, without intestines, was weighed and stored deep-frozen until dried at 60 °C to constant weight.

Dying eels were usually not dried or histologically examined. The same was the case for the eels with macroscopically well defined sex at the end of the experiment. The measurements of head dimensions were introduced during the experiment when the first large females subjectively looked different from the males. Additionally, missing values sometimes occurred due to damaged eyes or otoliths.

Absolute measurements of mouth width, mouth length and head length were taken as shown in Fig. 1. Corresponding relative indices were obtained by division with total length. Mouth shape was expressed as the ratio between width and length of the mouth. Otolith length was defined as the mean maximum length of the two sagittal otoliths. As the difference between the two otoliths was negligibly small ($N=1,812$, paired t-test, $P=0.014$), the measurement was based on one otolith when the other one was damaged. Water content was calculated as the difference between fresh and dry weight, in relation to fresh weight of eel without intestines. In order to compare eye size with published data, the eye index was expressed according to Pankhurst (1982). The eye area was thereby divided by total length. Fulton's condition factor was used according to Ricker (1975), i.e. total weight divided by the cube of total length. Two variables were given as present (=1) or absent (=0). "Lower jaw" was present when it, in dorsal view of the head, was visible all the way from the tip to at least just in front of the eyes (Fig. 1).

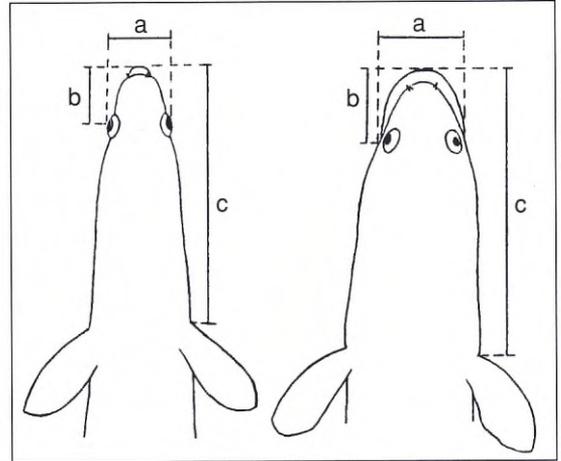


Fig.1. Head dimensions of eels in dorsal view: a. mouth width, b. mouth length and c. head length. The left eel has "protruding eyes"=1 and the right eel has "lower jaw"=1.

"Protruding eyes" was present when, in dorsal view of the head, the eye outlines were outside (covering) the mouth angles (Fig. 1).

Numerical and statistical analyses

The program package "SPSS/PC+, V4.0" (Norusis 1990a, Norusis 1990b) was used in computation and evaluation of data. Several variables were not perfectly normally distributed (Table 2) although each of them was well centered around the mean. The variables with significant deviations from normal distributions were not possible to transform to normal ones. All methods proposed by Sokal and Rohlf (1981) were applied without success, and therefore the untransformed data were used in every analysis.

Discriminant function analysis (DFA) is suitable in searching for variables to separate the two groups males and females (e.g. Camilleri and Shine 1990, Brennan et al. 1991). In this study, variables were selected by stepwise analysis based on minimizing the overall Wilks' lambda, while SPSS' default criteria were used for entering and removing variables. As the group covariance matrices were not equal (Box-M, $P<0.0001$), the separate group covariance matrices of the discriminant functions were used for the classification of cases.

Table 2. Descriptive statistics of 13 continuous variables. Tests for normal distributions (N.D.) (Kolmogorov-Smirnov) and for differences between males (M) and females (F) (Mann-Whitney).

Variable	Sex	N	Mean (SD)	Range = min - max	Skewness	N.D.* +/-	P-value Mann-Whitney
Total length (mm)	M	1719	387(35)	256-498	-0.50	-	<0.001
	F	203	432(75)	255-653	-0.23	+	
Total weight (g)	M	1719	110(31)	18-224	0.21	+	<0.001
	F	203	154(92)	22-608	1.31	-	
Head length (mm)	M	1491	46.1(4.0)	32.0-59.5	-0.27	-	<0.001
	F	196	54.6(9.0)	31.0-74.5	-0.49	-	
Mouth length (mm)	M	1458	12.2(1.2)	7.3-19.1	-0.05	-	<0.001
	F	189	14.2(2.4)	7.4-19.2	-0.56	+	
Mouth width (mm)	M	1458	14.7(1.6)	8.9-19.3	-0.70	-	<0.001
	F	189	16.4(3.3)	8.1-23.5	-0.36	+	
Otolith length (mm)	M	1663	2.29(0.24)	1.58-3.08	-0.14	-	<0.001
	F	202	2.57(0.36)	1.80-3.48	0.08	+	
Water content (%)	M	462	55.5(3.9)	47.7-71.3	1.25	-	<0.001
	F	97	63.6(4.6)	52.1-73.9	-0.37	+	
Eye index (Pankhurst)	M	1708	7.26(2.00)	2.46-12.54	-0.17	-	<0.001
	F	202	4.95(0.89)	2.76-7.84	0.09	+	
Condition factor (Fulton)	M	1719	0.185(0.021)	0.105-0.282	0.10	+	<0.001
	F	203	0.169(0.026)	0.110-0.302	0.81	+	
Relative head length (%)	M	1491	11.80(0.52)	9.96-13.96	0.22	+	<0.001
	F	196	12.67(0.75)	9.93-15.18	-0.35	+	
Relative mouth length (%)	M	1458	3.13(0.23)	2.31-4.46	-0.06	+	<0.001
	F	189	3.30(0.29)	2.61-3.96	-0.10	+	
Relative mouth width (%)	M	1458	3.76(0.29)	2.72-4.81	-0.27	+	0.984
	F	189	3.78(0.35)	2.91-5.21	0.59	+	
Ratio between mouth width and mouth length= mouth shape	M	1458	1.21(0.11)	0.81-1.74	0.50	-	<0.001
	F	189	1.15(0.12)	0.89-1.63	0.60	+	

* N.D. = + when $P > 0.05$, N.D. = - when $P < 0.05$

Results

Sex ratio and differences between sexes in single variables

In total 1719 males and 203 females were convincingly sexed. The total number of sexable eels (males or females) was somewhat different between temperatures (Table 1, Chi-square=12.44,

$P=0.002$), but the proportion of females, 10.6%, did not differ significantly between temperatures (2 x 3 contingency table, Chi-square=3.12, $P=0.210$). Each of the morphological variables (Table 2 and 3) was tested for differences between temperatures (Kruskal-Wallis-test, results not shown). Due to the nonrandom sampling of eels in different categories (Table 1), it was not possible to detect any clear-cut effect of temperature. For

Table 3. Absolute numbers (N) and relative frequencies (%) of dissected males and females with different values of the dichotomous variables "lower jaw" and "protruding eyes".

	Males		Females	
	N	%	N	%
"Lower jaw"				
Not visible = 0	1439	99	25	13
Visible = 1	17	1	164	87
Total number	1456		189	
"Protruding eyes"				
Not present = 0	30	2	145	77
Present = 1	1427	98	44	23
Total number	1457		189	

example, different distributions of age in culture might mislead the interpretation, by either synergistic or antagonistic interaction with temperature. Therefore the analysis of differences between sexes was performed without regard to temperature.

The examined females were significantly larger than the males, which was reflected in all of six variables given as absolute measurements (Table 2). The males were more close to the silver eel

stage than the females. This was shown by lower water content and higher eye index and condition factor. The relative head and mouth lengths were higher in females. The mouth shape displayed a higher mean value in males. The relative mouth width was not significantly different between sexes. Unfortunately, more or less protruding eyes often covered the mouth angles and thereby obscured the interpretation of data on relative mouth width. The distributions of the variables "lower jaw" and "protruding eyes" were significantly different between males and females (Chi-square-test, 2 x 2 contingency tables, in both cases $P < 0.0001$). "Lower jaw" was almost never visible in males and "protruding eyes" almost exclusively covered the mouth angles (Table 3, Fig. 1), while the inverse relation was true for most of the females.

DFA - selected variables and classification results

Firstly, 13 continuous (Table 2) and 2 dichotomous (Table 3) variables were offered to the DFA (Run 1). Seven variables were selected (Table 4), where, in descending order, "lower jaw", water content and relative head length showed the high-

Table 4. Discriminant analysis when 15 variables were offered (all variables in Tables 2 and 3). In the two groups, males and females, 255 and 84 cases had complete data sets. A. Selected variables, listed in the order in which they were entered in the analysis. B. Indicated power of the discriminant function.

A.			B.	
Variable	"Coefficient"*	"Correlation"*		
1. "Lower jaw"	1.89	0.706	Wilks' Lambda	0.1990
2. Water content	0.177	0.508	Chi-square	520.6
3. Total weight	0.0158	0.182	df	7
4. Rel. head length	0.478	0.305	P-value	<0.0001
5. Condition factor	-12.7	-0.185	Discriminant function at group means	
6. Eye index	-0.0762	-0.294	Males	-1.16
7. Mouth shape	1.03	-0.145	Females	3.44
(constant)	-16.6	-	Correctly classified cases (%)	
			Males	94.9
			Females	95.2
			Males+females	95.0
			Proportion (%) of females:	
			Actual	24.8
			Predicted	27.4

* "Coefficient" = unstandardized canonical discriminant function coefficient.

* "Correlation" = pooled within-groups correlation between discriminating variable and the canonical discriminant function.

Table 5. Discriminant analysis when 14 variables were offered (all variables in Table 2 and 3, except for water content). In the two groups, males and females, 1,454 and 189 cases had complete data sets. A. Selected variables, listed in the order in which they were entered in the analysis. B. Indicated power of the discriminant function.

A.

Variable	"Coefficient"*	"Correlation"*
1. "Lower jaw"	4.40	0.849
2. "Protruding eyes"	-1.68	-0.594
3. Eye index	-0.162	-0.250
4. Condition factor	-26.8	-0.119
5. Total weight	0.0224	0.157
6. Rel. head length	0.789	0.239
7. Rel. mouth width	0.477	0.012
8. Head length	-0.0127	0.273
(constant)	-0.733	-

* "Coefficient" and "Correlation" as in Table 3.

B.

Wilks' Lambda	0.1860
Chi-square	2171
df	8
P-value	<0.0001

Discriminant function at group means

Males	-0.76
Females	5.72

Correctly classified cases (%)

Males	97.9
Females	93.1
Males+Females	97.3

Proportion (%) of females

Actual	11.5
Predicted	12.6

est correlation between the variable and the discriminant function. The overall misclassification of cases was 5.0%, and the proportion of females was somewhat overestimated. In a second run (Run 2) water content was excluded in order to increase the number of cases with complete data sets. Eight variables were selected to the discriminant function (Table 5). However, the discriminating variable "lower jaw" had an extremely high correla-

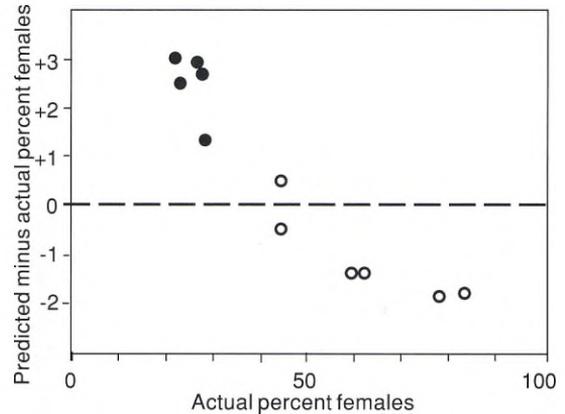


Fig. 2. Bias in predicted proportion of females in relation to actual sex ratio, in simulated samples for discriminant functions based on seven variables as in Table 4, ● five independent samples of 50% of sexed specimens, 148-174 classified eels, ○ two independent samples of each 10, 20 and 40% of sexed males, and each of six samples combined with the same 84 females, 108-191 classified eels.

tion of 0.849 to the function. The second selected variable was "protruding eyes", although it was highly intercorrelated to "lower jaw". By excluding water content, the number of classified cases was increased from 339 to 1,643. Despite decreased overall misclassification, to 2.7%, the proportion of correctly classified females was lower than in Run 1. By inspection of individual cases, this could be explained by an increased misclassification rate of females with "lower jaw" absent.

DFA - effect of skewed sex ratio

In order to illustrate the bias of predicted sex ratio in relation to actual sex ratio, different proportions of the sexes were randomly sampled from the total population of sexed eels. For each sample the selected variables from Run 1 were offered to a new DFA. The predicted percentage of females was overestimated when females actually constituted less than 50% (Fig. 2). When females were in excess the predicted proportion was underestimated. In the simulated range of 20 to 85% females, the difference between predicted and actual percentage of females never exceeded three units.

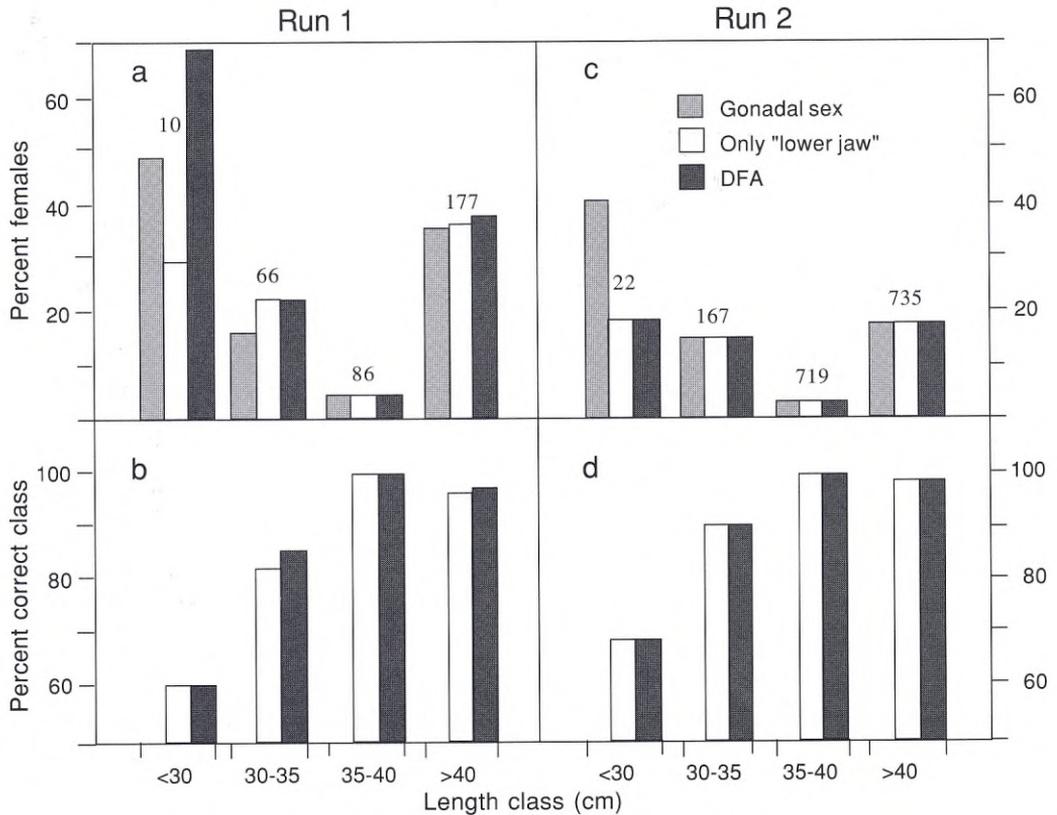


Fig. 3. Compared ability between the variable "lower jaw" and the discriminant functions (Run 1: a. and b., Run 2: c. and d.) to predict gonadal sex of eel in different size classes.
 a. predicted proportion of females, in 339 eels with observations of water content. The numbers of sexed eels in each size class is indicated above the bars,
 b. proportion of overall correctly classified eels per size class in Run 1,
 c. as a. but based on 1,633 eels with observations of "lower jaw",
 d. as b. but for Run 2 as in c.

Predicted sex in relation to eel size

The single variable "lower jaw" and the discriminant function was compared with respect to their ability to predict gonadal sex of different size classes of eels. For the 339 classified eels in Run 1, both methods were almost equally good in predicting sex ratio when the eels were at least 300 mm (Fig. 3a). The use of discriminant function (i.e. Six variables in addition to "lower jaw") slightly increased the proportion of overall correctly classified cases (Fig. 3b), but a misclassification rate of less than 5% was only found when the eels were more than 350 mm. In Run 2, where

water content was excluded, 1,633 eels were classified. "Lower jaw" and the discriminant function gave exactly the same predicted proportion of females (Fig. 3c) and the same percentage of overall correctly classified cases (Fig. 3d).

Water content, the second selected variable in Run 1, decreased with total length (Fig. 4). At any specific length within the observed interval, 250-600 mm, there was hardly any overlap in water content between sexes. Relative head length was correlated to the discriminant functions (Table 4 and 5), but it did not differ between sexes in eels less than 300 mm (Fig. 5). Females longer than 300

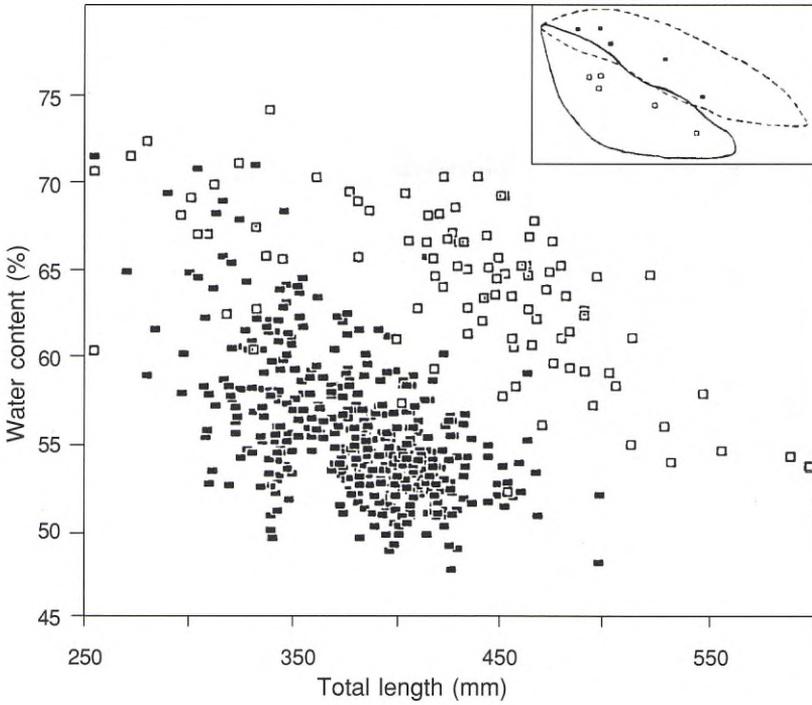


Fig. 4. Water content in relation to total length in males (filled boxes, N=462) and females (open boxes, N=97). Small figure: Areas of values, except for marked outliers, surrounded by solid line (males) and broken line (females).

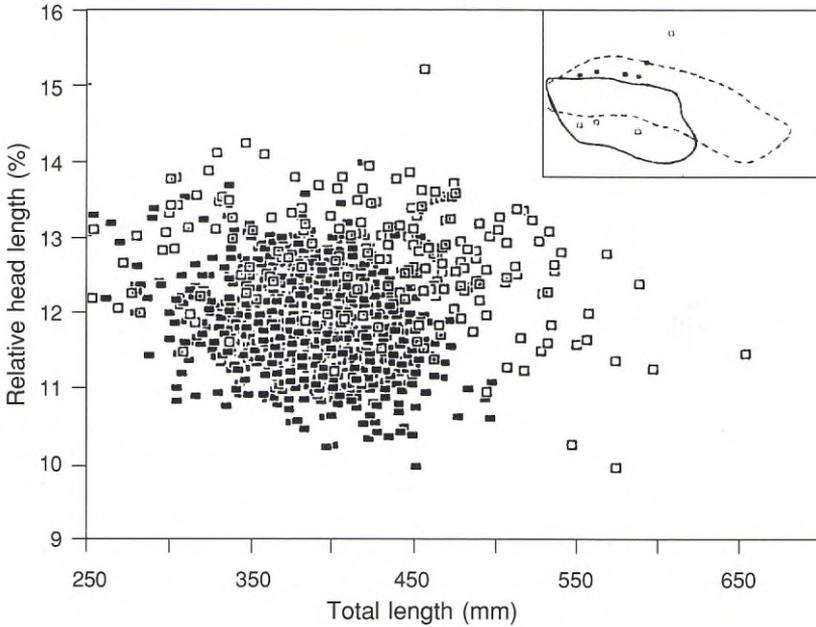


Fig. 5. Relative head length in relation to total length in males (filled boxes, N=1,491) and females (open boxes, N=196). Small figure: as in Fig. 4.

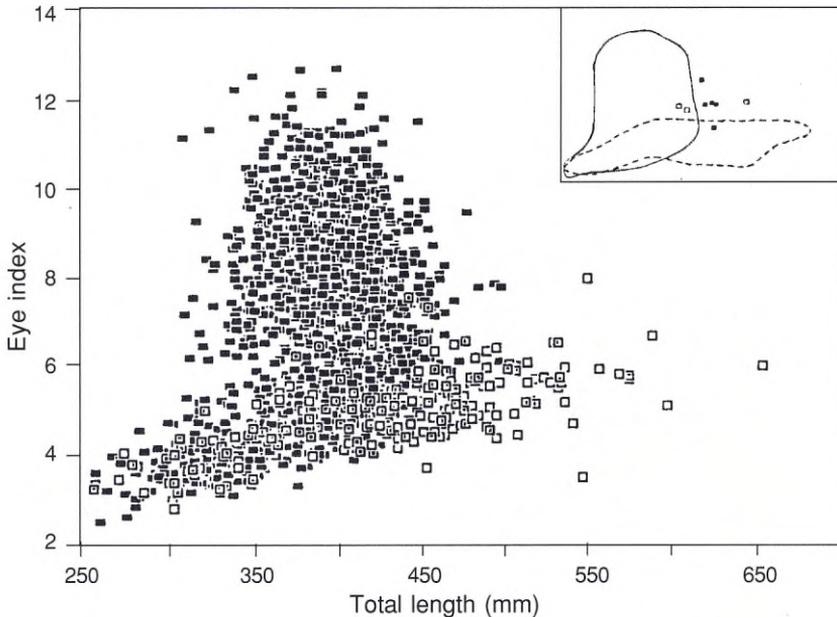


Fig. 6. Eye index in relation to total length in males (filled boxes, $N=1,708$) and females (open boxes, $N=202$). Small figure: as in Fig. 4.

mm had on average relatively longer heads than males, although the separation between sexes was not as distinct as for water content. The correlations between eye index and the discriminant functions were comparable to those between relative head length and the functions (Table 4 and 5). In females the eye index constantly increased with total length (as expected from the mathematical character of the index, a ratio between an area and a length measurement), but it seldom reached the value of 6 (Fig. 6). In males larger than 350 mm, there was no correlation between eye index and total length. On the other hand, larger males displayed a wide range in eye index, with values between 4 and 13.

Discussion

Sex dimorphism in size, shape and stage of maturity

In this experiment, females only constituted 10.6% of sexable eels. The females reached a higher

mean size than the males. This was explained by decreasing growth of most males during the last year of the experiment (Holmgren et al. 1993) while many females were allowed to reach more than 450 mm in total length before they were removed from the culture.

In 87% of the females, the lower jaw (or actually the lips of the jaw) was visible, in dorsal view of the head, from the tip to at least just in front of the eyes. This visibility of the lower jaw was absent in 99% of the males. A visible lower jaw has earlier been reported as normal for broad headed eels and as unusual for narrow headed eels (Törlitz 1922). When the present results on relative head and mouth lengths were compared to corresponding measurements by Törlitz (op. cit.) the mean values of cultured females were comparable to broad headed and the males to narrow headed eels. All eels in the cited study were females. With respect to relative mouth width, both females and males showed higher means than broad headed eels. However, in Törlitz's study the occurrence of eyes covering the mouth angles was not men-

tioned. This phenomenon (i.e. "protruding eyes" present) was true for 98% of the cultured males and for 23% of the females.

The fat content increases during the development from elver to silver eel (Boëtius and Boëtius 1985) with a corresponding decrease in water content. Males in the present study had a lower mean water content in spite of smaller mean size than the females. As the difference in water content between sexes was evident at comparable sizes of eels down to at least 300 mm in length, water content might be an earlier indicator of sex differentiation and maturation than for example the relative eye size. In the present study not more than ten females had eye indices indicating early maturation, according to Pankhurst (1982), while less than one third of the males, mainly those smaller than 350 mm, had eye indices below 6.5.

Prediction of sex - DFA and single variables

All performed DFA:s gave correct classification rates of well above 90% in each sex and the difference between predicted and actual proportion of females never exceeded three percentage units. Such an outcome would be fairly excellent if independent of eel size. Unfortunately, the results, when using DFA or the single variable "lower jaw" in sex determination of eels less than 300 mm, were hardly better than by chance. The variables relative head length and eye index displayed two more or less separated clusters in relation to total length, but the overlaps between sexes were complete when eels were smaller than 300 mm. The most promising discriminating variable for smaller eels was water content, but the number of observations was too low to confirm this suggestion statistically.

The morphological study thus failed in finding variables for sex determination of small eels. The main purpose could although still be fulfilled. Due to good separation between sexes in maturity dependent variables of larger eels, more than 300-350 mm, eels with low water content and high eye index but with only irregular lobed Syrski organs should certainly be regarded as males.

Interpretation of head shape

The visual distinction between sexes in this experiment was strongly improved by the tendency of females to be broad headed. Nordquist (1917) found the highest mean values of relative head length and mouth width in intermediate size classes of both male and female eels. A phenotypical adaption (thus not selection of genotypes) with change in the jaw apparatus has been confirmed in domesticated cichlids (Witte 1984). Later studies suggested that adaptional changes in relative mouth width of eel might occur within one growing season, in association with changed abundance and composition of prey organisms (Lammens and Visser 1989). In the studied lakes all eels larger than 400 mm were broad headed females, while 95% of smaller eels were males or just undifferentiated.

In the present study, no traditional grading was performed. Larger and growing eels were thus present together with small and almost nongrowing eels. As 30-50% of initial numbers just disappeared during the experiment (Holmgren et al. 1993), it was concluded that small eels were exposed to cannibalism by larger eels. A hypothesis of phenotypical adaption in cannibalistic females is still very speculative, but in an ongoing experiment, the head dimensions are repeatedly measured on individually tagged eels.

Concluding remarks

The appearing visual difference between larger males and females from the present eel culture, was supported by means of measurable variables of maturity dependent and shape describing nature. The presence of "lower jaw" was highly associated with female sex, while males usually had "lower jaw" absent and "protruding eyes" present. Next to the two dichotomous variables, water content, eye index and relative head length improved the discrimination between sexes.

The eels were cultured at different temperatures, but the sampling was not suited for testing temperature effects on allometric growth. The within sex variation of discriminating variables might be smaller in a comparably large sample of eels cultured at uniform temperature.

With known distributions of maturity and shape indices of females and males, it is probably useful to create discriminant functions for other eel populations as well. A practical recommendation for eel culturists could be to look for, and separate broad headed and potentially cannibalistic females from males. Further more, at the size when males cease to grow, females still have potential for a long period of growth.

Acknowledgments

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Differences in Reproductive Traits between Sea-ranched and Wild Sea-trout (*Salmo trutta*) Originating from a Common Stock

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Abstract

It has been hypothesized that the absence of breeding competition, resulting from artificial spawning technique, would result in sea-ranched trout and salmon developing less pronounced secondary sexual characteristics such as the kype, adipose fin, nose and lower jaw, but would result in increased fecundity. A comparative analysis of certain traits of sexually mature, male and female, wild and sea-ranched sea trout (from the River Dalälven) has revealed the following associations: (1) Wild males had longer bodies but the size of their secondary sexual characteristics, when compensated for body size, did not differ from those of the sea-ranched fish. A canonical discriminant analysis (CDA) revealed a significant difference between wild and sea-ranched trout, with high loadings found for body weight, size of the adipose fin and lower jaw, when all values were adjusted for body length. (2) There was no difference in body length between wild and sea-ranched females. Wild females, on average, had longer noses. Both categories of females produced about the same number and size of eggs. Wild females ovulated about one week before the sea-ranched ones did. A CDA revealed a significant difference between wild and sea-ranched females, with a high loading for nose size when adjusted for body length. Our analyses thus show in a limited way that the secondary sexual characteristics of both wild males and females were more pronounced than those of the sea-ranched fish. This finding accords with the hypothesis prediction. However, there was no significant difference between the primary sexual characteristics of the two categories of females. This contradicts the hypothesis. The observed weak response to artificial spawning could be due to (1) genetic introgression in nature, (2) wild individuals have been stripped and used for artificial breeding, (3) the two strains have been isolated for too short a period of time.

Introduction

Mariculture and the restoration of natural salmonid populations in Europe and North America during recent years have increased to such extent that the numbers of escaped, or deliberately released, farmed fish approaches or even exceeds the number of naturally produced, wild individuals in certain localities (Maitland 1989, Lund et al. 1991; cf. Gausen and Moen 1991). There is now concern that such fish farming will result in an evolutionary divergence of the farmed strains away from their wild phenotypic norms (e.g. Flem-

ing and Gross 1992), and that, furthermore, interactions will occur in nature between farmed and wild stocks in respect to diseases, parasites, behavioural ecology and genetics (Saunders 1991). Ecological concern has been mainly focused on how the elimination of distinctive gene pools by the breaking down of isolation mechanisms between stocks, will result eventually in a possible reduction in the Darwinian fitness of the wild stock, due to continuous introgression of non-indigenous genes, or gene combinations (e.g. Altuhkov 1981).

In contrast to conditions in the wild, sea-ranching involves raising eggs and fry in hatcheries,

with subsequent release of the smolts into the sea, where they stay for one or more years. After that time, the surviving adults return to their site of release, and form the brood stock for the next generation. This regime will almost certainly exert a selection pressure for new phenotypes capable of succeeding in this new environment, as well as relaxing selection for traits that were previously advantageous in the wild. This divergence of the farmed from the wild fish will probably result in the former becoming an inferior stock under natural conditions (Fleming and Gross 1992).

Another possible effect of sea-ranching is due to the absence of breeding competition resulting from artificial spawning. Hence, selection on competitive ability and elaborate secondary sexual traits, such as the relative size of the kype, nose, lower jaw, adipose fin, and body size will be relaxed for both males and females.

The aim of this study was to discover whether, after six generations, hatchery reared sea-ranched trout (*Salmo trutta* L), having been exposed to different sexual selection pressure, due to the absence of breeding competition, manifested any changes in either their body size, primary or secondary sexual characteristics, compared to wild conspecifics from the same original genetic stock.

Material and Methods

The study was carried out during October and November in 1991 at the Fishery Research Station at Älvkarleby, central Sweden. The research station is situated on the River Dalälven, which flows into the Baltic Sea. Seven kilometres upstream of the estuary, anadromous fish are hindered from continuing their natural migration by a hydro electrical power plant and dam. Baltic salmon (*Salmo salar*) and sea trout migrating upstream are caught by using a trap in a fish ladder. The fish is then transported, without being handled, via a pipe-line system to a big storage tank (130 m³) placed in a sorting hall where they are kept and eventually used for artificial breeding. Sea trout migrate upstream from May to October each year. All the sea trout caught during any week (i.e. the

arrival date) are marked with a unique combination of dots tattooed beneath the pelvic fins. These marks are noted later when the fish is used for breeding, which can be some months later. Each week the maturity of the females are checked and if they have ovulated they are stripped. The date of stripping, thus ovulation, is noted.

Two categories of sea trout are today present in the River Dalälven, both of which are descendants of the native population that existed prior to the construction of the dam in 1915. The first category is a strict cultivated strain, which was established in 1967. A large number of adults were caught at the Fishery Research Station and used for artificial breeding and cultivation. The offspring of these fish were marked by cutting off the left pelvic fin on their release. After the start of the 'sea-ranched' group only fin-clipped trout have been used as parents. The second category is mainly wild conspecifics from the River Dalälven. They are identified on having both pelvic fins intact. The fish in this group are also to some extent descended from sea-ranched parents spawning in nature and strayers from other rivers. Furthermore, they could be descendants from two introduced strains in the river. Those strains are originating from the River Weichsel (northern Poland) and from the River Klarälven (southern Sweden). However, according to unpublished records of the fish used for artificial breeding at Älvkarleby, the numbers of smolts of these two strains released have never accounted for more than 10% of the total number of trout smolts originating from the River Dalälven. It should be noted that farmed sea trout have also been released into the river at Älvkarleby long before 1967 (since 1872), but then mainly as fry, or one-summer parr, and without being marked. Nevertheless, all the unmarked brown trout will be referred to as the "wild" group.

In this study we measured morphological characters on the 134 males (109 sea-ranched and 25 wild) and the 145 females (109 sea-ranched and 36 wild) caught in the fish-trap in 1991. Measurements included body weight, total length, the post-orbital to caudal peduncle length (POCP) and the sizes of the following secondary sexual characteristics viz., kype, nose, jaw and adipose fin (Fig. 1).

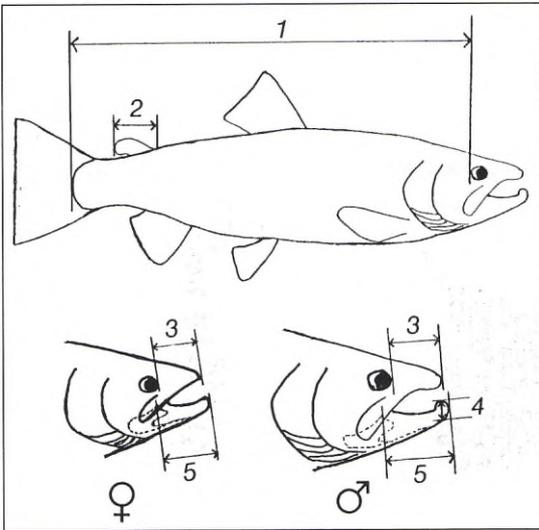


Fig. 1. The morphological traits recorded for each fish: (1) post-orbital-caudal-peduncle-length (POCP), (2) adipose fin length, (3) nose length, (4) height of kype (note the difference in structure between the skulls of males and females), (5) jaw length.

The kype data for the females were not analysed statistically, because it is not a pronounced character in females (Fig. 1). To estimate the age of the fish 5-10 scales were sampled from each male. It proved possible to establish the age of 113 males. Each female was weighed before and after stripping, and the volume their eggs was estimated. The number of eggs produced by each female was estimated from the egg volume and from the number of eggs needed to fill a 25 cm scale (i.e. the Brofeldt-scale, Edwards 1978). At time for artificial spawning, the tattooed dots, assigning the arrival date, could only be read for 77% of the males and 59% of the females.

Comparison of the data for the wild and the sea-ranched groups of trout was made in two different ways. Firstly, by using Bonferonni's method pairwise comparisons were made for each variable (the two sexes were treated separately), both for the raw data and for the relative values compensated for POCP. The residuals from multiplicative regressions ($y=a \cdot x^b$; x being the POCP, y the trait and a, b constants) were used as relative values. Secondly, a canonical discriminant analysis was

carried out on the relative values for some of the measured traits (weight, jaw, adipose fin, kype and nose). All tests were two-tailed and all analyses were made using SAS statistical software.

Results

Males

Wild males were on average about 4.5 cm longer than sea-ranched ones (Table 1). In consequence, wild males also were heavier, had longer noses and jaws, larger kypes and adipose fins. No differences were found in ages, arrival dates, or condition index values (Table 1). The two groups did not

Table 1. Comparison of different traits of adult male sea trout from wild and sea-ranched strains from the River Dalälven. The values presented here are original values (POCP=Post-orbital-caudal-peduncle-length; N=sample size; W=wild strain; S=sea-ranched strain).

Variable	Strain	N	mean+SD	P
Total length (cm)	W	25	78.3+7.38	<0.005
	S	109	73.8+6.44	
POCP (cm)	W	25	65.0+6.20	<0.005
	S	109	61.2+5.37	
Weight (kg)	W	25	5.92+1.40	<0.01
	S	109	5.11+1.36	
Nose length (cm)	W	25	7.78+0.97	<0.005
	S	109	7.19+0.88	
Jaw length (cm)	W	25	7.72+0.88	<0.001
	S	108	7.10+0.81	
Kype height (cm)	W	25	2.43+0.48	<0.05
	S	109	2.22+0.36	
Adipose fin length (cm)	W	20	7.36+0.83	<0.001
	S	92	6.68+0.69	
Condition index	W	25	20.7+2.27	NS
	S	109	21.1+2.17	
Age (years)	W	21	4.3+0.80	NS
	S	90	4.1+0.66	
Arrival date (week no.)	W	20	33.4+4.73	NS
	S	83	33.6+3.98	

Table 2. Comparison of different traits of adult male sea trout of wild and of sea-ranched origin, using values adjusted multiplicatively for post-orbital-caudal-peduncle-length (N=sample size; W=wild strain, S=sea-ranched strain).

Variable	Strain	N	mean+SD	P
Weight	W	25	-0.16+0.67	NS
	S	109	0.05+0.50	
Nose length	W	25	0.10+0.62	NS
	S	109	-0.01+0.60	
Jaw length	W	25	0.11+0.47	NS
	S	108	0.00+0.43	
Kype height	W	25	0.05+0.38	NS
	S	109	0.01+0.29	
Adipose fin length	W	20	0.17+0.56	NS
	S	92	0.00+0.50	

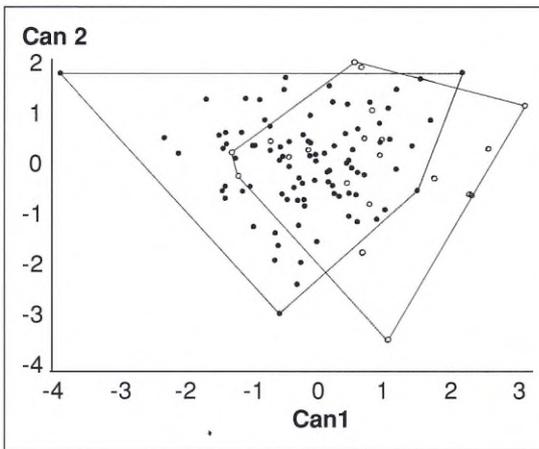


Fig. 2. The first two axes of a canonical discriminant analysis based on the residuals of five secondary sexual characteristics of male sea trout after multiplicative value adjustment for post-orbital-caudal-peduncle-length. The first axis had especially high positive loadings for the relative size of the adipose fin and the lower jaw and high negative loading for relative body weight. The second axis had especially high positive loading for the relative size of the nose. Circles indicate wild males, dots indicate sea-ranched males. Squared Mahalanobis distance between classes=0.909, $F=2.87$, $P<0.019$.

differ in regard to the relative sizes of any of the measured traits (Table 2). When the relative values for five of the measured traits were subjected to canonical discriminant analysis, the wild and the sea-ranched males were found to differ significantly (Fig. 2). The first canonical axis explained more than 95% of the overall variation and revealed an especially high negative loading for relative body weight and a high positive loading for the relative sizes of the adipose fin and the lower jaw.

Females

Wild and sea-ranched females did not differ significantly in any of the measured traits except in nose size; wild females had, on average, longer noses than sea-ranched ones (Table 3). The relationships were the same for the relative measurements (Table 4). The mean arrival dates of the two groups did not differ significantly, but the wild females, on average, ovulated about one week earlier than the sea-ranched females (Table 3). When the relative values of the four measured traits were subjected to canonical discriminant analysis, the wild and sea-ranched females differed significantly (Fig. 3). The first canonical axis explained more than 97% of the overall variation and revealed an especially high positive loading for the relative size of the nose.

Discussion

For salmonids it has been suggested that breeding competition is important in the evolution of body size and primary and secondary sexual characters in males, as well as of the females (e.g. van den Berghe and Gross 1989, Fleming and Gross 1989, Järvi 1990, Fleming and Gross 1992). Differences in the selection mechanisms for choosing mates during artificial spawning and during natural spawning may result in morphological and behavioural differences arising between sea-ranched and wild offspring. Due to the absence of breeding competition, sea-ranched males and females may develop less pronounced secondary sexual charac-

Table 3. Comparison of different traits of adult female sea-trout from wild and sea-ranched strains from the River Dalälven (POCP=Post-orbital-caudal-peduncle-length; N=sample size; W=wild strain, S=sea-ranched strain).

Variable	Strain	N	mean+SD	P
Total length (cm)	W	36	71.6+4.54	NS
	S	109	71.7+4.85	
POCP (cm)	W	36	61.0+3.66	NS
	S	109	61.3+4.22	
Weight before stripping (kg)	W	36	4.73+0.97	NS
	S	109	4.63+1.01	
Weight after stripping (kg)	W	36	3.94+0.82	NS
	S	109	3.86+0.85	
Weight of all eggs (kg)	W	36	0.79+0.20	NS
	S	109	0.78+0.24	
Nose length (cm)	W	36	5.67+0.83	<0.001
	S	109	5.23+0.58	
Jaw length (cm)	W	36	5.43+0.60	NS
	S	109	5.27+0.52	
Adipose fin length (cm)	W	34	5.12+0.48	NS
	S	95	5.18+0.61	
Estimated number of eggs	W	36	6346.6+1564.6	NS
	S	98	6402.1+1218.9	
Diameter of eggs (cm)	W	36	0.570+0.021	NS
	S	98	0.567+0.022	
Total volume of eggs (L)	W	36	1.01+0.23	NS
	S	98	0.98+0.26	
Condition index	W	36	18.6+2.06	NS
	S	109	18.0+2.02	
Arrival date (week no.)	W	17	35.8+2.43	NS
	S	68	34.9+3.69	
Date of ovulation	W	36	290.3+6.30	<0.001
	S	109	298.0+8.97	

Table 4. Comparison of different traits of adult female sea trout of wild and sea-ranched origin, using values adjusted multiplicatively for post-orbital-caudal-peduncle-length (N=sample size; W=wild strain, S=sea-ranched strain).

Variable	Strain	N	mean+SD	P
Weight	W	36	0.06+0.43	NS
	S	109	-0.09+0.41	
Weight of all eggs	W	36	0.04+0.11	NS
	S	109	0.01+0.17	
Nose length	W	36	0.37+0.69	<0.001
	S	109	-0.08+0.50	
Jaw length	W	36	0.10+0.44	NS
	S	109	0.00+0.36	
Adipose fin length	W	34	-0.01+0.39	NS
	S	95	0.02+0.50	

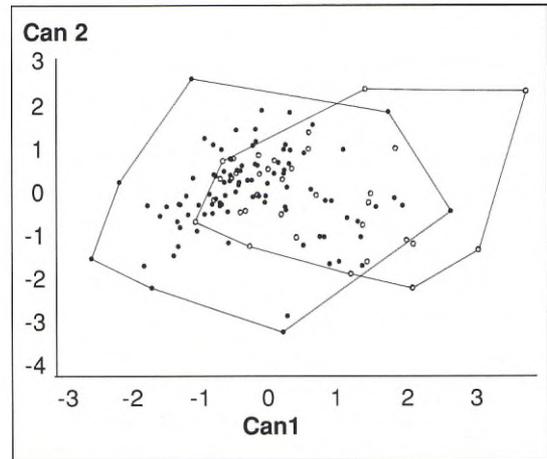


Fig. 3. The first two axes of a canonical discriminant analysis based on the residuals of four secondary sexual characteristics of female sea trout after multiplicative value adjustment for post-orbital-caudal-peduncle-length. The first axis had especially high positive loadings for the relative size of the nose. The second axis had high negative loading for the relative weight. Circles indicate wild females, dots indicate sea-ranched females. Squared Mahalanobis distance between classes=0.647, $F=3.95$, $P<0.005$.

ters, such as the kype, adipose fin, nose and lower jaw, but show an increased fecundity (Fleming and Gross 1989). Few studies have examined the reproductive behaviour and reproductive success of sea trout and the relation of these factors to mor-

phological traits. It is therefore difficult satisfactorily to outline the implications of the differences between the wild and the sea-ranched strain, that we have found from a canonical discriminant analysis of the data.

Fleming and Gross (1992) showed that sea-ranched male coho salmon (*Oncorhynchus kisutch*), despite investing more in primary sexual characteristics (expressed as testes size), exhibited less spawning activity, were generally less active and were less aggressive than wild males. In stream tank experiments, Petersson and Järvi (unpublished data) have studied the reproductive behaviour of wild and sea-ranched trout. Amongst other associations there was a strong correlation between male reproductive success, the relative size of his adipose fin and social rank. Adipose fin size had a high loading on the first canonical axis in our present study, suggesting that sexual selection for a large-sized adipose fin in males diminished in the course of artificial breeding. The weight of wild males, adjusted for body length, tended to be relatively less than of sea-ranched males, suggesting that wild males were on average more "streamlined". Body shape is generally supposed to be under conflicting selection pressures in teleost fishes (e.g. Riddell and Leggett 1981, Taylor and McPhail 1985a, Swain and Holtby 1989). The optimal body shape for burst and for sustained modes of swimming differs. A deep body confers superior burst-swimming performance, whereas a fusiform or "streamlined" shape is superior for sustained swimming (Webb 1978, Taylor and McPhail 1985b). Studies on juvenile coho salmon (Swain et al. 1991) and on adult female coho salmon (Fleming and Gross 1989), have shown that body shapes of sea-ranched strains were more streamlined and those of wild strains were deeper-bodied, suggesting that the former were better adapted to sustained swimming and the latter burst swimming. However, among female coho salmon, there was a negative relationship between sea-migration distance and body depth (Fleming and Gross 1989). Hence, assuming that the migration patterns of wild and sea-ranched trout in the sea are identical, it seems reasonable to predict that wild sea trout should be more deeper-bodied, while sea-

ranched ones should be streamlined. The results of the present study do not support this prediction.

Sea-ranched, female coho salmon had smaller kypes, body depths and body lengths compared to wild females (Fleming and Gross 1989). In the present study, the sea-ranched females, on average, had relatively shorter noses than the wild females. Because the definition of kype size in the coho salmon study corresponds with the definition of nose length in our study, there is therefore a concordance between the results of the two studies, i.e. sea-ranched females of both species showed less pronounced secondary sexual characteristics. Female coho salmon allocate more energy resources to their primary sexual characteristics by producing larger eggs (Fleming and Gross 1989). We found no such difference between the wild and the sea-ranched females. However, the wild, female sea trout ovulated one week earlier than the sea-ranched ones. This implies that the ovulation of sea-ranched females is physiologically inhibited due an unintentional selection favouring delayed ovulation during the artificial breeding process.

We found differences between the wild and the sea-ranched trout in the River Dalälven, and these were valid for both sexes. Nevertheless, the differences are not of such a kind, or magnitude, that differences in any single character could be used to separate the two strains. There are several possible reasons for this. (1) The two strains of trout are most likely interbreeding in the field, i.e. the gene pool of the sea-ranched strain dilutes that of the wild. This process is most likely sped up because the sea-ranched population outnumbers the wild one. (2) Since 1986, unmarked sea-ranched trout have been stripped and used for artificial breeding, i.e. in part, the wild, unmarked population has been subject to the same kind of selective pressures as the sea-ranched one. This fact, together with the one previously mentioned, makes it difficult to separate differences due to genetic causes and environmental ones (cf. Swain et al. 1991). (3) The sea-ranched strain was established in 1965, which means that inbreeding in that strain has been going on for about six generations (generation time = 4.5 years). Depending on the selec-

tion pressure operating on the specific quantitative character and the heritability of the character, six generations may be too few to lead to manifest differences in specific characters between the wild and the sea-ranched strains. However, Fleming and Gross (1992) have reported differences in the reproductive behaviour of wild and of fourth generation, hatchery-reared, sea-ranched, coho salmon. In general, the response to sexual selection pressure by the sea-ranched, coho salmon would seem to be stronger than by the sea trout. This applies to differences in the development of both primary and secondary characteristics. One reason for this discrepancy between coho salmon and sea trout is probably due to the fact that the former only reproduce once during its lifetime (i.e. semelparous, cf. Schaffer (1974)) and the latter several times (i.e. iteroparous, Mills (1971)). In semelparous species, during natural spawning, competition is more intense than in iteroparous ones, and, hence, selection for secondary sexual characteristics is more pronounced in coho salmon than in sea-trout.

The circumstantial, evidence presented in this study, indicates that differences between wild and sea-ranched trout in their natural and sexual selection patterns have been manifested in different reproductive traits, such as secondary sexual characters and date of ovulation.

Acknowledgments

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NOTES AND COMMENTS

B-type Otolith Structure in Perch, *Perca fluviatilis*, Maintained in the Laboratory

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Fish otoliths usually grow by continuous deposition of increments or daily increments. Recently Umezawa and Tsukamoto (1991) reported that under prolonged starvation and/or low temperature in the laboratory the otoliths of Japanese eel, *Anguilla japonica*, grew peculiarly without deposition of apparent increments. They categorized this kind of otolith structure as B-type structure and believed that occurrence of this structure could be the reason for very low rate of increment deposition in some cases. B-type structure was also found in perch maintained in the laboratory, as reported in this paper.

Perch (fork length 11.9-18.1 cm) were collected from the Trawsfynydd Lake in North Wales, U.K., using a seine net during April-July 1987. Twenty-six healthy fish were selected and transported back to the laboratory. They were reared in 3 600-L tanks: 9 fish were held under constant light and a constant temperature of 22 °C, 9 fish under constant light and diel temperatures of 25 °C and 22 °C for 14 and 10 h respectively, and 8 fish under a diel photoperiod of 14 h light and 10 h dark period at a constant temperature of 22 °C. Oxygen was provided to each tank through bubbling air. As none of the fish ate provided food (live fly larvae and earthworms), it was assumed that no feeding took place. To mark the otoliths the fish were injected with tetracycline at a dose of 100 mg tetracycline per kg fish weight 5 d after acclimatization to the experimental conditions. The fish

under the diel photoperiod were sampled 15 d after the injection, while fish under the constant light died in 3-13 days following the injection. Otoliths (sagittae) were removed and cleaned. Excess material was removed through grinding from both sides of each otolith to produce a thin section, which was studied using a light microscope.

Tetracycline administration introduced a clear fluorescent mark in the otoliths, which showed growth under any one of the three regimes despite no food intake. However, the marginal region of the otolith formed during the experimental period did not contain apparent increments, while the region formed during the pre-experimental period (in the wild) exhibited distinct increments (Figs. 1A-B).

This kind of peculiar otolith growth (B-type structure) may be more than of academic interest. Formation of B-type structure alternately with deposition of daily increments, if this could happen, will cause underestimation of increment deposition rate.

B-type structure, noted in some of laboratory-reared fish, has often coincided with tetracycline administration. Campana (1983) reported that some starry flounder, *Platichthys stellatus*, stopped increment deposition at various times after tetracycline injection. Hettler (1984) failed to observe any increments beyond the fluorescent band after immersion of larvae of spot, *Leiostomus xanthurus*, and pinfish, *Lagodon rhomboides*, in tetracy-

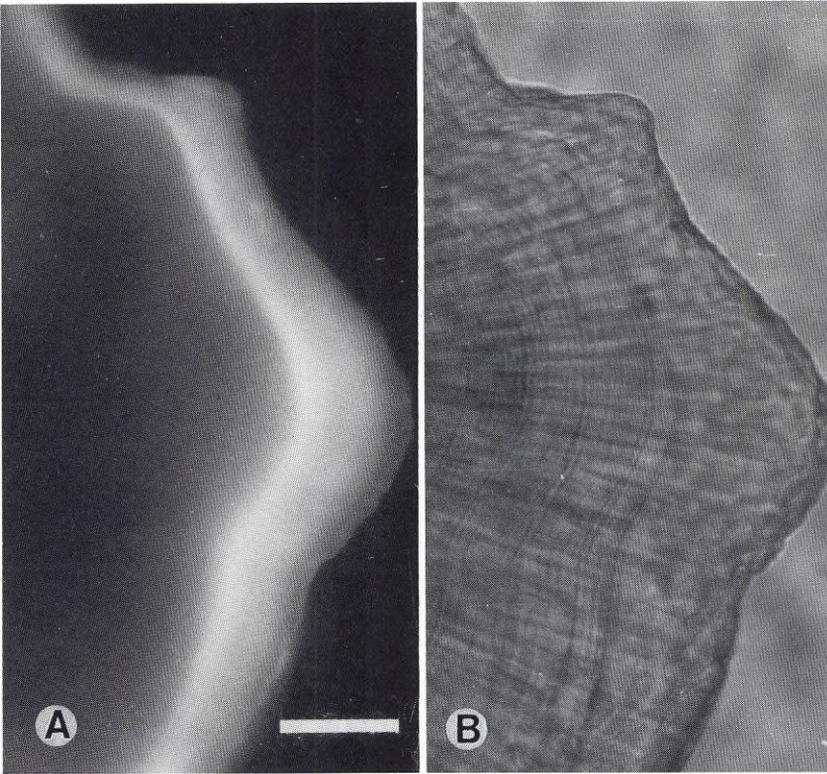


Fig. 1. A ground otolith section of a perch reared at constant temperature and constant light in the laboratory. The fish was injected with tetracycline and died 13 days afterwards. Scale Bar = 70 (μm). (A) Viewing under ultraviolet light, showing the fluorescent band introduced by the tetracycline injection. (B) Viewing under the bright field illumination. No evident increments, but wrinkled structures are visible after the fluorescent band, while clear increments are present before it.

cline solution. The increments deposited in most otoliths of juvenile black rockfish, *Sebastes melanops*, were very faint after injection with tetracycline (Yoklavich and Boehlert 1987). Tetracycline was also administered to the Japanese eel, the otoliths of which exhibited B-type structure (Umezawa and Tsukamoto 1991). It appears possible that cessation of increment deposition is partially associated with administration of tetracycline, which, as an antibiotic drug, is able to affect the normal growth of hard tissues. When tetracycline was used to temporarily mark bones of dog and rat (Harris 1960) and goldfish (Kobayashi et al. 1964), both authors found that it could produce partial inhibition of mineralization in hard tissues. However, tetracycline alone can not, at least in most cases, cause cessation of increment deposition. Tetracycline has been well used as a marker to validate daily increments (see the review by Campana and Neilson 1985). When feed-

ing was sufficient at high temperature, daily increment deposition was maintained in the otoliths of Japanese eel (Umezawa and Tsukamoto 1991) and milkfish (Tzeng and Yu 1992). Furthermore, cessation of increment deposition has also been reported in some laboratory-reared fish which had not received tetracycline treatment (Laroche et al. 1982, Hettler 1984).

The perch probably suffered severe stress in the laboratory, as they did not even attempt to eat. The fish died shortly after being reared under the constant light condition, suggesting that constant light caused additional stress. The stress, along with the administration of tetracycline, may adversely affect the mechanism for increment deposition in these fish, causing the production of B-type otolith structure.

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Predation by the Noble Crayfish, *Astacus astacus* (L.), on Emerging Fry of Sea Trout, *Salmo trutta* (L.)

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In many water systems, crayfish and trout may live sympatrically. In those water systems, the crayfish may interact with the trout population directly or indirectly. For example, the noble crayfish, *Astacus astacus* (L.) and the signal crayfish, *Pacifastacus leniusculus* (Dana) are opportunistic omnivores, feeding on living plants and animals as well as on detritus, and readily feeding on benthic invertebrates (Abrahamson 1966, Mason 1975). Thus, crayfish may act as food competitors to young trout. Furthermore, the influence of crayfish on aquatic vegetation can be considerable (Abrahamson 1966, Hogger 1988), which may lead to an alteration of growing areas of fish juveniles. Thereby the vulnerability of small fish to other predators can also be increased by evicting them from shelters and causing increased activity (Rahel and Stein 1988). Crayfish may also have a

direct effect on a trout population by predation on eggs and/or younger stages of juveniles.

Sea trout, *Salmo trutta* (L.), generally spawn from October to December. Embryonic development and hatching of the fry take place inside the gravel of the spawning grounds. After hatching fry stay inside the gravel for one to three weeks until their yolk sac is mostly completely resorbed, and then emerge from the gravel. This is a period full of risk for the fry. They have to reach the water surface to fill their swimbladder with air, to hide, to begin to swim, to exogenously feed and to establish a territory. All these adaptations make them very vulnerable (Elliott 1989). On Gotland, a Swedish island of the Baltic Sea, the emergence of the fry generally coincides with the warming-up of the stream water (Rubin in prep.), which is probably the period during which crayfish begin to

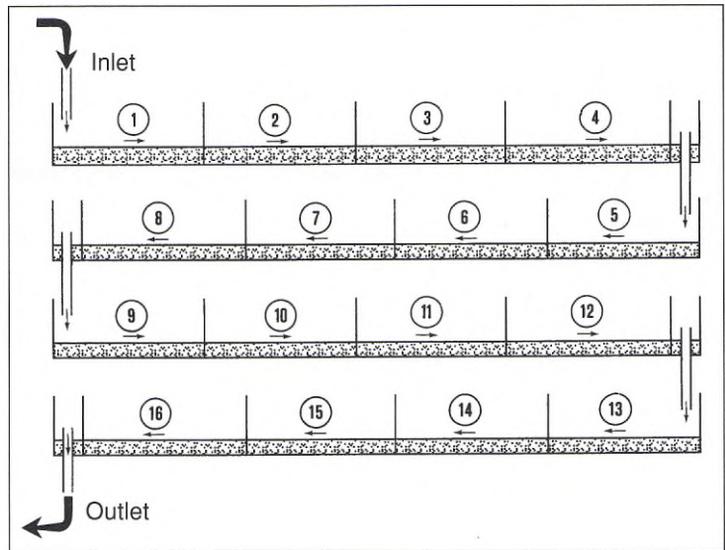


Fig. 1. Design of the experiment. Compartments No. 1, 6, 11 and 16 are controls without crayfish. Compartments No. 1, 5, 9 and 13 are compartments where the water supply came as a waterfall.

search for food more actively after the winter starvation. If crayfish have a direct effect on trout populations, then it should be evident at this particular time.

The aim of the presented experiment was to study in the laboratory the possible predation of the noble crayfish on sea trout eggs and fry during the incubation period in the gravel and the short period of the emergence of the trout juveniles.

The experiment was run from 18.03.93 to 17.05.93 at the Ar laboratory of the Institute of System Ecology, Stockholm University, located on the north part of Gotland (58°N, 19°E), Sweden. Unfiltered freshwater was obtained from Lake Bästeträsk, a large lake located just 100 m from the laboratory. Four plastic aquaria were placed one above the other (200 x 40 cm). Each aquarium was divided into four parts by a plastic net of 2 mm mesh size. Thus 16 different compartments (40 x 50 cm) were obtained. A layer of 8 cm of clean gravel (geometrical mean diameter: 23.9 mm) was deposited on the bottom of each aquarium to constitute the "streambed". This gravel composition corresponded to the usual Gotlandic sea trout spawning ground substrate, which is known to give high survival for both trout eggs and emerging fry (Rubin in prep.). Freshwater was added in

the first compartment of the upper aquarium. Water then flowed through all the compartments, falling from one aquarium to the next lower one (Fig. 1). The waterfall created turbulence in the first compartment of each aquarium. Then water became gradually more laminar in the other compartments. Water temperature ranged from 2.4 °C in the beginning of the experiment to 16.0 °C at the end (Fig. 2). Light was supplied from fluorescent tubes above each aquaria. The light was regulated in order to obtain natural photoperiod during the study (from 10 h of light in the beginning of the experiment to 14 h at the end).

One adult *A. astacus* female was placed inside each test compartment, except in four compartments which were used as controls. The control compartments were positioned regularly along the experimental installation (Fig. 1). Thus in total 12 crayfish were used whose mean total length was 9.8 ± 0.5 cm (range: 9.2-10.4 cm). Each compartment was equipped with a claypipe as shelter for the crayfish and with a cluster of *Chara fragilis*, an algae that is readily eaten by crayfish. A total of 150 fertilized eggs of sea trout were placed 8 cm inside the gravel in the middle of each compartment. These eggs came from 13 females (range: 54-78 cm in total length) caught in Arån and Ireån.

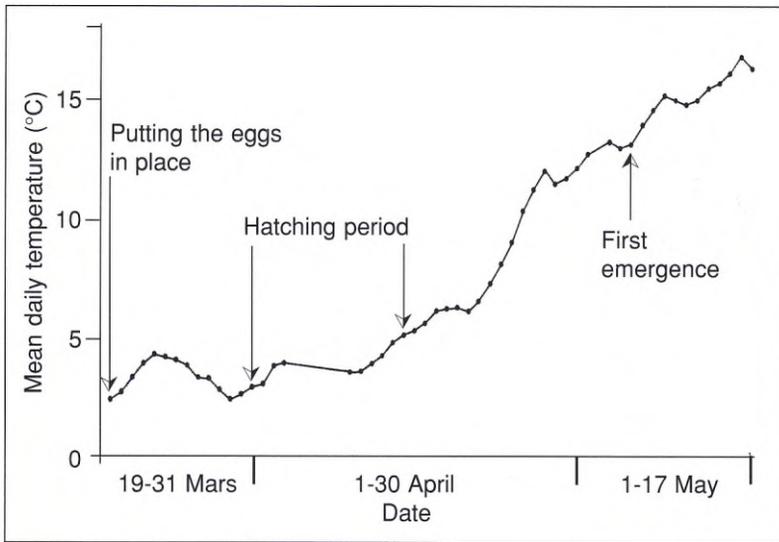


Fig. 2. Water temperature during the experimental period.

Females were stripped during the spawning season and the eggs were kept at the Ar hatchery. Before stocking the compartments with eggs, all the eggs from the different females were mixed together, and then divided into different batches. Thus, the same biological material was found in each compartment. In the control compartments, sea trout eggs were also placed above the gravel, inside a perforate plastic box, through which water could flow but from which fry could not escape. By checking the egg-to-fry survival in these boxes, the variation of the water surface quality could be detected and time of hatching determined. In total 2,750 eggs were used. The stage of development reached by the eggs was determined at least three times a week. Indication of possible crayfish digging was also checked at the same time, and crayfish activity was observed for 10 min at least 2 hours after full darkness. Hatching of the eggs took place between 01.04.93 and 15.04.93. The first emerging fry were observed on the 06.05.93. The experiment was ended the 17.05.93 (Fig. 2). The number of remaining alive fry was then determined in each compartment.

No signs of crayfish digging activity (displaced stones, holes in the gravel, digging crayfish) was observed. Thus, no predation by crayfish on the trout eggs probably occurred. But after the emer-

gence of the fry, crayfish were observed after the light had been turned off moving outside the shelter and chasing fry. It was observed that some crayfish had eaten a lot of the *chara* algae but there was no correlation as to the degree of predation on fry. The mean number of fry found in the control compartments was 101 ± 59 and only 32 ± 38 in the compartments with crayfish (Table 1). This reduction in the number of fry in the compartments with crayfish was significant (Mann-Whitney U-test, $Z = -2.18$, $P < 0.05$, $N = 16$). On average $68.6 \pm 37.9\%$ of the emerging fry disappeared in the compartment with crayfish. At the end of the experiment, fry had not started to feed exogenously, thus food competition between crayfish and fry could not have been a cause of increased fry mortality. Therefore, since the presence of crayfish was the only difference between the test and the control compartments, the disappearance of fry had to be attributed to crayfish predation. In the compartments where the water came as a waterfall, significantly more fry were found at the end of the experiment (Mann-Whitney U-Test, $Z = -2.50$, $P < 0.05$, $N = 16$). This variation may be explained either by a higher egg-to-fry survival due to a local increase of the interstitial dissolved oxygen concentration caused by the waterfall or by a disturbance of the crayfish due to the water turbulence.

Table 1. Estimation of the Noble crayfish predation on sea trout fry. WF is a compartment with a waterfall.

A

Control in the waterbox without crayfish	Compartment No.			
	1 (WF)	6 (WF)	11	16
N of fry	86	49	59	104
N of dead eggs	0	0	27	25
% survival	100	100	68.6	80.6
N of alive fry found	107	142	138	15

B

Experiment	Compartment No.												
	2	3	4	5 (WF)	7	8	9 (WF)	10	12	13 (WF)	14	15	
N of alive fry found	1	0	2	86	46	3	102	26	6	84	23	1	
Expected N of fry without predation	101	101	101	101	101	101	101	101	101	101	101	101	
% predation	99.0	100	98.0	14.8	54.4	97.0	0.0	74.2	94.0	16.8	77.2	99.0	

Some damaged but alive fry were found only in compartments with a waterfall (compartment 9 and 13). The damage appeared as a parallel wound on both sides of the fry, generally between the dorsal and the caudal fin, clearly caused by the crayfish chelae. Fry were probably caught by the crayfish and could escape but were wounded.

In nature crayfish may avoid the most streamy parts of rivers. Westman et al. (1986) showed that no crayfish were found in the "swiftest rapids" in a Finnish river. On the contrary trout are generally located in more streamy areas, although fry seem to chose calmer parts in shallow areas (Heggens 1988). Hence, it could be argued that interactions between the two species may be low under normal natural environmental conditions. But if both species are forced to use the same habitat, for instance if the water flow is reduced, then the impact of the crayfish predation may be important, although probably not as high as observed in the present laboratory experiment. As a matter of fact, in nature crayfish have more feeding choices and fry have more space to escape and more shelter to

hide. Nevertheless, crayfish are used to hunt at night, that is to say during the period when fry are the most vulnerable to predators. Efficiency of this predation in nature is not at present computable now from our existing knowledge. Probably the substrate composition, the water temperature and the water velocity are important factors effecting the efficiency of the crayfish predation. In nature crayfish predation on trout fry has never been demonstrated. However, it may be because it has never been studied. Thus, the present experiment shows that investigations under natural conditions should be performed before introducing new crayfish populations in streams where vulnerable trout populations exist. For example, crayfish were introduced in the River Svartån (Southern part of Sweden), a stream previously known to possess an important trout population. After some years, the crayfish population increased enormously and the trout population declined to the level of extinction. One explanation of this drastic decline of the trout population is that crayfish predated on fry of the trout (T. Järvi, pers. comm.).

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Guide to authors

General editorial practice

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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.

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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.

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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

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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 resubmission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program (e.g. wp 5.1, ws, ms-world).

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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.

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Use SI units as far as possible.

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

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

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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.

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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 figures or figure captions. A variable divided with another variable should be noted as the following example L per min is $L \text{ min}^{-1}$.

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	$^{\circ}\text{C}$
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.)	R
correlation or regression coefficient (multiple)	r
correlation or regression coefficient (simple)	ρ
degree (angular)	$^{\circ}$
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

para
 pascal
 per mille (per thousand)
 siemens
 tesla
 trishydroxymethyl-aminomethane
 volt
 watt
 weber

p
 Pa
 ‰
 S
 T
 tris
 V
 W
 Wb

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.)

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

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 inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

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