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Recovery of Piscivorous Brown Trout and its Prey, Arctic char, in the Acidified Lake Selura after Liming

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Abstract

Lake Selura has been exposed to acid rain for many decades. This led to reductions in both the brown trout *Salmo trutta* and the Arctic char *Salvelinus alpinus* populations from the beginning of the 1960's onwards. A large-sized brown trout phenotype, known locally as "lugg", disappeared during the early part of 1970's. We have studied the effects of liming on two discrete brown trout populations and the Arctic char population. After liming of Lake Selura in 1985 the Arctic char population increased initially due to increased recruitment, eventually reaching high numbers between 1988-90. The mean size of the Arctic char individuals subsequently decreased. presumably due to increased intraspecific competition. Also the brown trout increased in numbers, and eventually the large-sized piscivorous phenotype reappeared in 1991. The large-sized trout were caught at two different spawning grounds, suggesting that individuals from both populations had the potential of becoming piscivorous. We suggest that this reappearance is due to the increase in small sized Arctic char which occurred prior to 1990, facilitating an ontogenetic niche shift in the brown trout populations.

Keywords: Brown trout, Arctic char, liming, recruitment, population structure, predation.

Introduction

Acidification of freshwater is the most severe environmental problem in Norway today (Henriksen et al. 1988, 1989). In large areas (over 70,000 km²) especially in the southern part of the country fish stocks have been lost at high degrees. In 1992 it was estimated that a total of 2,471 populations of brown trout, *Salmo trutta*, were lost due to acidification. A further 2,033 populations were severely affected, showing clear signs of decline (Berger et al. 1992). The brown trout is one of the most affected species in Norway, both due to its sensitivity (Bulger et al. 1993) and because it originally was widespread in the most acidification-sensitive areas.

Populations experiencing sublethal stress due to increased acidity and elevated levels of toxic aluminium may show different kinds of responses. Increased adult mortality leading to juvenilization or reproductive failure leading to senescence are the most common population responses (Andersen et al. 1984, Muniz et al. 1987). Since the acidification process will selectively affect different components of the biotic community in the lake (Haines 1981, Muniz 1991), changes in prey composition or competitive interactions within the fish community may also lead to other marked changes in the target fish population.

If important prey organisms are lost this may lead to reduced growth rates, since in order to sustain high growth rates throughout life suitably sized prey must be available, especially during critical transitional stages in the ontogeny of the individual. For the brown trout such a

stage may be the transition from a benthivorous to a piscivorous mode of prey selection (L'Abée-Lund et al. 1992a). If suitably sized prey is not available this transition will not occur, and stunting may be the consequence.

In Lake Selura, South Norway, the fish stocks (brown trout and Arctic char, *Salvelinus alpinus*), have been severy affected by acidification since at least the early 1970's (Andersen et al. 1984, Bravington et al. 1990). Evidence from the Arctic char population suggests that serious acidification problems were present by 1968. Up to the early 1960's a large-sized brown trout phenotype, locally known as "lugg" (it could reach 5-6 kg), was commonly caught by local fishermen (Andersen 1994). The common name for such trout is ferox (Campbell 1979). This phenotype represented piscivorous brown trout demonstrating large size and rapid growth associated with a transition to a piscivorous prey selection. Large-sized brown trout dissappeared in the early 1970's, and has not been recorded either in our own experimental fisheries or in the sports fisheries. After the implementation of a liming programme in the lake, large sized brown trout again appeared in the samples. Before liming of the lake started, the lake spawning brown trout was strongly affected by the acidification, and a median time before extinction was estimated to 16 years (Bravington et al. 1990). One of the stream spawning populations suffered a 30 per cent decrease in survivorship (Bravington et al. 1990).

Material and Methods

Study area

Lake Selura is an oligotrophic lake located in the Vest-Agder county, SE Norway (Fig. 1). The area receives annual rainfalls of about 1,900 mm. With a geology dominated by gneisses and small amounts of glaci-fluvial deposits the area is susceptible to acidification. The Lake Selura watershed is 45 km² and includes 15 lakes and tarns. All lakes are oligotrophic with low colour values (1 mg Pt L⁻¹) and have practically no alkalinity. The water is influenced by marine spray
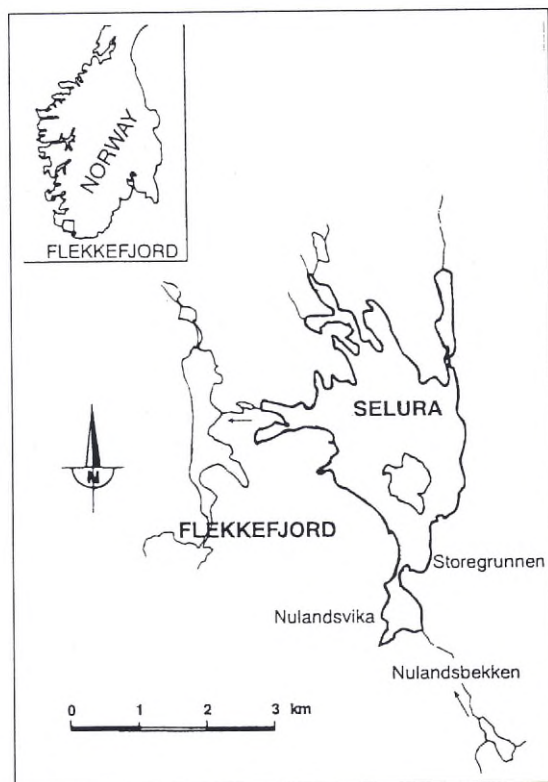
Fig. 1. The Lake Selura catchment area. The different sampling stations are indicated.

and have consequently relatively high conductivity (40-55 μS cm⁻²). Lake Selura has been acidified by 0.5-1.5 pH units during the last decades, and pH rarely exceeded 5.0 (Fig 2) during the period prior to 1980 when the liming programme was initiated. The amount of aluminium (Al) is less known, but measurements from 1984 (before partial liming of Lake Selura had been initiated) show levels of labile (mainly inorganic) monomeric Al between 100-180 μg L⁻¹ (Andersen, unpublished data). After liming, pH reached 5.5-6.5, with the low values in early spring and the high values in autumn (Fig. 2) The autumn rises is mainly due to the fact that liming is normally done in August-September. For a more detailed description of the study area see Andersen et al. (1984). Liming of the lake and tributaries started in 1980; a short description of the liming history is given in Table 1.
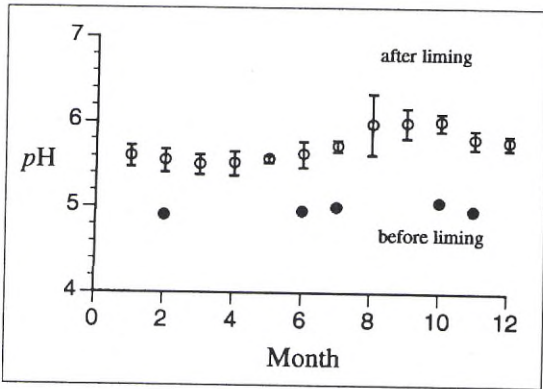
Fig. 2. Seasonal variation in pH in Lake Selura prior to and after liming was initiated. The data before liming are single measurements, the data after liming are mean ± standard deviation (SD).

The fish community include mainly brown trout and Arctic char, but also a moderate population of European eel *Anguilla anguilla*. The brown trout spawn both in the lake itself (at Storegrunnen) and in a series of tributaries (Andersen 1982), but all populations use the lake as the feeding habitat. There are no clear indications of genetic differentiation between the different spawning stocks (a total of 41 loci have been screened using enzyme electrophoresis; Ryman, Andersen and Hindar, unpubl. data). The char population is mainly composed of small, slender individuals, but Hindar et al. (1986) did find evidence for two genetically distinct phenotypes in the lake during the early 1980's. The rare dwarf phenotype which were caught by Hindar et al. (1986) has not been caught in recent years. In 1994 a large piscivorous char weighing 3 kg was caught.

Methods

Brown trout has been sampled since 1976 both in the stream Nulandsbekken, the main spawning tributary, and at Storegrunnen, the most

Table 1. The liming history in Lake Selura and its tributaries.

Year	Activity
Tributaries	
1980-1983	Use of small, simple shellsand drums (Andersen et al. 1987). Small if any effects.
April 1984	A large (2.5 m³) shellsand drum was built in Nulandsbekken. pH increased from 5.3 to around 7.0. The drum was effective even during spring spates (Andersen et al. 1987, Muniz et al. 1987),
1984 onwards	Unsystematic liming using shellsand deposited directly into streams, and shellsand drums in streams in the northern part of Lake Selura
1985	Extra shellsand drum (3 m³) built in Nulandsbekken
1993	It is decided to discontinue the use of the shellsand drums in Nulandsbekken to reduce trout recruitment
Lake Selura	
1985	100 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1986	155 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1987	75 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1988	86 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1989	107 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1990	107 ton $CaCO_3$ deposited in Nulandsvika and two bights in the northern part of Lake Selura
1991	135.5 ton $CaCO_3$ deposited along the eastern shore of Lake Selura
1992	127 ton $CaCO_3$ deposited along the eastern shore of Lake Selura
1993	127 ton $CaCO_3$ deposited along the eastern shore of Lake Selura
1994	130 ton $CaCO_3$ deposited along the eastern shore of Lake Selura

important spawning area in the lake (se Fig. 1) (Andersen 1980). During 1976-78 the brown trout in Nulandsbekken were collected with electric fishing and fyke nets. From 1983 all sampling of this population has been done using benthic gillnets (mesh size 29 mm bar mesh) set near the outflow of the tributary, in Nulandsvika (Fig. 1). This net catches trout in the length interval 10-39 cm, with a modal length about 24-26 cm. The size selectivity of the nets varies with condition factor (see Jensen 1995), such that the modal length of a net will differ between samples taken at different times. However, since the sampling was done at a fixed location and at the same time each year the data is suitable for our purposes. Tagging experiments have shown that most brown trout caught in Nulandsvika during autumn actually will ascend Nulandsbekken for spawning (Andersen 1980). At Storegrunnen 1976-78 the sampling was done using fyke nets and a gang of gillnets (1.5 • 25 m) with mesh sizes between 15 and 39 mm (bar mesh) (Andersen 1980). From 1983 onwards the brown trout were sampled yearly using standard gillnets with mesh size 29 mm operated by the landowner during the spawning season each year (October-December). In addition, we have received samples from local fishermen of most of the large brown trout (larger than 1 kg) caught in the lake during the last 15 years (scale samples, length, weight and sex).

Historical data on the total length and weight of brown trout in Lake Selura in 1939 were found in the archives of Flødevigen Biological Station (sampled and tabulated by G. Dannevig), together with individual data on back-calculated length based on scale samples. We have used these data as an example of the pre-acidification situation. How and where in the lake these fish were sampled is not known in detail.

The Arctic char has been sampled in a less systematic manner, but we feel that the data warrants a detailed treatment. In 1976 we caught the char during November using beach seines (see description in Vøllestad and Andersen (1985)). Thereafter the char has been sampled using gillnets (mostly benthic gillnets, but in 1978 also using pelagic gillnets) with mesh sizes ranging 16-39 mm (bar mesh). Most of the sampling have been done during autumn (October-November), except in 1978, 1985 and 1994 when the sampling took place in May-June. As a consequence we do not present growth data, only age and length distributions. In addition, one fisherman have been fishing at Storegrunnen and in Nulandsvika each autumn since 1983, using gillnets with mesh size 29 mm. These data were used for calculating catch per unit of effort (CPUE). The condition factor of the Arctic char is much lower than for the trout, thus the modal lengths of Arctic char caught in 29 mm nets is larger than for the trout. Further, if the condition factor decreases between samplings this will lead to further increases in the modal length. Thus, the 29 mm nets will only catch the larger-sized Arctic char in the population.

The CPUE is calculated as number of fish (Arctic char or brown trout) caught per net, each net being set for one night. A CPUE was calculated for each night, and we estimated a mean CPUE using from 4 to 20 nights a given year. In this way we get an indication on the variability of the catches.

The individual fish was measured for total length (mm), total weight (g) and sexed. Scales and otoliths were sampled for age determination (Nordeng 1961, Jonsson 1976). Piscivorous brown trout were identified based on the growth structure of the scale. Trout with scales showing an increase in sclerite width after a period of slow growth, and all brown trout larger than 1.0 kg, were classified as piscivorous. Growth-curves were based on individual back-calculated lengths using the Dahl-Lea method. Last years growth increment were included for trout caught during the spawning season when growth had ceased.

We use data on both Arctic char and brown trout sampled prior to 1985 as indicative of the pre-liming situation. Liming during 1980-85 was limited, and did not significantly influence the water qualtiy in Lake Selura (see Table 1).
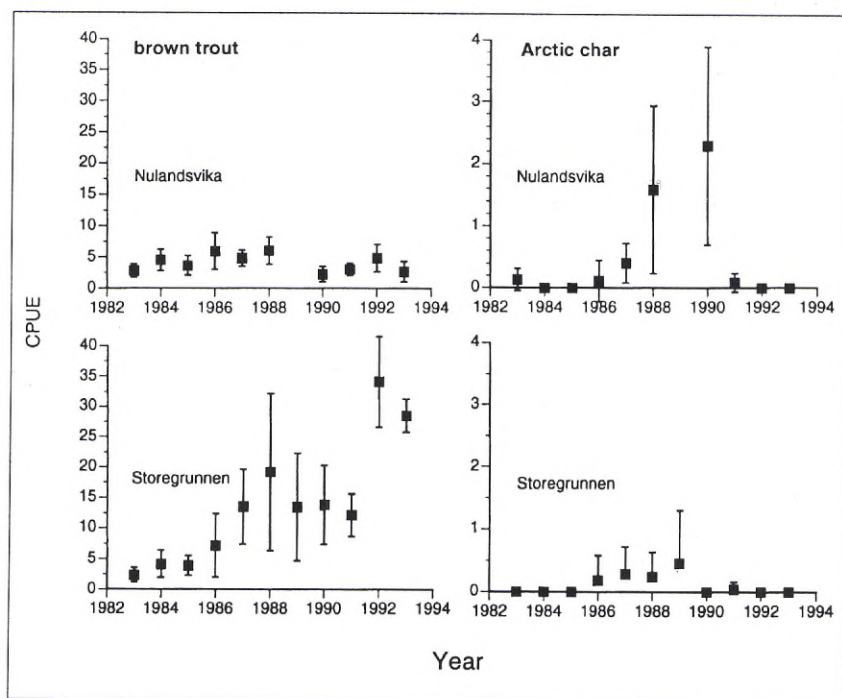
Fig.3. Catch per unit of effort (CPUE - mean and SD) of brown trout (left panels) and Arctic char (right panels) in benthic gill nets with mesh size 29 mm prior to and after liming in Lake Selura. The two different locations (Storegrunnen - lower panels - and Nulandsvika - upper panels) where sampling was done are indicated in Fig. 1.

Results

Arctic char

The CPUE of Arctic char caught in 29 mm gillnets increased from 1986 to 1990 at both sampling stations, but decreased drastically after 1990 (Fig. 3). The gillnets used select Arctic char in the length interval 150-350 mm, with a modal length around 250 mm. The increase in CPUE was most pronounced at Nulandsvika, where it more than tripled between 1982 and 1990, and then decreased to almost zero in 1993.

The mean length of the char increased from the 1976-78 period to the 1982-85 period and further to the 1988-90 period, but then decreased reaching a low mean value in 1994 (Fig. 4). In 1994 the population consisted mainly of char smaller than 200 mm, whereas char larger than 20 cm were common in the earlier periods. The length distributions were significantly different in the different periods (ANOVA, $P<0.001$).

The age distribution has changed drastically between 1976 and 1994 (Fig. 5). During the periods 1976-78 and 1982-85 the proportion of old char increased, indicating a low reproductive success (i.e. recruitment). After liming the recruitment is assumed to have increased, and in 1994 the population was dominated by very young individuals (Fig. 5). The age distributions were significantly different in the different periods (ANOVA, $P<0.001$).

The length-weight relationship of the char has also changed significantly during the study period (full model ANCOVA, with period as treatment variable and ln-transformed length as covariate, ln-transformed weight as dependent variable; $F_{7,699} = 1880.5$, $P<0.001$). The cross-effect was highly significant, indicating that the shape of the length-weights curves differ between periods (Table 2). Typically, the weight at length of the char increased during 1976 to 1990, but then decreased dramatically in 1994.

Brown trout

The CPUE of brown trout caught in the 29 mm gillnets at Storegrunnen increased between the
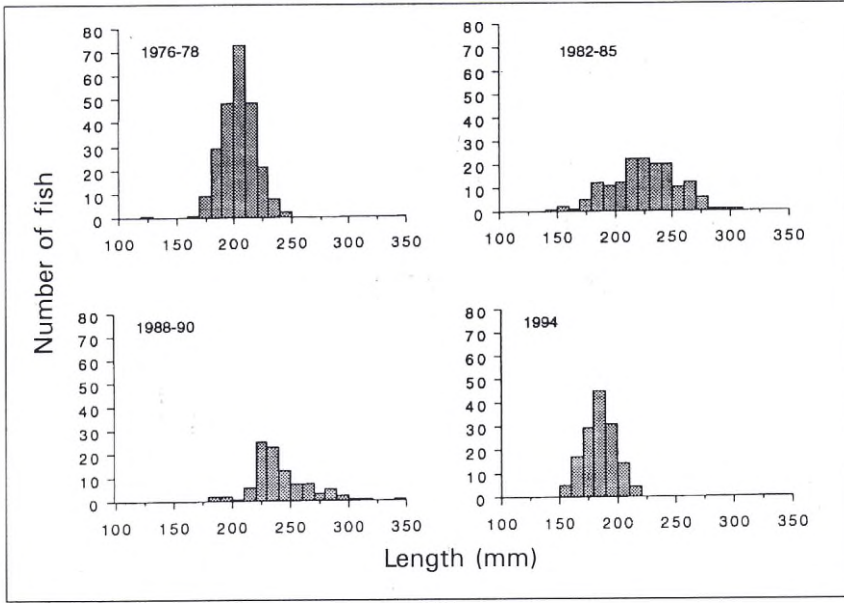
Fig. 4. Length distribution of Arctic char in Lake Selura during two periods prior to liming (1976-78; 1982-85) and two periods after liming (1988-90; 1994).

early 1980's and 1988, decreased between 1988 and 1991, and reached its highest levels during the investigation in 1992 and 1993 (Fig. 3). The CPUE of brown trout in Nulandsvika was more or less constant in the same time period.

In 1939 the brown trout stock in Lake Selura comprised fish with a mean size around 220-250 mm, with a few individuals reaching sizes around 500 mm (Fig. 6). In the period prior to liming (1976-78, 1983-85) the mean size in-
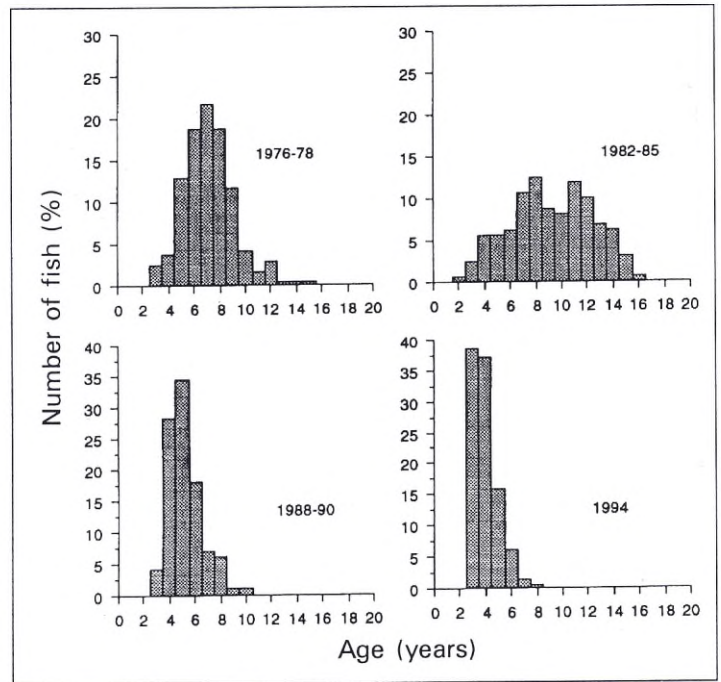
Fig. 5. Age distribution of Arctic char in Lake Selura during two periods prior to liming (1976-78; 1982-85) and two periods after liming (1988-90; 1994).
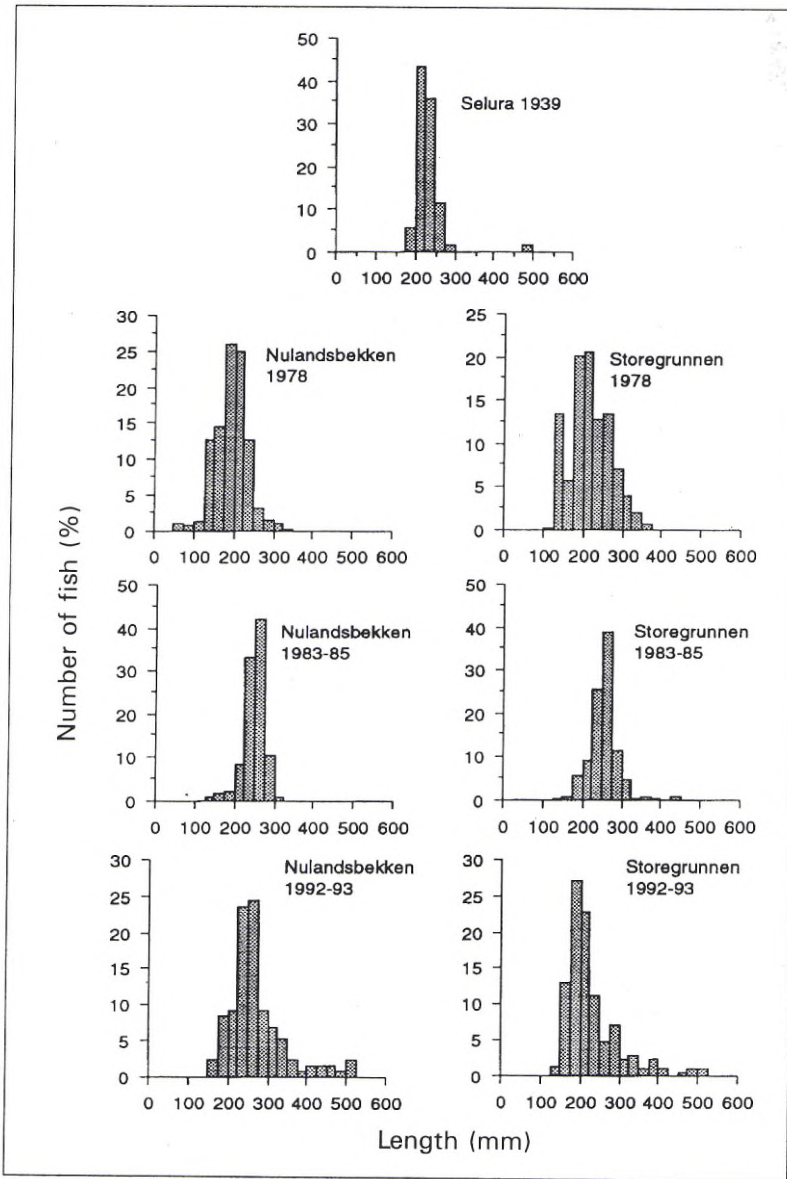
Fig. 6. Length distribution of brown trout sampled in Nulandsvika and Storegrunnen in Lake Selura during a pre-acidification period (1939), two periods prior to liming and thus exposed to acidification (1978; 1983-85) and one period after liming (1992-93).

creased significantly with time. With two exceptions, large-sized trout were never reported. The two trout, caught at Storegrunnen in 1983 (lengths ca. 420 mm, weights ca. 900 g), did not exhibit the typical growth rate change often associated with a change to piscivory. After some years of liming the mean size decreased (1992-93), although large-sized brown trout again occured in the catches. In addition, large-sized

trout were reported in the catches of local fishermen.

The age distributions did also change between the different periods. In 1939 most of the brown trout were in age groups 3, 4 and 5 (Fig. 7). In 1978 the most common age group was two year old, with a larger number of older fish. In 1983-85 these older fish had disappeared, and most fish were in age group 3. After liming, the fish
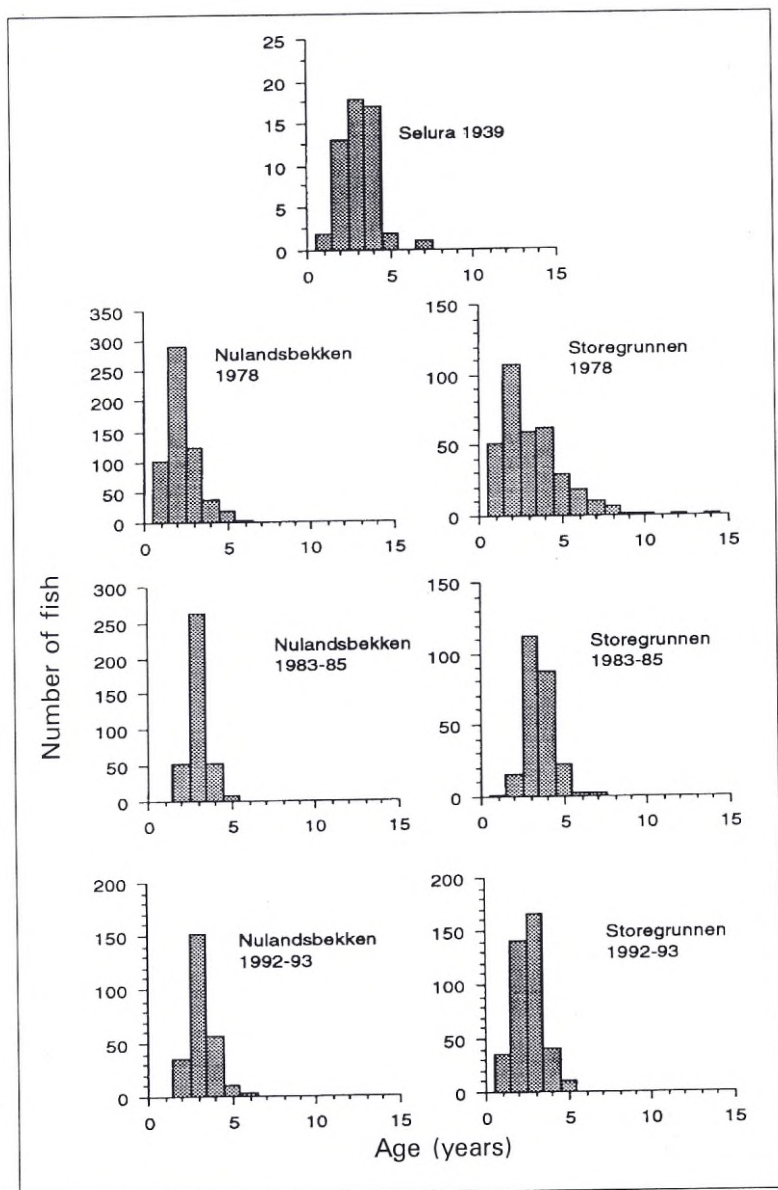
Fig. 7. Age distribution of brown trout sampled in Nulandsvika and Storegrunnen in Lake Selura during a pre-acidification period (1939), two periods prior to liming and thus exposed to acidification (1978; 1983-85) and one period after liming (1992-93).

in age group 3 was still most common. The piscivorous brown trout were found among age groups 4 and 5.

The length-weight relationships of the brown trout varied significantly between time periods (ANCOVA, with time period as treatment variable and ln-transformed length as co-variate, ln-transformed weight as dependent variable, $P<0.001$), but not between localities (ANCOVA,

$P>0.05$). The differences in length-weight relationships were small, as indicated by Table 2.

Large, piscivorous brown trout were not recorded in the catches of 1978 or 1983-85. Neither were any such fish reported by local fishermen. The piscivorous brown trout was first recorded in the catches in 1991. This year one trout was caught during test fishing in Nulandsvika (53 cm - 2,500g) and two were caught by local

Table 2. Length - weight relationships (lnW(g) = a +blnL(mm)) of Arctic char and brown trout in Lake Selura, Norway, during 1939 to 1994. We give the regression coefficients, r, N, and the estimated mean weights (g) at lengths of 200 mm (W_{200}) and 250 mm (W_{250}). All regressions were significant at the $P<0.001$ level.

		a	b	r	N	W_{200}	W_{250}
Arctic char							
Lake Selura	1976-78	- 8.51	2.41	0.860	214	70.7	121.1
"	1985-86	-13.97	3.43	0.963	170	66.9	143.8
"	1988-90	-13.00	3.27	0.964	170	75.6	156.8
"	1994	- 7.87	2.23	0.854	146	51.7	85.0
Brown trout							
Lake Selura	1939	- 9.34	2.59	0.843	53	80.0	142.7
Nulandsbekken	1978	-11.24	2.94	0.994	584	76.5	147.4
Nulandsbekken	1983-85	-10.09	2.77	0.951	177	98.1	182.1
Nulandsbekken	1992-93	-13.44	3.36	0.986	262	75.4	166.0
Storegrunnen	1978	-11.47	2.98	0.993	351	75.1	146.1
Storegrunnen	1983-85	-10.86	2.90	0.983	219	90.5	172.8
Storegrunnen	1992-93	-12.43	3.17	0.993	412	78.7	159.7

fishermen (44 cm - 1,100 g; 53 cm - 2,500 g). In 1992-93 an increasing number of these fishes were caught (Fig. 6) both at Storegrunnen and in Nulandsbekken.
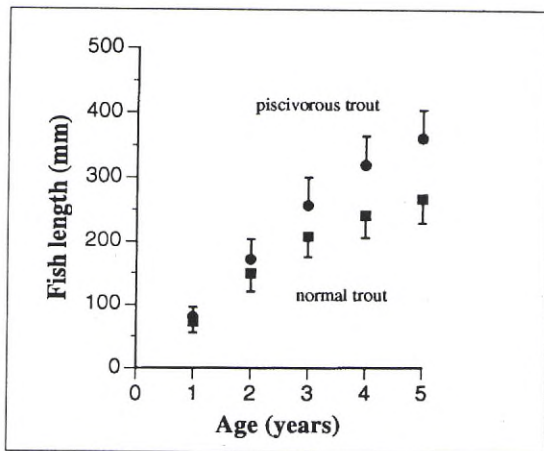
Fig. 8. Growth rate of brown trout categorized as piscivorous and non-piscivorous caught in Nulandsbekken and at Storegrunnen (Lake Selura) during spawning in 1992-93. Included among the piscivorous trout are also fish caught by local fishermen.

The back calculated growth rate of the fish categorized as piscivorous in 1992-93 was significantly higher than that of the "normal" trout (Fig. 8). As two year old both normal and piscivorous trout were around 180 mm, but the growth curves diverged strongly from age 3 onwards.

Discussion

The two most important fish species in Lake Selura are the brown trout and the Arctic char. Prior to the acidification of the lake the Arctic char was the most abundant fish, i.e. having the larger "standing crop". In Lake Selura the Arctic char mainly utilizes the deep benthic and the pelagic zone, however they co-occur with the brown trout in the littoral zone during the spring hatching of chironomids and other aquatic insects (Andersen and Nilssen 1984, Vøllestad and Andersen 1985). This kind of habitat segregation is commonly observed where brown trout and Arctic char lives in sympatry (Svärdson 1976, Langeland et al. 1991, L'Abée-Lund et al. 1992a, b). The Arctic char spawn within the lake, whereas the brown trout spawn both within the

lake and in different tributaries entering the lake (Andersen 1982).

This study shows that prior to the start of the liming program in Lake Selura the Arctic char populations was strongly affected by the acidification. The remaining individuals exhibited clear indications of scenecence, the age and size increased, and the recruitment was reduced (see Fig. 4 and 5). After liming the char recruitment has increased considerably, and the char population now comprises mainly small individuals with low weights (low condition).

Compared to the Arctic char, the brown trout was not so dramatically affected by the acidification. The lake spawning population was more affected than the stream-spawning populations, and a median time before extinction of the lake spawning population of 16 years was estimated (Bravington et at. 1990). The large sized piscivorous phenotype had dissapeared during the early part of the 1970's. In this study we have shown that this phenotype returned in 1991 after the successful implementation of the liming program. Its reappearance was probably due to the changes occuring in the Arctic char population after liming. The Arctic char population was reduced in numbers due to the acidification, producing few but relatively large char. After liming, the reproductive success of the char increased leading to increased recruitment and increased population size.

The liming of Lake Selura and its tributaries has had a pronounced influence on the population structure of both the brown trout and the Arctic char. Before liming brown trout and Arctic char spawning at Storegrunnen were at its way towards extinction, and the population spawning in River Nulandsbekken had a survival reduced by 30 per cent compared to pre-acidification data (Bravington et al. 1990). After liming was implemented on a larger scale in 1985, the brown trout spawning at Storegrunnen increased strongly in strength, whereas the Nulandsbekken population seemed to be stable (stream spawning brown trout are often regulated by density-dependent factors, due to limited access to territories (Elliott 1994)). For Arctic char the catch per unit of effort data shows an extensive increase from 1986 leading to a strong decrease after 1990. This is probably due to increased intraspecific competition leading to reductions in growth rate and weight-at-length ratios. Since our CPUE data are based on catches in 29 mm nets, most of the reduction in catch after 1990 is probably due to reduced catchability (due to gear selectivity) (Hamley 1975) of small-sized and slender (low condition) Arctic char.

The large-sized piscivorous brown trout in Lake Selura disappeared during the early part of the 1970's. This loss could have been due to the selective loss of a distinct population spawning at a specific spawning ground either in the lake or in one of the tributaries. Tagging studies have shown that the brown trout at two of the more important spawning grounds (Storegrunnen, Nulandsbekken) are more or less reproductively isolated (Andersen 1980), and also that they exhibit local adaptation to their spawning grounds shown as differences in O_2-metabolism of brown trout eggs (Kildal 1980) and differences in the frequency of white fin margins (Taugbøl et al. 1988).

It has previously been documented in a large number of studies that sympatric and genetically distinct populations of brown trout may exist within the same river system and also within the same lake (Allendorf et al. 1976, Ryman et al. 1979, Ferguson and Mason 1981, Ferguson and Taggart 1991, Skaala 1992). In some of these studies the sympatric populations have been shown to differ in certain life history trait (Ferguson and Mason 1981). However, in a thorough study on the genetics and life history variation of brown trout in a river system in western Norway, Hindar et al. (1991) did show that the different phenotypes of brown trout present (anadromous vs. freshwater resident) were not genetically different, but rather individuals from the same gene-pool responding to different environmental opportunities (see Skúlason and Smith (1995) for a general discussion on resource polymorphisms in vertebrates).

It is most reasonable to conclude that the disappearance and subsequent reappearance of this

phenotype is due to changes in availability of suitable food organisms. This contention is further supported by the fact that even though the two brown trout populations responded quite differently to the acidification, the large-sized brown trout reappeared in both populations at the same time. If piscivory have a genetic basis (as suggested by L'Abée-Lund et al. 1992a) it is to be expected that this trait is retained in a population for some generations, even if the population is experiencing a genetic bottleneck. Recent studies by Damsgård (1993) and Amundsen et al. (1995) indicates that there are individual differences in the propensity for becoming piscivorous, and that these differences are genetic. The time period from the disappearance of the piscivorous trout in Lake Selura to its subsequent reappearance was less than 20 years, which is a too short time interval for any "piscivory" genes to disappear. This makes us certain that the reasons for the changes in trout population structure has to be sought in the lake itself, and most probably in the availability of suitably sized prey.

Minimum size of piscivorous brown trout has been documented to exceed 130 mm (L'Abée-Lund et al. 1992a), but trout rarely feed on fish before reaching sizes around 200 mm. Further, the gape size of the brown trout puts constraints on the size group available for feeding. Prey size of piscivorous brown trout increases linearly with predator size, and mean prey size seldom exceeds 30-40% of predator length (L'Abée-Lund et al. 1992a, Damsgård 1993). In Lake Selura the large sized brown trout has had increased growth rates after reaching lengths of about 18 cm (see Fig. 8). For a trout of 180 mm char in the size range of 50-80 mm will be the suitable prey category. During the latest phase of the acidification of Lake Selura, the Arctic char population was reduced in number due to recruitment failure and the individual mean size increased. This implies that the availability of suitably-sized Arctic char was too low to sustain a piscivorous habit. Piscivory will only occur if the largest sized brown trout and the smaller sized Arctic char share habitat. Such habitat

sharing probably will not occur if the Arctic char population is small in numbers, as was the case in Lake Selura.

The liming program in Lake Selura has been highly successful. In the early phase of the programme the brown trout populations increased in numbers, especially the lake-spawning Storegrunnen population increased significantly. Further, the Arctic char stock responded by an increase in population size and a subsequent reduction in mean size and age (probably caused by reductions in individual growth rates and increases in mortality due to intraspecific competition). As a consequence of the Arctic char response, the brown trout found suitably sized prey at adequate densities to sustain a piscivorous habit. The result of this is the reappearanc of increasingly larger numbers of large-sized piscivorous trout increasing the value of the sports-fisheries in the lake.

Acknowledgements

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New and Unusual Records of Freshwater Oligochaeta from the Scandinavian Peninsula

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Abstract

Nine species of freshwater Oligochaeta are reported from various sites on the Scandinavian Peninsula. Taxonomic descriptions and/or remarks are given for all species. *Rhyacodrilus subterraneus* Hrabě, *Peipsidrilus pusillus* Timm (both Tubificidae), *Lamprodrilus isoporus* Michaelsen, *Rhynchelmis tetratheca* Michaelsen (Lumbriculidae), and *Propappus volki* Michaelsen (Propappidae) are recorded from Sweden, *R. subterraneus* also from southern Norway, for the first time. *Rhyacodrilus subterraneus* inhabits moderately eutrophic streams in Stockholm and Oslo and is thus not restricted to groundwater. Some of the old records of *Rhynchelmis limosella* Hoffmeister from Lake Vättern (Sweden) and other Scandinavian sites are likely to have been based on misidentifications of *R. tetratheca*. *Rhyacodrilus falciformis* Bretscher, which has been regarded as an indicator of oligotrophic conditions in lakes, is reported from wet soils, probably associated with groundwater seeps, in the Norra Djurgården park in Stockholm. *Potamothrix heuscheri* (Bretscher), a Ponto-Caspian tubificid characterized by its tolerance to weak salinity, and a recent invader in the Swedish Lake Mälaren, is described from heavily eutrophic, stratified urban lakes within Stockholm. A note on the rarely occurring reproductive organs of the lumbriculid *Lumbriculus variegatus* (Müller), and an unusual find of the enchytraeid *Cognettia* cf. *sphagnetorum* Vejdovský in the profundal of Lake Vättern, are presented.

Keywords: Freshwater Oligochaeta, taxonomy, biogeography, new records, Scandinavian Peninsula.

Introduction

The abundance of cool and oxygen-rich oligotrophic waterbodies on the Scandinavian Peninsula is favourable for a diverse freshwater fauna. This fauna, however, is young, as the area was covered by continental ice only 10,000 years ago. Refugia for relics of preglacial fauna do not seem to have existed here, and as the history of the Scandinavian waterbodies appears to be too short for local speciation, all freshwater animals must be regarded as recent invaders, primarily belonging to a more widely distributed Palaearctic fauna. However, the presence of some endemic species (perhaps of preglacial origin) on the neighbouring Kola Peninsula was supposed by Timm and Popcenko (1978).

The history of research on the local oligochaete fauna started with Linnaeus (1767) describing *Nereis lacustris* (now *Stylaria lacustris*), presumably on the basis of material from Sweden. Later, papers by Eisen (1879, 1885), Ekman (1915), Alm (1916), Piguet (1919a,b, 1928), Almstedt (1946), and Sperber (1948) made good contributions to the knowledge on this topic, not to mention numerous short notes. In the last decades, they were followed by Milbrink (1969, 1970, 1973a-b, 1978, 1983a-b, 1993, 1994), Holmquist (1975, 1978, 1979, 1983, 1985), and Bremnes and Sloreid (1994). To date, 62 spe-

cies of freshwater Oligochaeta have been documented in Sweden and Norway.

The Swedish Worm (SWORM) Project launched by the Swedish Museum of Natural History (SMNH) in 1993 includes among its targets an inventory of the Oligochaeta and their distribution in Sweden. This paper presents some new and unexpected distribution records and ecological data, revealed for some freshwater species during this project. In one case, Norwegian material is included.

Material and methods

The sources of material used in this study are summarized as follows.

1. Urban freshwaters and wet soils of the Ekoparken area, i.e. the royal parks Norra Djurgården, Ulriksdal and Haga, in Stockholm and Solna, were sampled for the "Ekoparken project" within SWORM, largely in 1994-95. The total material includes over 2,500 oligochaete specimens from 49 different samples, but only the species of particular interest are treated here.
2. A collection of oligochaetes maintained in the SMNH, originating from bottom grab samples collected in Lake Vättern by Ekman (1915) and identified by Piguet (1919a, 1928) was revised by T. Timm. *Rhyacodrilus falciformis* and *Cognettia sphagnetorum* from this collection are dealt with here.
3. A number of smaller lots of oligochaetes collected in various Swedish waterbodies by different authorities, consulting firms and individuals in 1990-94; a majority of these lots placed at our disposal by the courtesy of the Service Center for Taxonomic Zoology, SMNH.
4. One sample (containing *Rhyacodrilus subterraneus*) from the Ljanselva River in Oslo, Norway, collected by L. Kleboe.

As the material studied comes from many different sources, the procedures of collection, fixation and preservation vary. Most specimens were studied as whole-mounts on microscope slides, either as temporary mounts in glycerine, or permanently mounted in Canada balsam. Prior to mounting, the material of *Peipsidrilus pusillus* and *Propappus volki* was stained in paracarmine. A few specimens of five of the species were transversely or longitudinally sectioned and stained after Mallory or Hauser. Most of the material is deposited in the SMNH.

In the descriptions, segment numbers are referred to by Roman numerals.

Systematic account

Family Tubificidae

Rhyacodrilus subterraneus Hrabě, 1963
(Fig. 1)

Hrabě 1963: 249
Giani and Martinez-Ansemil 1981: 206

Material

Nineteen specimens: Igelbäcken Stream, Solna, 26-30 August 1994, coll. T. Timm (3), 20 February 1995, coll. S. Lundberg (3), 23 May 1995, coll. T. Timm (2); Edsviken Bay at the mouth of this stream, 23 May 1995, coll. T. Timm (1); Söderbrunn, W of Uggleviken, Norra Djurgården, meadow, wet soil in bed of an intermittent streamlet, 31 August 1994, coll. B. Healy and E. Rota (1); Ljanselva River, Oslo, Norway, 24 May 1995, coll. L. Kleboe (9). Mature individuals with clitellum and eggs were found in May only. Five specimens serially sectioned, the others whole-mounted.

Description

Length 6-17 mm, width 0.3 mm (up to 0.5 mm at clitellum when slightly compressed), 43-63 segments. Anterior ventral bundles with (2)3-5(6) bifid crotchets, 71-103 µm long in Igelbäcken material, only 61-85 µm in Oslo material, with distal nodulus, and with upper tooth at least twice longer than lower (Fig. 1C). At each male pore a single penial seta, 72-95 µm long, with simple-pointed, hooked tip and strongly distal nodulus (Fig. 1D). Anterior dorsal bundles with (1)2-3(5) pectinate setae, 47-80 µm long, upper tooth straighter and about
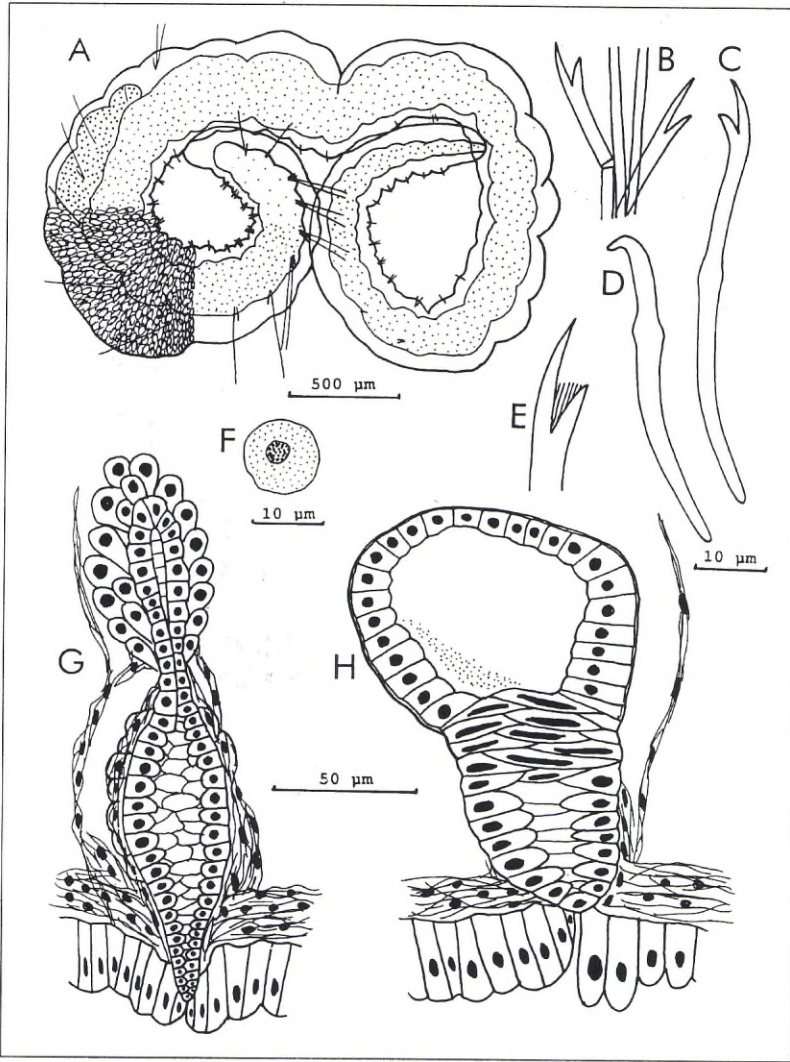
Fig. 1. *Rhyacodrilus subterraneus* (A-E from Igelbäcken Stream, whole-mounted specimen; F-H from Ljanselva River, sagittal sections). A, general appearance; B, portion of dorsal bundle of setae, VI (intermediate teeth of pectinate setae not visible under this magnification); C, ventral seta, VI; D, penial seta, XI; E, distal end of a dorsal pectinate seta, VI (free-hand drawing); F, coelomocyte; G, atrium; H, spermatheca.

twice longer than lower, intermediate teeth very fine, numerous (Figs 1B, 1E); and (0)1-2(3) smooth, thin hair setae, 135-350 µm long. In posterior bundles, hair setae soon disappearing, while bifid crotchets, 1-4 per bundle, 47-97 µm long, having teeth of equal length or upper tooth being slightly shorter than lower. Chloragogen tissue on oesophagus beginning in VI, but weakly developed, transition into intestine smooth. Coelomocytes round (Fig. 1F), 13-30 µm wide, transparent, hardly visible in whole mounts, in some specimens stuck together in an amorphous mass. Clitellum up to 25 µm thick, usually in

X-XII (Fig. 1A), with male pores in XI, but a forward shift by two segments occurred in one Igelbäcken worm. Testes usually in X, sperm sac in IX, also extending backwards, sometimes as far as XIII. Large, erect ovaries in XI, egg sac may reach as far as XIV-XVI. Male funnel beaker-shaped, with (larger) upper lip up to 60 µm long. Vasa deferentia and female funnels not seen. Atria (in XI) erect, 100-190 µm long, bipartite (Fig. 1G); proximal part an oval ampulla, merely consisting of epithelial wall, about 80 µm long, 20 µm wide (30-50 µm, if dense cover of prostatic cells included); distal part an oval

pseudopenis, 75-100 μm long, 30-50 μm wide, without prostatic cells, but with wall consisting of 10-13 μm thick epithelium and 2-3 μm thick muscular layer, latter attaching atrium to body wall (Fig. 1G). Lumen of pseudopenis about 10 μm wide, opening to exterior through tiny male pore near penial seta. Spermathecal pores located in line with ventral setae, anteriorly in X. Spermathecae (Fig. 1H) 115-140 μm long, with globular or sac-like empty ampulla measuring from 64 x 43 μm to 110 x 140 μm in sections; the epithelial wall being 6-18 μm thick (thickest on anterior side) and covered with delicate muscular layer. Spermathecal duct 43-72 μm long, up to 32-55 μm wide (widest either at base of ampulla or at middle), with thick epithelium and narrow lumen. The long, transversally oriented cells of epithelium give the duct a striped appearance. Sperm not observed in spermathecae studied.

Remarks

The new material conforms well to the original description. Previously known from subterranean waters (wells) in Germany (Hrabe 1963) and clean mountain streams in France (Lafont 1989) and Spain (Martinez-Ansemil and Giani 1980; Giani and Martinez-Ansemil 1981), the species is here recorded from Sweden and Norway for the first time. In spite of its name, *R. subterraneus* is apparently not a specialized groundwater animal. It has now been found as a member of diverse oligochaete communities of moderately eutrophic urban watercourses in two Scandinavian capitals, Stockholm and Oslo.

Worms identified as *R.* cf. *subterraneus* were reported from underground waters in New York state, USA (Strayer and Bannon-O'Donnell 1988).

Rhyacodrilus falciformis Bretscher, 1901
(Fig. 2)

Bretscher 1901: 205
Piguet 1913: 123

Material

Twenty-five specimens from wet soils in Norra Djurgården, Stockholm, coll. B. Healy and E. Rota: shore of Lake Laduviken, 23 August 1994 (9); Ugglebo, on a slope with oak forest, 24 August 1994 (12); Söderbrunn, W of Uggleviken, meadow, in the bed of an intermittent streamlet, 31 August 1994 (4). Three specimens from Lake Vättern, Sweden, coll. S. Ekman: at 3-15 m depth, 25 July 1911 (1); at 34-43 m depth, 10 August 1911 (2). All specimens whole-mounted.
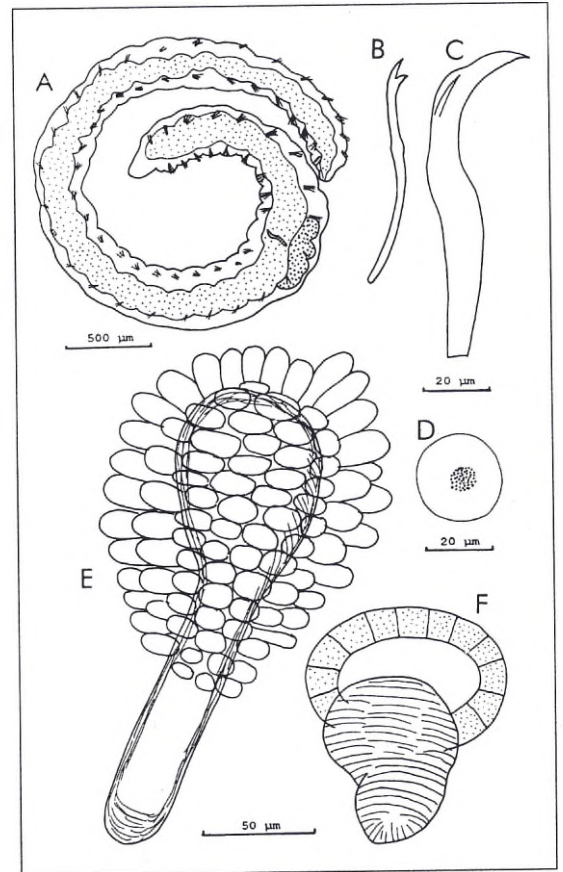

Fig. 2. *Rhyacodrilus falciformis* (from wet soil at Ugglebo, Stockholm, whole mount). A, general appearance; B, somatic seta; C, penial seta, XI; D, coelomocyte; E, atrium; F, spermatheca.

Description

Length about 5 mm, width 0.3 mm, 44 segments (2 complete specimens). Whitish and agile like enchytraeids when alive, not congregating in clumps or spirally contracting as most tubificids do. Prostomium prolonged oval. When preserved, body strongly bent to its ventral side (Fig. 2A), with deep intersegmental furrows. All somatic setae (Fig. 2B) similar, anteriorly 3-5, on mid-body 1-3, near posterior end 3-4 per bundle, 51-74 µm long, 3 µm thick, with upper tooth twice as long as lower, and with distal nodulus. Dorsal bundles often containing one seta less than ventral bundles of same segment. In XI, a single penial seta (Fig. 2C) at each male pore; this seta 100-122 µm long, with straight proximal portion 11 µm thick, and sickle-shaped, crest-bearing distal portion up to 14 µm thick. Coelomocytes (Fig. 2D) abundant, round, 18-26 µm wide, granular without apparent nuclei, in living worms whitish opaque. Clitellum thin, invisible when mounted in Canada balsam. Atria (Fig. 2E) pear-shaped, 185 µm long, up to 65 µm broad, excluding dense, 15-70 µm thick, cover of prostatic cells. Male pores externally imperceptible. Spermathecal pores lateral, located anteriorly in X. Spermathecal ampulla round, 80-97 µm wide, with 13-18 µm thick wall; duct 48-70 µm long, proximally 48-64 µm broad, with wall consisting of high epithelium (Fig. 2F).

Remarks

This species is known from many lakes, watercourses and springs in Central and Southern Europe (see e.g. Juget 1987). It was noticed also in the profundal of the Swedish Lake Vättern in 1911 (Ekman 1915, Piguet 1919a; identity now confirmed by T. Timm). Since it has been regarded as an indicator of oligotrophic conditions in lakes (Milbrink 1978), its occurrence in wet soils, although already mentioned by Piguet and Bretscher (1913), largely has remained unnoticed. Recently, the species was found in soil samples together with enchytraeids also in two different places in Germany (Beylich et al. 1995, Römbke and Federschmidt 1995). According to

our observations, this rarely found tubificid belongs to the soil fauna in Ekoparken, Stockholm, but it appears to be associated with groundwater seeps. This conclusion finds support in the occurrence of *R. falciformis* only in springs in Estonia and neighbouring Northern Russia (Timm 1987).

In Scandinavia, *R. falciformis* also occurs in Sørumsbekken in southern Norway (Bremnes and Sloreid 1994). The species has also been reported from a few North American localities (Brinkhurst 1978, 1986).

Potamothrix heuscheri (Bretscher, 1900) (Fig. 3)

Bretscher 1900: 11 (as *Tubifex heuscheri*)

Material

237 (mature and juvenile) specimens from Norra Djurgården, Stockholm, coll. T. Timm: Lake Laduviken, 2-3 m depth, 25 August 1994 (17), 22 May 1995 (176); Lake Brunnsviken, 4 m depth, 22 May 1995 (42); Husarviken, *Glyceria maxima* zone, 24 May 1995 (2). Twenty-four specimens from Lilla Värtan Strait, Stockholm, 3 samples at 5-10 m depth, brackish water, 16-21 October 1992, coll. Stockholm Water Co. One specimen serially sectioned, all others whole-mounted.

Description

Length 6-12 mm, width at VIII before compression 0.5-0.7 mm, 36-77 segments (9 complete specimens measured). Prostomium conical. Segments short, intersegmental furrows deep. Clitellum extending over XI-1/2XII. Genital segments in mature individuals broad, with male pores located at edges of flattened ventral surface. Anterior ventral setae 3-5 per bundle, 119-153 µm long, with upper tooth thinner and up to twice as long as than lower (Fig. 3C); followed by a single modified spermathecal seta representing each ventral bundle in X (Fig. 3A, ss), and small bifid crotchets, 2 per bundle, in XI. Postclitellar ventral setae 2-3 per bundle,
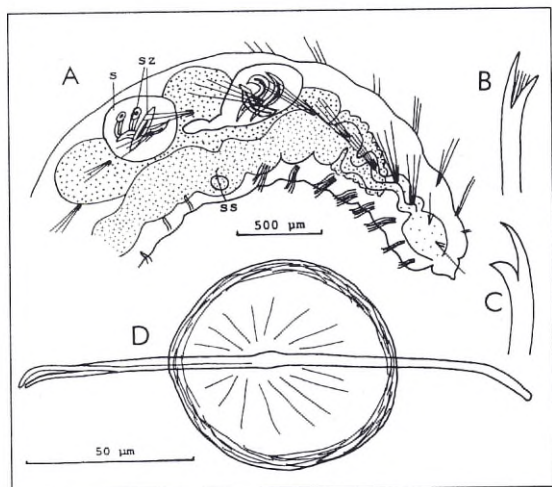
Fig. 3. *Potamothrix heuscheri* (from Lake Laduviken, whole mount). A, general appearance of forebody; B-C, distal ends of dorsal pectinate and ventral seta, respectively (both free-hand drawings); D, spermathecal seta with its gland. Abbreviations: s, spermatheca; ss, spermathecal seta; sz, spermatozeugma.

shorter than anterior setae, and with teeth about equally long. Anterior dorsal bundles with 2-4 pectinate setae, 109-144 µm long, with rather straight, uniform ordinary teeth (upper tooth mostly longer than lower) and several short intermediate ones (Fig. 3B), and 2-4(5) smooth hair setae, 267-554 µm long. Posterior dorsal bundles usually with 2-3 hair and 2-3 bifid setae, latter similar to the ventral ones. Spermathecal setae (Fig. 3D) (in X) 121-224 µm long, 5 µm thick, almost straight, slender, with long furrow with parallel edges in their distal half, one edge (corresponding to the upper tooth) distinctly longer than the other and distally hooked. Nodulus of each spermathecal seta surrounded by spherical gland, 50-72 µm wide, with about 5 µm thick external muscle layer. Pharynx (in I-III) thick-walled throughout, pharyngeal glands reaching IV; no glands found along oesophagus. Chloragogen tissue beginning in VI, cells growing taller in VII; intestinal dilatation in VIII. One nephridium seen in IX. Testes in X, ovaria in XI; sperm sac reaching as far as XII, egg sac considerably further back. Sperm funnels, large,

directed forwards, with opening 100 x 115 µm, and with epithelium 13 µm thick. Vasa deferentia 115 µm long, 25 µm wide, ciliated. Prostate glands not seen. Atria tubular, densely winding in XI, partly in egg sac; their width 35 µm at inner end, at middle up to 80-84 µm (their epithelial wall being 16-32 µm thick, their external muscle layer not more than 1 µm), then narrowing again. Atrial lumen 10-35 µm wide, ciliated. Distal portion of each male duct a 100-110 µm long, up to 63-78 µm wide penial sac, with external muscular layer about 5 µm thick, and with main part of wall consisting of folded epithelium. Penis and external male pore small, hardly distinguishable. Spermathecal ampullae sac-like, about 200 µm broad, their wall about 16 µm thick, including 1-2 µm of muscular layer. They may contain one or several spermatozeugmata (Fig. 3A, sz) of variable shape, from nematoid (up to 640 µm long, only 15 µm thick) to spindle- or lemon-shaped (about 200-250 µm long, 40-70 µm thick). Each spermatozeugma with longitudinally or (in the periphery) spirally arranged filiform regular spermatozoa enclosed in a 3-8 µm thick compact envelope of modified sperm cells. Spermathecal ducts small, only 50 µm long, 27-30 µm wide, pores dorso-lateral, opening below and slightly anterior to dorsal bundles of X.

Remarks

Potamothrix heuscheri is an element of the Ponto-Caspian freshwater fauna, characterized by its tolerance to weak salinity. The species is common in many South European and West Asian lakes, and locally in some areas of Africa. It has also been observed as a recent invader into some estuaries of the Baltic Sea (Laakso 1969; Timm 1987; Finogenova et al. 1987), and in the Swedish Lake Mälaren (Milbrink 1970).

Being most tolerant to long-term anaerobic conditions, *Potamothrix heuscheri* is known to replace *P. hammoniensis* as the dominating species in the profundal of some eutrophic lakes, e.g. in Spain (Rieradevall and Real 1994), Italy (Bazzanti and Lafont 1985) and Israel (Gitay 1968). The same may have happened in the heav-

ily eutrophic, stratified urban lakes in Stockholm, perhaps accentuated under the influence of the extremely hot summer of 1994. In May 1995, *P. heuscheri* densely inhabited most of the deeper zones (i.e., deeper than about 2.5 m) in Laduviken, while in Brunnsviken it was a dominating species (although accompanied by *P. hammoniensis* and *P. bavaricus*) at the very border of the deeper, anaerobic zone. In the better mixed Lilla Värtan Strait, *P. heuscheri* was a second-ranked member of the bottom fauna.

The shape of the spermathecal setae of *P. heuscheri* varies in some South European lakes, as described by Bazzanti and Lafont (1985) for the Italian Lake Nemi. The first author also observed broad spermathecal setae (similar to those of *P. hammoniensis*) in specimens of *P. heuscheri* collected in the desert Lake Jashan, Turkmenistan. All Stockholm (and other Baltic) specimens studied, however, revealed a typical, thin and straight shape of this seta.

Peipsidrilus pusillus Timm, 1977

Timm 1977: 279
Hrabě 1981: 73
Finogenova 1982: 200-201

Material

Five specimens from the Fryken Lakes, province of Värmland, south-western Sweden, all from clayey sediments at 5 m depth, coll. A.-C. Norborg and K. Johansson (Norborg 1992): middle part of Lake Övre Fryken, at Stöpafors, 25 October 1990 (2); southern part of Lake Övre Fryken, at Björkefors, N of Sunne, 24 October 1990 (2); Lake Mellanfryken, at Västra Ämtervik; 23 October 1990 (1). All specimens whole-mounted.

Description

Length (3 complete specimens) 5.7-9.9 mm, 0.24-0.33 mm wide at XI, with 45-71 segments. Prostomium small. Somatic setae bifid, anteriorly with upper tooth somewhat longer than lower, in postclitellar segments with upper tooth about as long as, or slightly shorter than, lower.

Setae 25-47 µm long, up to about 1.5 µm thick, (1)2-4 per bundle in preclitellar segments, 2(3) per bundle thereafter. Spermathecal setae, one at each spermathecal pore, 36-41 µm long, present in two specimens. Clitellum extending over XI-XII in one specimen, not developed in the others. Male and spermathecal pores paired, located in line with ventral setae, somewhat posterior to middle of XI and X, respectively. Pharynx cavity voluminous. Pharyngeal glands in III only. In VIII, oesophagus widening into voluminous intestine. Male ducts poorly developed and/or poorly visible in available material; vasa deferentia about 11 µm wide in one specimen, atria 14-19 µm wide in another. Prostate glands not seen. Penes appear somewhat cylindrical, 18-19 µm in diameter, with somewhat crumpled cuticular sheaths, but exact shape not observed. Spermathecae, when developed, with short, distinct ducts and roundish ampullae, latter 40-50 µm wide; sperm never observed in any material.

Remarks

Although on average a little longer and with a greater number of segments, the new individuals fit Timm's (1977) original description of *Peipsidrilus pusillus* well. A small prostate gland, attached to each atrium, was noted by Hrabě (1981), who therefore regarded the species as a member of the subfamily Aulodrilinae. The latter taxon was merged with the Tubificinae by Giani et al. (1984), who also regarded *Umbadrilus* Timm, 1978 (in Timm and Popčenko 1978) and *Neoaulodrilus* Giani et al., 1982 as junior synonyms of *Peipsidrilus*.

Known so far only from Lake Peipsi-Pihkva at the border between Estonia and Russia (Timm 1977), Lake Onega and the estuary of Neva River in Russia (Finogenova 1982; Finogenova et al. 1987), and a small lake near Česke Lipy in Czechia (Hrabě 1981), *P. pusillus* is here reported from Scandinavia for the first time.

This species may be rare even when present. In Lake Peipsi-Pihkva, only six specimens were sorted from a total of about 25,000 worms, and they were found only in the middle and deeper parts of the sublittoral zone, at depths between

6.5 and 8.4 m (Timm 1977). In the Fryken Lakes (which make up one continuous water body), the five specimens of *P. pusillus* were collected at three different stations, all at 5 m depth. No specimen was found at the other Fryken stations, located at 10, 15 and 25 m and sampled at the same time and with an equivalent effort (Norborg 1992). This strengthens the view that this species has a restricted habitat preference (Timm 1977). In the Fryken study, however, the total number of collected and identified oligochaetes (including all stations) was not more than 276, which indicates a frequency of *P. pusillus* two orders of magnitude higher than that in Lake Peipsi-Pihkva.

Family Lumbriculidae

Lamprodrilus isoporus Michaelsen, 1901 (Fig. 4)

Michaelsen 1901: 3; 1902: 47
Svetlov 1936: 89 (as *L. isoporus* f. *variabilis*)
Hrabě 1962: 311 (*L. isoporus variabilis*)
Popčenko 1988: 236 (*L. isoporus variabilis*)

Material

Forty-nine specimens from bottom grab samples, Lake Siljan, Sweden, courtesy B. Jonsson (Allumite Konsult, Fors): Solviken, at 110 m depth, 3 April 1991 (43); Storsiljan, 35-125 m depth, 18 April 1991 (2); Rättviken, 60-70 m depth, 18 April 1991 (4). About one half of specimens sexually mature; three of these were serially sectioned, all other specimens were whole-mounted.

Description

Fully grown individuals 9-12 (rarely up to 16.5) mm long, 0.7-1.0 mm wide (0.8-1.4 mm at clitellum), with 50-63 segments. Smaller juveniles 6-9 mm long, 0.5-0.75 mm wide. Thus, several cohorts seem to co-exist. Prostomium short, rounded or obtuse, hollow, often pointing upwards. Intersegmental furrows indistinct. One individual with regenerated tail. Setae (Fig. 4B) pointed and slightly sigmoid, with a weak distinct nodulus, 2 per bundle, in IV-IX 120-180 µm long, 6 µm thick, in II-III and posteriorly often smaller, 75-150 µm long, 4-5 µm thick. Body wall epithelium 11-14 µm thick (in clitellum up to 21-27 µm), circular musculature 1-3 µm, longitudinal musculature 10-40 µm (thickest in forebody). From XIII on, body cavity lined with high, loose, coeloepithelium. Digestive tract filled with mud, transition between different regions gradual. Pharynx in II-III with 13-35 µm thick epithelial wall, and a weak muscular and glandular cover; pharynx seven- or eight-angled in cross section, due to muscle bundles connecting it with body wall. Dissepiments 3/4, 4/5 and 5/6 somewhat glandular; no free pharyngeal or oesophageal glands present. Oesophageal wall about 23 µm, intestinal wall 11-21 µm thick; internal ciliation beginning in IV, external chloragogenous cover in VI or VII. Dorsal vessel adhering to intestine, often covered with chloragogen cells. Long winding transversal vessels (Fig. 4C, v) present in anterior segments as well as in sperm and egg sac walls, but not seen in posterior segments. Brain in I-II, nerve cord thin without any accessory glands. Clitellum extending over X-XIII or -XIV. Two pairs of testes, in X and XI. One pair of ovaries, in XII. Paired sperm and egg sacs, latter ones extending backwards at least into XVI; in one specimen an odd anterior egg sac in XI. Large sperm funnels on 10/11 and 11/12, at least 150 µm wide, filling anterior part of sperm sacs. Free portions of vasa deferentia (Fig. 4C, vd) 200-250 µm long, 12-24 µm broad, penetrating dissepiment and then returning to their testicular segment, entering efferent duct; distal portions of vasa deferentia 6 µm broad, proceeding up to middle region of atrium inside atrial wall. Paired atria in X and XI tubular (Figs. 4A, a; 4C, a), erect or, these of anterior pair, bent forward, 300-380 µm long, 50-80 µm wide, with external muscular layer 8-12 µm thick, and uneven ciliated epithelium 10-20 µm thick. Atrial lumen from imperceptible to 35 µm wide, filled with cilia, sometimes also containing spermatozoa. In one specimen, one atrium has a small (50 µm wide) round lateral diverticulum. Atria
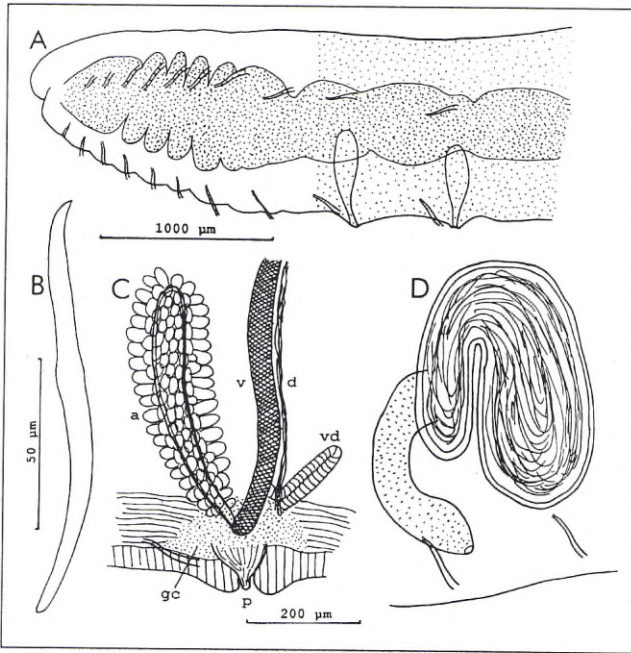
Fig. 4. *Lamprodrilus isoporus* (from Lake Siljan, whole mounts). A, general appearance of forebody; B, seta; C, details of first pair of male ducts, at dissepiment 10/11 (duct of one side of worm only); D, spermatheca, XIV. Abbreviations: a, atrium; d, dissepiment; gc, glandular cushion; p, penis; v, transversal blood vessel; vd, vas deferens.

irregularly covered with 25-50 µm high prostatic cells. Efferent ducts of atria at least 100 µm long, 25-35 µm wide, with gradually lowering and disappearing prostatic cover. Penes (Fig. 4C, p) 24-64 µm long, 29-75 µm broad, in large penial sacs; ends of some cells of the internal epithelium protruding from penial aperture like a small knob. Penial sac surrounded by a 50-100 µm wide glandular cushion (Fig. 4C, gc). Male pores posterior to ventral setae of X and XI (see Fig. 4A). Egg funnels on 12/13, funnel-shaped, their upper lips up to 215 µm high and 190 µm broad. Oviduct inside body wall, 80 µm long, 35 µm wide, opening in line with ventral setae. One pair of spermathecae (Fig. 4D), opening posterior to ventral setae of XIII. Spermathecal ampullae located in XIV, or partly extending into XV, sacculate or roughly tubular, about 500 µm long, 58-150 µm wide, sometimes widening to 170-290 µm at proximal end; epithelial wall of ampulla 2-30 µm thick, external muscular cover not thicker than 1 µm. Ampullae full of irregular bundles of spermatozoa. Spermathecal ducts about 500 µm long, erect, 64-85 µm wide for most parts, but narrowing to 24 µm distally; wall

of ducts consisting of 17-43 µm thick epithelium, and 2-8 µm thick external muscle layer. Lumen of ducts up to 8 µm wide, empty or with spermatozoa in its proximal portion.

Remarks

The Swedish material is morphologically identical with *L. isoporus variabilis* Svetlov, 1936, which has been found (sometimes abundantly) in several lakes of Karelia, Finland, north-western Russia and Estonia, and also in the estuary of the Neva River. The only valid difference from the nominate, Baikalian subspecies seems to be the size: *L. isoporus isoporus* has a length of 30-40 mm and a diameter of about 1.7 mm according to Michaelsen (1901, 1902). The variable number of spermathecae (2-3) in the European subspecies mentioned by Svetlov (1936) was perhaps accidental, and has never been confirmed by subsequent studies. The asexual reproduction with fragmentation supposed by Svetlov (1936) has not been verified either. The species is maturing and laying cocoons in the cold season (and only then) both in Estonia (Timm 1979) and Karelia (Popčenko 1988); the

abundance of reproducing individuals in Lake Siljan in April matches this rule.

The record from Lake Siljan (already noticed by Dr. Ralph O. Brinkhurst while examining other Siljan material in 1979; Brinkhurst, pers. comm.) is the first and so far only known occurrence of *L. isoporus* in Scandinavia. The species is supposed to have colonized the North European water bodies over the periglacial lakes (Timm 1987). Thus, its apparent lack in the large Scandinavian lakes, Mälaren, Vättern and Vänern, once closely connected with the former freshwater stages of the Baltic Sea, remains an enigma. *Lamprodrilus isoporus* was not found by the first author when reexamining S. Ekman's collection from Lake Vättern lodged in the SMNH.

Lumbriculus variegatus (Müller, 1774) (Fig. 5)

Müller 1774: 26 (*Lumbricus variegatus*)
Mrázek 1906: 381
Semernoj 1971: 31
Timm 1979: 158
Rodriguez 1988: 204

Material

Besides numerous immature individuals, three mature specimens were collected in Norra Djurgården, Stockholm, coll. T. Timm: Karpdammen Pond, 23 May 1995 (1); ditch at Husarbron Bridge, 24 May 1995 (1); shallows of Lake Brunnsviken, 25 May 1995 (1). Two specimens were sectioned, the third one whole-mounted.

Remarks

This common species normally reproduces by fragmentation and individuals with reproductive organs are rare.

The Karpdammen specimen (Fig. 5B-D) has one pair of testes, atria (Fig. 5C) and male pores in IX, two pairs of ovaries in X and XI (specimen hologynous), a single spermatheca in XII, and three pairs of spermathecae in XIII-XV. The Husarbron specimen possesses two pairs of testes in IX-X, but with atria and male pores in X only, one pair of ovaries in XI, paired sperma-

thecae in XII-XV, with an additional unpaired one in XV. The Brunnsviken specimen (Fig. 5A) bears atria and male pores in X, the other internal elements were not studied.

Mrázek (1906) discovered and described the huge degenerative variability in the number and disposition of separate elements of the genital system in *L. variegatus*, caused by the prevailing asexual reproduction. This is why Brinkhurst and Jamieson (1971) and other workers regard most of the nominal species of *Lumbriculus* as intraspecific variations of *L. variegatus*. According to Semernoj (1971) and Timm (1979), the double bend of the atrial efferent duct (Figs 5A, 5C) is a specific character not described in other congeners apart from the genuine *L. variegatus*. This character was depicted by Rodriguez (1988) too. Dorsolateral spermathecal openings near the dorsal setae (Fig. 5D) are also characteristic of this species. Both characters were observed in the Stockholm specimens.
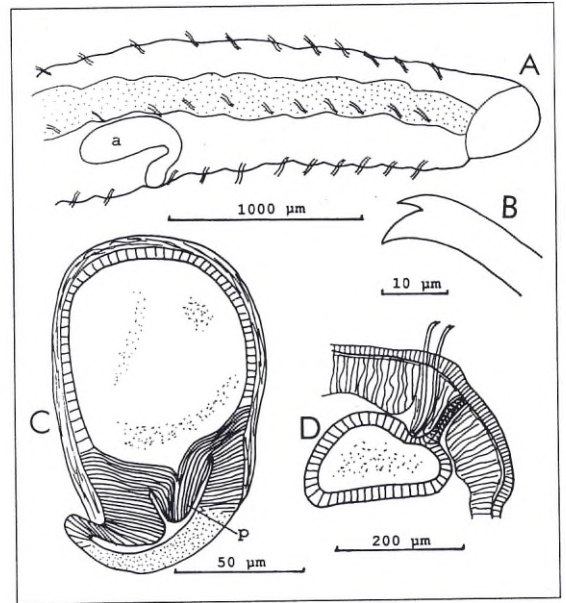

Fig. 5. *Lumbriculus variegatus* (A from Lake Brunnsviken, whole mount; B-D from Karpdammen Pond, cross sections). A, general appearance of forebody; B, distal end of a seta; C, distal end of atrium with penis, IX; D, spermatheca, XIV. Abbreviations: a, atrium; p, penis.

Rhynchelmis tetratheca Michaelsen, 1920

Ekman 1915: 300 (as *R. limosella*)
Michaelsen 1920: 130
?Hrabě 1962: 321 (*R. granuensis onegensis*)

Material

Two immature specimens from Lake Vättern, 98 m depth, 26 July 1911, coll. S. Ekman. Four immature specimens from Svartån River, about 10 km N of Västerås, fast flowing reach, abundant growth of sponges (*Spongilla*), 18 October 1994, coll. P.-E. Lingdell and E. Engblom (Limnodata HB, Skinnskatteberg).

Remarks

The worms from both Vättern and Svartån have a small, but distinct upper tooth in all setae, distinguishing them from another common European species, *R. limosella* Hoffmeister, 1843. Ekman (1915) and Piguet (1919a) apparently treated the Vättern material as *R. limosella* without any closer examination, since all other European species of *Rhynchelmis* were described later. According to Ekman, there were numerous mature specimens and even cocoons in his material from Lake Vättern. They may have remained in Piguet's collection for the possible description of a new species. However, such a description never appeared, maybe anticipated by Michaelsen's publication of *R. tetratheca* in 1920.

Rhynchelmis limosella was reported from the two largest lakes in Sweden (Vättern and Vänern) as well as from Lake Tyrifjorden in southern Norway by Milbrink (1973b, 1994).

Following Ekman's (1915) classical paper on Lake Vättern, *R. limosella* was mentioned also as a member of profundal fauna of the large Karelian lakes by Gerd (1950; referring to identifications by P.G. Svetlov, D.A. Lastočkin and C.I. Ioffe). Another problem arises with *R. granuensis onegensis* Hrabě, 1962 described from the profundal of Lake Onega and resembling *R. tetratheca* in having a tiny upper tooth in some setae. Hrabě (1962) pointed out the risk of it being confused with *R. limosella* in the

Karelian lakes. When mature, it can easily be distinguished from *R. tetratheca* by the lack of an unpaired, atrium-like, structure in IX.

Rhynchelmis tetratheca has not been mentioned for Scandinavia before, but it was recently found also by H. Torstensson (KM lab, Karlstad) in the Alsterån River, southern Sweden (identification confirmed by T. Timm).

Family Enchytraeidae

Cognettia cf. *sphagnetorum* (Vejdovský, 1877) (Fig. 6)

Vejdovský 1877: 304 (as *Pachydrilus sphagnetorum*)
Ekman 1915: 301 (as "fadenförmige Enchyträidenart")
Nielsen and Christensen 1959: 42
Kasprzak 1986: 124

New material

Twenty-seven specimens from Lake Vättern, Sweden, coll. S. Ekman: at 26 m depth, 2 August 1911 (6); 102 m, 5 August 1911 (1); 34-43 m, 10 August 1911 (4); 18-33 m, 5-11 August 1911 (15); 63-73 m, 11 August 1911 (1). Among them, one individual was mature and another partially mature. The mature specimen was serially sectioned, all others were whole-mounted.

Description

White filiform worms, 0.35 mm wide, without clear intersegmental furrows, the longest (maturing) individual 23 mm long with 96 segments; others mostly fragmented, on average about 14 mm long with about 52 segments. One shorter (regenerating?) worm only 9.5 mm long with 40 segments. Body wall thick, but smooth and transparent. Setae (Fig. 6B) 3 (rarely 2) per bundle, 60-106 μm long and up to 6 μm thick, sigmoid without nodulus, lacking only at the male pores (ventrally in XII or X). Clitellum (in mature worm) extending over XII-1/2XIII, reticulate. Primary pharyngeal glands (Fig. 6A, pg) 4 pairs, fused on 4/5 and 5/6, dorsally connected at 6/7, separate on 7/8, plus a single asymmetrical gland
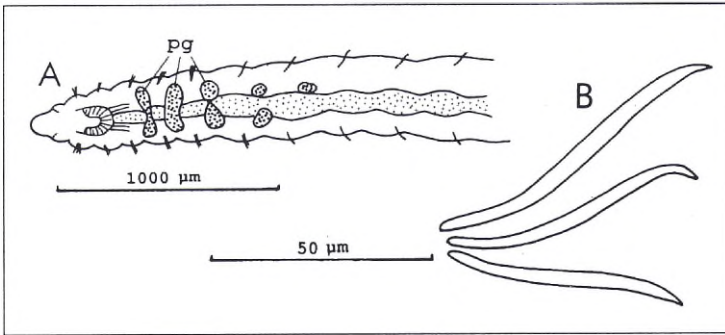
Fig. 6. *Cognettia sphagnetorum* (from Lake Vättern, whole mount). A, general appearance of forebody; B, bundle of setae. Abbreviation: pg, pharyngeal glands.

in VIII, reaching 8/9 on one side only. Secondary pharyngeal glands absent. Oesophagus thick-walled, gradually transiting into the chloragogen-covered midgut from IX on. Dorsal vessel traced in VI-X only in sectioned (mature) worm, in X-XIV in partially mature one. The only nephridium seen in sections located at 13/14. In posterior dorsal portion of VII-XIV, however, unknown paired or unpaired (one side) globular or oval organs were observed; these apparently free in body cavity, globular or oval, about 40 µm wide, smooth, with closely packed round nuclei. Coelomocytes scarce, round, granular, about 15 µm wide. In sectioned worm, small testes in XI, weakly developed unpaired sperm sacs in X and XII. Ovaries in XII, continuing inside egg sac in XIII; one single large egg with yolk. Male ducts degenerated in sectioned worm: only simple oval bodies, 50-68 µm wide, representing sperm funnels on 11/12; a third, similar but globular body occurred in egg sac in XIII. Male pores not found in (sectioned) mature worm, but female pores distinguishable in 12/13. Maturing individual with developing penial bulbs in X, and erect, bent sperm funnels at 9/10, funnels 180 µm long, 50 µm wide. Spermathecae with broad (about 50 x 90 µm in sections), free ampullae in VIII, their wall 5 µm thick, lumen full of granular matter. Spermathecal ducts directed forward, for their most parts only 15-16 µm wide, with a 32-45 µm thick valve containing spermatozoa in posterior half of V. Spermathecal openings at 4/5 in line with dorsal setae, with a 40-48 µm tall, compact bundle of gland cells.

Remarks

Cognettia sphagnetorum is a common terrestrial species in Europe, dominating in the acid litter of coniferous forests in Scandinavia (Nurminen 1967, Abrahamsen 1968). It reproduces mainly by fragmentation, therefore mature specimens are rare. Like other terrestrial Enchytraeidae, immature *Cognettia* sometimes occur in shallow waters. One mature specimen from the littoral of the small Lake Tänavjärv in Estonia was recently identified as *C. sphagnetorum* (Timm, unpubl.). However, no *Cognettia* species has previously been reported from deep lake bottoms, and profundal records of Enchytraeidae in general are scarce. The above-described specimens belong to one of the two enchytraeid taxa found by Ekman (1915) at 18-120 m depth in Lake Vättern that has remained unidentified like several other deep-water enchytraeids reported in the literature.

The scarcity and irregular structure of the mature individuals suggest an asexual reproduction of *C. sphagnetorum* even in the lake profundal. The location of the clitellum in XII (as normal for the family) has not been described for this species to date; usually it is shifted 3-4 segments forward. Dorsal connections within the pairs of the pharyngeal glands have not previously been described for *C. sphagnetorum* (see e.g., Nielsen and Christensen 1959), but with regard to the number of pharyngeal glands and most other characters this unusual profundal enchytraeid population is most similar to *C. sphagnetorum.*

Family Propappidae

Propappus volki Michaelsen, 1916

Michaelsen 1916: 51
Coates 1986: 423

Material

Five specimens from Svartån River, at Karlslund, Längbro, W of Örebro, province of Närke, southern Sweden, at site of collection about 20 m wide, 0.3 m deep, bottom mostly rocks, stones and gravel, 30 May 1995, coll. U. Ericsson; courtesy M. Medin (Medins Sjö- och Åbiologi, Mölnlycke). All specimens whole-mounted.

Remarks

The family Propappidae Coates, 1986, with only one genus containing three species, was thoroughly reviewed by Coates (1986). Her work includes a careful redescription and illustrations of *P. volki*. The present specimens, representing the first record of *P. volki* from Fennoscandia, conform in all details (even dimensionally) to these. The worms from Svartån are 4.3-5.0 mm long with 36-39 segments. The prostomium is anteriorly prolonged into an annulated, non-retractile proboscis, and the setae are bifid, with much reduced upper teeth, and arranged (2)3 per bundle.

Propappus volki is widely distributed in the Palaearctic (Coates 1986). It is characteristically found in springs, moving ground waters and stony streams, or in sandy substrates of lakes, reservoirs and large rivers (Bird 1982).

Conclusions

1. With this contribution, the list of Swedish freshwater Oligochaeta is augmented by five nominal species, thus reaching a total of 67.
2. *Rhyacodrilus subterraneus* and *R. falciformis*, generally regarded as clean-water animals with a primarily Middle European distribution, inhabit moderately eutrophic urban streams in Scandinavian capitals: *R. subterraneus* is known from both Stockholm and Oslo, *R. falciformis* from Stockholm only. Both species are also documented from wet soils in Stockholm.
3. The recent Ponto-Caspian invader in Sweden, *Potamothrix heuscheri*, has found a suitable niche for mass development in some shallow, highly eutrophic lakes in Stockholm.
4. Two rare lacustrine species, *Peipsidrilus pusillus* and *Lamprodrilus isoporus*, previously known only from east of the Baltic Sea, as well as the widely distributed Palaearctic rheophilous psammobiont *Propappus volki*, are now known to occur in Sweden.
5. A study of some mature specimens of *Lumbriculus variegatus* has confirmed the identity of this largely asexual species in Sweden.
6. *Rhynchelmis tetratheca* has been identified in old as well as new Swedish collections. The old material was earlier erroneously regarded as *R. limosella*.
7. A form very similar to *Cognettia sphagnetorum*, a common enchytraeid in acid soils, occurs in the deep lake profundal in the Swedish Lake Vättern.

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Reduced Recruitment in Brown Trout *Salmo trutta*, the Role of Interactions with the Minnow *Phoxinus phoxinus*

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Abstract

Annual recruitment, measured as the cohort size of age-class 4, and individual growth of brown trout, was studied in a Norwegian subalpine lake for ten years before and three years after introduction of minnows into a previously allopatric brown trout population. The cohort size of age-class 4 was approximately halved in sympatry with minnows, without any significant change in annual individual length increments. We have been unable to relate the reduced trout recruitment to other factors than interactions with minnows. It is uncertain whether the reduction of trout recruitment was the result of direct interactions between the two species in the nursery streams, or an indirect effect caused for example by increased brown trout cannibalism.

Keywords: brown trout, minnow, species interactions, cohort size

Introduction

As a result of introductions of fish species to new localities, changes in predation or competition pressures may considerably change the native fish fauna as well as modifying whole ecosystems (Zaret and Paine 1973, Svärdson 1976, Brabrand and Faafeng 1993). In Norway, the minnow, *Phoxinus phoxinus*, has extended its distribution during the present century, especially to mountain localities where the brown trout, *Salmo trutta*, was formerly the sole fish species (Borgstrøm 1973). Due to the overlap in diet between brown trout and minnow in these mountain localities (Lien 1981, Borgstrøm et al. 1984), it has frequently been predicted that the spread of minnows would have a negative effect upon brown trout populations (Borgstrøm 1973, Tysse 1995), corresponding to the effect on

rainbow trout, *Onchorhynchus mykiss*, after introductions of redside shiner, *Richardsonius balteatus* (Johannes and Larkin 1961). Decreased population densities of brown trout have been reported after introductions of minnows (Tysse 1995). Most information on changes in brown trout numbers after such introductions are, however, more or less anecdotal, because population data on both minnow and brown trout are lacking.

We have had the opportunity to study the dynamics of brown trout after the establishment of minnows in a lake where the brown trout population have been thoroughly studied over a period of ten years before minnows were recorded (Jensen 1977, Lien 1978, 1981). If minnows negatively affect brown trout, it is hypothesized that this would manifest itself in reduced individual growth rates and reduced cohort size.

Material and methods

Lake Øvre Heimdalsvatn

Øvre Heimdalsvatn, on the eastern slope of the Jotunheimen Mountains at 1,090 m a.s.l., has an area of 0.78 km^2, an average depth of 4.7 m, and a maximum depth of 13 m (Vik 1978, Grøterud and Kloster 1978). It is usually ice-covered from mid-October to early June (Grøterud and Kloster 1978). Brown trout was the only fish species recorded in the lake before 1969. In this year the first minnows were collected near an inlet from a small lake (Lien 1978, 1981). From 1969 to 1976, minnows gradually colonized the whole lake (Lien 1981).

Population data

The trout population was monitored from 1957 onwards, with annual estimates based on both the biostatistical method and the Petersen method (mark-recapture), and with good agreement between the two set of figures (Jensen 1974, 1977). In 1993-95, we estimated the number of brown trout by the Petersen method (Ricker 1975). Just after ice-break in June, trout were caught in a 50 m long beach seine, with a height of 4 m at the bag, and with a mesh size of 3 mm in the bag. The fishing was carried out between about 22:00 and 02:00-05:00. All fish were anaesthetized, and total length measured in mm. Fish with length ≥13 cm were marked with Alcian blue at the base of the pelvic, ventral, anal or caudal fins, by the use of a Jet inoculator (Hart and Pitcher 1969), with different fin marking codes each year. Sampling for control of marked fish was performed with series of gillnets, set randomly both in the littoral and in the pelagic part of the lake. The mesh sizes used were 16, 19.5, 22.5, 26, 29, 32, 35, 39, and 45 mm (bar measure). In addition, catches from the ordinary sport and gillnet fishery were also controlled for marks.

During our own fishery, scales and otoliths were sampled for age determination. Scale and otolith readings gave the same age for the first 9-10 years, while higher otolith ages usually gave lower scale age. When scale and otolith readings gave identical age, back-calculation to length at the start of the growing season in year of marking was carried out by use of the scales. When otoliths showed a higher age than scales, length at capture was considered identical to length at marking, due to growth stagnation.

An adjusted Petersen estimate (Ricker 1975) was obtained for size-classes above 13.0 cm, according to the equation:

$$N = (M + 1)(C + 1)/(R + 1)$$

where N = estimated number in population, M = number of marked fish, C = number captured and controlled for marks, and R = number of recaptures. Confidence limits of the estimates were obtained by using R as the entering variable in the Poisson distribution (Ricker 1975). By assuming that fish within particular length-intervals had equal catchability using the beach seine, the estimated number of fish within each length-class could be divided into cm-classes in proportion to the number caught in the beach seine.

The total number of fish within each year-class was calculated by apportionating the number within each cm-class according to the frequency of each year-class within the cm-class, and the numbers obtained summed for all cm-classes.

Survival rates (S) were obtained by using recaptures of marked fish, according to the equation:

$$S = (M_2 \cdot R_{12})/M_1 \cdot (R_{22} + 1)$$

in which M_1 and M_2 = number of fish marked at the start of the first and second year, respectively, and R_{12} and R_{22} recaptures of first year and second year marks, respectively, in the second year (Ricker 1975). Additionally, survival rates were obtained by $S = N_1/N_0$, in which N_1 and N_0 is estimated number of fish in the same cohorts in the second and first year, respectively.

Results

Population numbers and biomass

According to the length frequency in beach seine catches (Fig. 1) and catches from the ordinary fishery and gillnet control fishery during the period 1993-95 (Fig. 2), the brown trout popu-

lation in the lake mainly includes fish with lengths below 35 cm. From June 1993 to June 1995, the number of brown trout in length-class 27.0-34.9 cm was halved, from about 1,600 to about 800 fish (Table 1). The number of fish in the length-class 21.0-26.9 cm was more or less unchanged, varying between 1,400 and 1,900 fish. A high number of fish in length-class 13.0-
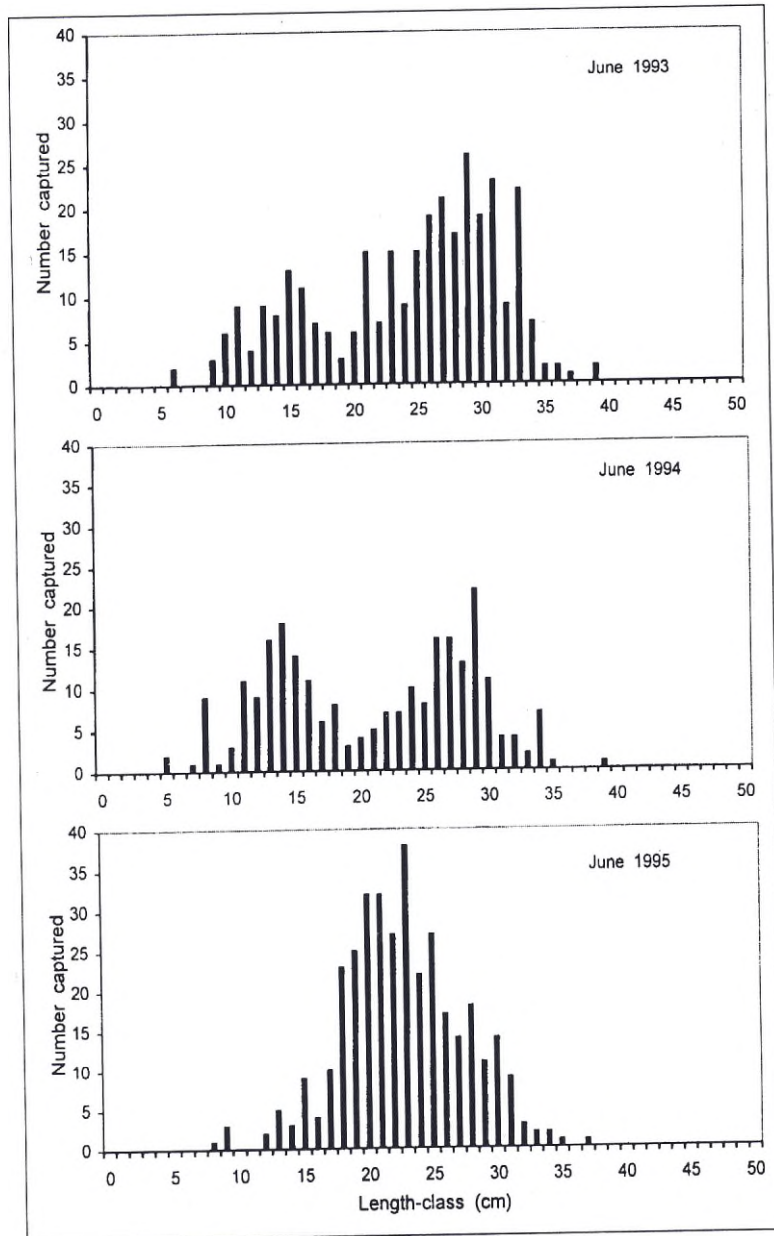
Fig. 1. Length distribution of brown trout captured by beach seine in Lake Øvre Heimdals-vatn, in June 1993-June 1995. Fish with lengths ≥13.0 cm were marked for estimation of numbers in population.
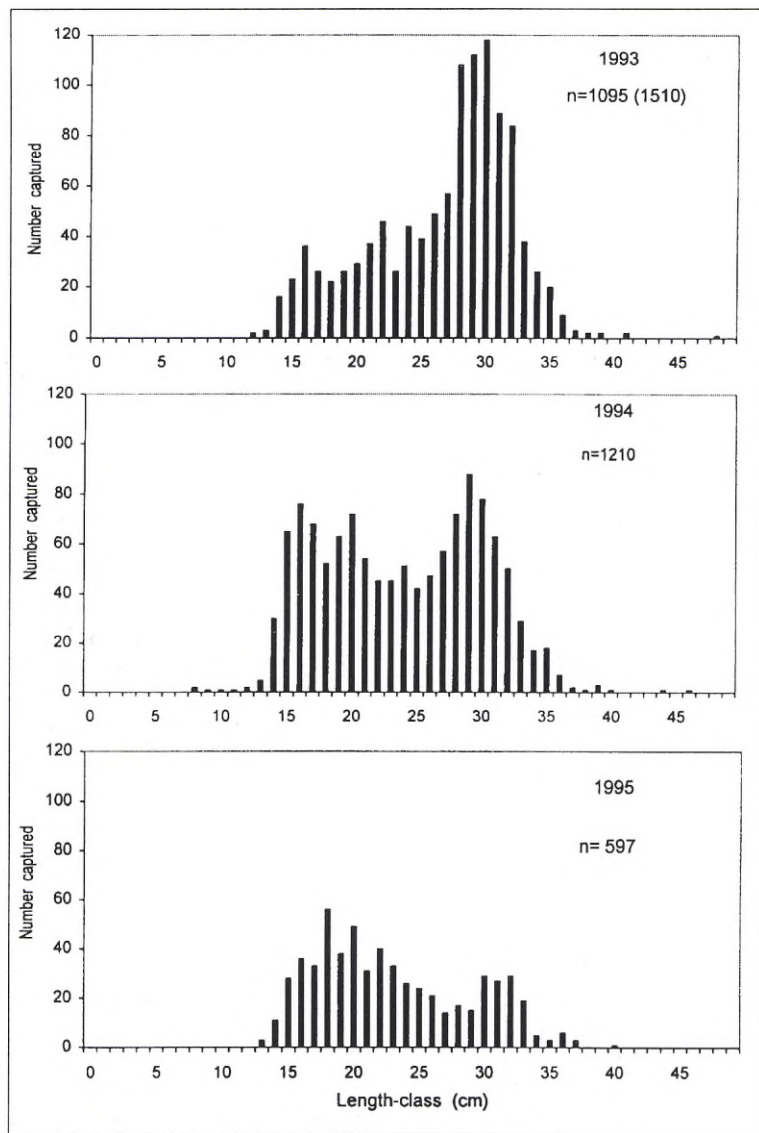
Fig. 2. Length distribution of brown trout in Lake Øvre Heimdalsvatn captured by ordinary fishery and experimental fishery in 1993-95. n=total number of fish measured. Number in parenthesis gives the total number captured.

15.9 cm was recorded in June 1994, and correspondingly, the length-class 16.0-20.9 cm, more than doubled in number from 1994 to 1995 (Table 1). The increase in number of fish within the length-class 16.0-20.9 cm, and the decreased number of fish within length-class 27.0-34.9 cm in June 1995, was also reflected in the beach seine catches in 1995 compared to the catches from 1993-94 (Fig. 1).

The estimated biomass of brown trout ≥13.0 cm fell from 814 kg (10.4 kg ha^{-1}) in June 1993

to 676 kg (8.7 kg ha^{-1}) in June 1994, and declined further to 570 kg (7.3 kg ha^{-1}) in 1995.

Cohort strength

In the period 1958-63, the range in numbers of age-classes 4 and 5 was 2,207-5,048 and 1,540-3,596, respectively (Table 2). In 1993-95, the calculated number of brown trout in age-classes 4 and 5 was in the range 1,202-2,466 and 851-2,294, respectively (Table 2). The number of fish

Table 1. Estimated number of brown trout in Lake Øvre Heimdalsvatn, in June 1993-95.

Year	Length-class cm	Number marked M	Number controlled C	Number recaptured R	Estimated number N	95% Confidence limits
1993	16.0-20.9	34	290	9	1,019	563-2,037
	21.0-26.9	79	311	12	1,920	1,135-3,467
	27.0-34.9	133	395	32	1,608	1,151-2,327
1994	13.0-15.9	64	256	6	2,386	1,185-5,220
	16.0-20.9	36	267	8	1,102	590-2,254
	21.0-26.9	58	142	5	1,406	664-3,245
	27.0-34.9	79	148	8	1,324	710-2,709
1995	16.0-20.9	94	205	6	2,796	1,388-6,116
	21.0-26.9	163	93	8	1,713	918-3,504
	27.0-34.9	73	101	8	837	449-1,715

in age-class 4 was significantly lower in 1993-95 compared to the numbers in 1958-63 (*t*-test, *P*=0.02). In 1994, the number in age-class 4 was much higher than in the two other years, and this gave a corresponding high number of the same year-class in 1995. In 1993, the number of fish in age-classes 6 and 7 was low, despite a light fishery in the years before, indicating that the number of fish in these two year-classes had also been low at age 4 and 5. From 1993 to 1995, the number of fish in age-classes ≥8 declined from nearly 2,200 to less than 500 fish (Table 2) as a result of the opening of ordinary gillnet and sport fishery from 1993.

Average survival rates, based on recaptures of marked fish in length-class 20.0-39.9 cm, mainly corresponding to fish in age-class 5 and older, was 0.51 from June 1993 to June 1994, and 0.56 from June 1994 to June 1995 (Table 3). According to the calculated cohort abundance (Table 2), the survival of age-class 5 and older from June 1993 to June 1994, and from June 1994 to June 1995, was 0.53 and 0.65, respectively. At the same time, about 1,510 and 1,210 trout have been reported captured in 1993 and 1994, while in 1995, a marked decline in captured fish was reported, with a total of 597 fish (Fig. 2).

Mean length and annual length increments

During the period 1960-68, the annual variations in mean back-calculated length increments were

Table 2. Calculated number of brown trout in age-class as 4-8 and ≥9 in Lake Øvre Heimdalsvatn, June 1958-63 (After Jensen 1977) and June 1993-95.

Age-class	1958	1959	1960	1961	1962	1963	1993	1994	1995
4	5,048	3,857	2,387	3,304	2,207	4,702	1,202	2,466	1,470
5	3,338	3,596	2,775	1,649	2,149	1,540	851	1,071	2,294
6	2,649	2,418	2,486	1,765	928	1,168	654	718	1,038
7	2,254	1,768	1,511	1,271	724	401	506	392	619
8	1,786	1,174	959	585	394	189	811	216	257
≥9	1,283	936	897	588	289	161	1,376	888	208

Table 3. Survival rates based on marked fish in length-class 20.0-39.9 cm in June, in year 1 and year 2, and based on estimated number of fish in age-class ≥5 in year 1 and ≥6 in year 2.

Period	Number marked Year 1 M_1	Number marked Year 2 M_2	Number recaptured from year 1 R_{12}	Number recaptured from year 2 R_{22}	Survival rate S
1993-94	236	138	14	15	0.5117
1994-95	138	270	6	20	0.5590

large (Table 4). The summed growth increments for the age-classes 4-7 were in the range 12.2-20.7 cm during this period, while in the period 1992-94 the range was 13.5-16.6 cm. Although the average back-calculated total annual length increment for age-classes 4-7 in 1992-94 was 14.8 cm, compared to an average of 16.8 cm in 1960-68, there is no significant difference in total length increments for these age-classes (Table 4) (*t*-test, $P=0.32$). By back-calculating from age-class 5 in 1960-68, the average length of age-class 4 at the start of the growing season was 16.0 cm, with a range of 15.6-16.7 cm. During the period 1993-95 the average length was 15.6 cm, with a range of 15.2-16.0 cm, when back-calculated from age-class 5. The difference in average length between these two periods was not significant (*t*-test, $P=0.21$).

Fulton's condition factor was calculated as average values for brown trout in length-classes from 13.0-14.9 cm through to 33.0-34.9 cm, captured at the end of June and the beginning of July, 1993-1995. Values increased for practically all length-classes from 1993 to 1994, while the values in 1995 were lower (Fig. 3). Condition progressively increased in larger fish both in 1994 and 1995, but not in 1993.

Discussion

The observed decline in brown trout recruitment coincides with the minnow establishment, but is not necessarily an effect of interaction between the two species, because there is a risk that brown trout recruitment has been affected by other conditions. To test the minnow effect would require at least one additional independent experiment. Recruitment to lacustrine brown trout populations may be density dependent, which means that annual recruitment from the streams is low when the lake population is dense (Borgstrøm 1992, 1994). For several years prior to 1993, exploitation rates in the lake were low compared to the period 1957-72. Before 1957, exploitation

Table 4. Average back-calculated annual individual growth in length (cm) of brown trout in age-classes 4-7 in Lake Øvre Heimdalsvatn, 1960-68 (After Jensen 1977) and 1992-94.

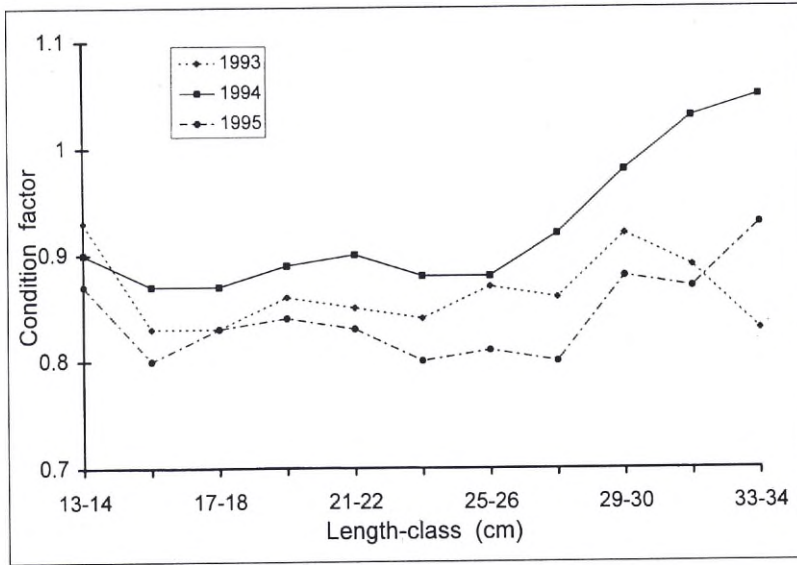| Age-class	1960	1961	1962	1963	1964	1965	1966	1967	1968	1992	1993	1994
4	4.5	5.0	3.5	5.5	6.0	4.7	5.0	4.2	5.8	4.3	3.8	4.3
5	4.0	4.2	3.3	5.4	5.6	4.4	5.3	3.9	5.7	5.7	3.6	4.1
6	3.4	3.5	2.9	4.9	4.8	3.7	4.3	3.4	4.6	3.9	3.4	3.1
7	2.7	2.7	2.5	4.5	4.3	3.2	3.5	2.8	3.8	2.7	2.7	3.1
Total length increment	14.6	15.4	12.2	20.3	20.7	16.0	18.1	14.3	19.9	16.6	13.5	14.6

Fig. 3. Fulton's condition as average for two-cm classes of brown trout captured in Lake Øvre Heimdalsvatn, during the period from the end of June to the beginning of July, 1993-95.

was also low, and fish density was high (Jensen 1977). However, annual recruitment was much greater before 1957, as well as during the period 1957-72 (Jensen 1977), when compared to the period 1990-95. Therefore, it is very unlikely that intrinsic density dependent factors have caused the reduction in recruitment.

Potential interactions between minnows and brown trout resulting in reduced recruitment of trout age-class 4 could take place both in the lake and in the inflowing and outflowing streams.

In 1976, the estimated total biomass of minnows was 221 kg wet weight, with an estimated production of 108 kg wet weight (Lien 1981). The population probably continued to increase after 1976. The total biomass of the brown trout population, age-class 4 and older, during the period 1958-70, varied between 616 and 1,510 kg (Jensen 1977), but as a result of the intensive fishing, the biomass declined to the range 616-851 kg during the period 1962-69. Thus, the minnow biomass was considerable, especially when compared to the biomass of young trout (Lien 1978). The diets of minnow and brown trout in the lake overlap (Lien 1978, 1981, Bruun 1988, Hansen 1988), and the abundance of *Gammarus lacustris* and *Lepidurus arcticus* in

the littoral zone has declined (Brittain et al. 1988). However, as no significant reduction in annual growth rates of brown trout has been recorded, the reduced recruitment to the brown trout population can hardly be explained as a direct result of food competition in the lake. Jensen (1977) found a significant correlation between brown trout growth rates, June temperature and population density. In 1994-95, the late ice break resulted in low mean water temperatures in June, and according to Jensen's model (1977) this would considerably reduce trout growth rates. However, the growth rates are still not significantly different from the growth rates observed in the absence of minnows.

During summer, minnows in the lake remain in shallow water, frequently in large shoals (Lien 1981). Also small brown trout usually occupy this zone (Thorpe 1974, Haraldstad and Jonsson 1983, Jonsson and Gravem 1985, Schei and Jonsson 1988, Hegge et al. 1989), probably reflecting an antipredator behaviour. Food competition between minnow and small brown trout may cause the trout to shift habitat and diet, comparable to the shift from zooplankton feeding to macroinvertebrate feeding in juvenile perch (*Perca fluviatilis*) in competition with roach (*Rutilus rutilus*) which is a more superior

zooplankton feeder (Persson and Greenberg 1990). With a large minnow population in the stony, shallow areas, the small brown trout may be displaced into deeper water with less cover, and thus become more exposed to predation by older trout. Lien (1981) examined the stomach contents of a large number of brown trout from Lake Øvre Heimdalsvatn, but from 1969 to 1972 no minnows or brown trout were found in the stomachs of 6,300 trout examined. From 1973 to 1976, when at least 100 trout were examined annually, no fish were found in trout stomachs. Later minnows have frequently been found in trout stomachs (Lien 1981, Bruun 1988, Hasle and Skjølås 1995). Two small brown trout were found in a brown trout stomach in 1994 (Hasle and Skjølås 1995), despite that the number of small brown trout in the lake was much lower compared to the period when minnows were not present. Sandlund and Forseth (1995) found that some larger brown trout, stocked in an Arctic charr-brown trout lake, consumed up to about 5 kg Arctic charr annually. This corresponds to about 500 prey fish with average length around 10 cm. Even if only a few brown trout turn to cannibalism, the annual number of predated brown trout may become substantial, thus explaining the reduced recruitment to the brown trout population.

Competition between brown trout parr and minnows in running water may also affect the recruitment. The outlet stream is the main nursery area for brown trout parr in Øvre Heimdalsvatn (Lien 1978). According to Lien (1978), age-class 3 and 4 constitute more than 65% of the immigrating brown trout from the nursery streams. Although the average length of age-class 4 was lower in 1992-94 than the average for the period 1960-68, the difference was not significant, indicating that growth in length of brown trout parr has not been affected by the presence of minnows. Interaction between brown trout and minnows in streams may take place from the swim-up stage of brown trout, i. e. a reduction in numbers of brown trout may occur at an early stage, while those surviving have the same access to food resources as before the min-

now establishment. However, at present there are no data for either brown trout parr or minnows in the streams, and it also has to be stressed that further studies would be needed to test a possible negative interaction between the two species in running waters, and correspondingly, for the possible interaction between the two species in the lake.

The decline in catch and number of catchable fish during the period 1993-95 is most likely due to the combined effect of low recruitment and high fishing mortality. During the same period the trout biomass declined from 814 kg to 570 kg, while during the period 1958-70, with even lower survival rates, the annual biomass was in range 616-1,510 kg for age-class 4 and older (Jensen 1977). If fishing pressure continues at the same level, and with the same average recruitment, i. e. 1,700 in age-class 4, the population is expected to decline further. Unless individual growth rates increase considerably, as a consequence of the reduction in numbers, the yield potential of the population will become much lower compared with the period before the minnow introduction, when the average annual recruitment of age-class 4 was 3,539 (Jensen 1977).

If independent experiments confirm that the observed decline in trout recruitment is caused by minnow introduction, a reduction of the minnow population would seem necessary to restore the recruitment potential of brown trout.

Acknowledgments

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Physiological Status of Vendace (*Coregonus albula* L.) Escaping from a Trawl Codend

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Abstract

Small vendace (*Coregonus albula* L.) escaping from a trawl codend are known to suffer high post-capture mortality. The purpose of this study was to examine whether physiological disturbances caused by the trawl capture process significantly contribute to the mortality of escapees. Fish that escaped through the trawl codend meshes during 10-min experimental tows were captured into a small-meshed hooped cage (volume 20 m³) that covered the codend. Muscle glycogen and total fish chloride concentrations were measured from escapees immediately after capture and at 1 h to 14 d post-capture. Muscle glycogen was low in escapees immediately after the 10 minutes trawl tow and remained low during the first post-capture hours indicating that the trawling process caused rapid exhaustion. Glycogen began to increase after one day of recovery and was restored in survivors within a few days after capture. Chloride levels in escapees tended to decrease during the first day after trawling suggesting osmotic disturbances. After three caging days chloride levels were restored in survivors. The greatest physiological stress in escapees coincided with the highest mortality, i.e., during the first post-capture day. Stress levels observed for purse-seine-caught comparison fish were similar to that observed for trawl escapees but they did not suffer high post-capture mortality. Hence, trawl-induced stress cannot be the only source for escapee-mortality. High mortality of trawl escapees is likely caused by a combination of physiological and physical (mechanical damage) factors.

Keywords: vendace, stress, glycogen, chloride, trawling.

Introduction

Vendace (*Coregonus albula* L.) is the most important species in Finnish commercial inland fisheries. In the late 1980s there were more than 100 paired trawling units (i.e., two trawlers towing one trawl) in Finnish freshwater lakes, mainly targeting on adult vendace. A considerable number of young vendace (0-group) pass through trawl codends during trawling and under certain conditions these escapees may suffer high mortality (Suuronen et al. 1995). The exact cause of death of these fish is not known and in particular, the relationship between capture stress and other possible mortality factors is unclear.

The general physiological responses of fish to stress, especially of salmonids, are well documented (e.g. Pickering 1981, Wedemeyer et al. 1984, 1990, Barton and Iwama 1991). However, little information is available regarding stress of pelagic fish captured in commercial fishing conditions (see the overview by Chopin and Arimoto 1995). Furthermore, only a few stress studies exist dealing with trawl fishing in fresh water (Soivio et al. 1991, Turunen et al. 1994).
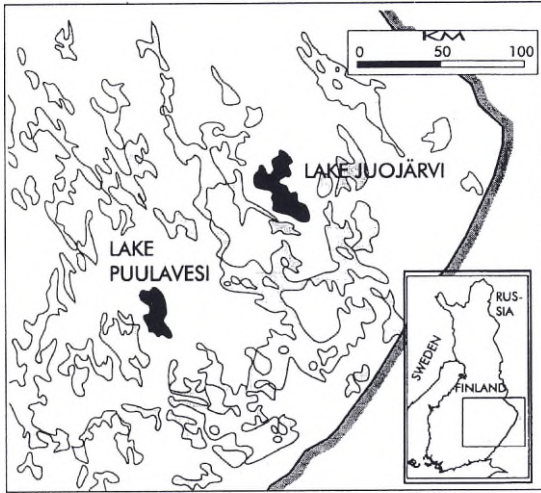
Fig. 1. Study lakes.

No published data exist of physiological responses of vendace to stress besides that of Pasanen et al. (1979).

The purpose of this study was to examine the levels of two stress-related physiological indicators (muscle glycogen and total fish chloride concentrations) in vendace escapees and determine if disturbances in these indicators could be identified as an important source of mortality.

Material and methods

Vendace (age group 0, length 5-10 cm) were sampled for physiological examination at the same time as fish for survival experiments (see Suuronen et al. 1995) carried out in Lake Juojärvi (July-August, 1992) and Lake Puulavesi (July-August, 1993) in eastern Finland (Fig. 1). Experiments were conducted using a commercial vendace midwater trawl towed by a paired trawling unit (Fig. 2). A 24-mm square mesh codend (stretched whole mesh length) was used for the experimental hauls. The trawl was towed near the surface in the evening (usually 19:00-23:00 h) at an average towing speed of 2.0 ± 0.2 knots. Fish that escaped through the codend meshes during 10-min experimental tows were captured into a small-mesh hooped cage (volume 20 m^3) that covered the codend (Fig. 2). After the haul, the cage was released, closed and anchored at the towing depth. Suuronen et al. (1995) provide details of the experimental set-up. During the study period, water temperature at caging depth varied between 12-18 °C in 1992 and 14-20 °C in 1993.

Codend escapees were sampled from cages immediately after capture and at 1 h to 14 d post-capture. To avoid extra stress to fish in cages
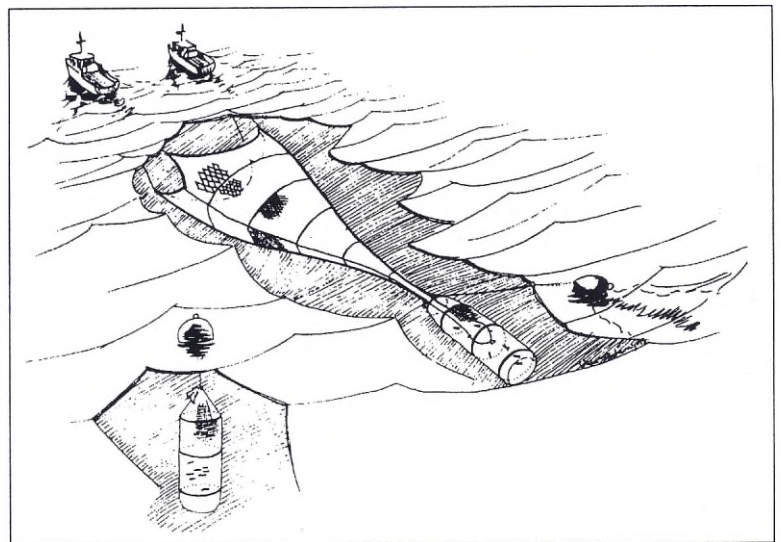

Fig. 2. Experimental set-up for capturing and caging of vendace that have escaped from a trawl codend.

Table 1. Number, and average length and weight of trawl and purse-seine caught vendace in the 1992 and 1993 experiments.

Sampling year	Lake	Number of trawl-caught fish	Number of seine-caught fish	Mean length (cm)	Meanweight (g)
1992	Juojärvi	57	9	7.3	3.2
1993	Puulavesi	164	40	7.7	3.3

(due to handling), each cage was sampled only once. Only live fish were sampled for the physiological study (we were not able to collect dying or moribund fish in adequate numbres). Fish were lifted by a dip-net and quickly frozen using dry ice (-79 °C; in 1992) or liquid N_2 (-196 °C; in 1993). We attempted to collect 10 fish in each sample but in some cases there were fewer than 10 individuals per cage. The length and weight of fish were measured in the laboratory. The biochemical data included 221 individually analysed codend escapees (Table 1).

For comparison, 29 vendace (3 samples; 9.July.1992, 14.July.1993, 4.August.1993) were caught with a small (10 x 250 m), manually operated purse-seine. In addition to these "0-h" samples, 20 seine-caught vendace (2 samples; 19.July.1993, 10.August.1993) were sampled after 5 and 20 days of caging (Table 1). Seining was conducted as gently and slowly as possible to minimize injury and capture stress. Moreover, one sample of small vendace (n = 10, mean length 5.6 cm; range 5.1-6.2 cm) were sampled in 5.July.1993 from a pound-net moored in a small lake nearby the study lakes. These fish had voluntarily swam into the bag of the pound-net. Fish caught by the seine and pound-net were sampled and frozen immediately after catching (hauling) and their physiological status was measured identically with the codend escapees.

Due to the differences in blood sampling from small vendace (in average 1.6-4.8 g/fish/sample), the biochemical study included dorsal white muscle glycogen and total (powdered) fish chloride analyses. Glycogen was determined by the method of Siu et al. (1970). Chloride was measured by a radiometric CMT10-chloride titrator within one month after sampling.

The data of trawl-caught vendace were pooled in order to facilitate the interpretation of recovery trends. Statistical differences in stress parameters between separate catching methods were analysed by Tukey's test having significance level at $P=0.05$.

Results

Muscle glycogen concentrations of codend escapees were at low levels (0.22-0.45 µg/mg) immediately after the tow and remained low during the first four post-capture hours (Fig. 3). After one day of recovering, muscle glycogen began to increase, and levels continued increasing throughout the 2-week monitoring period.
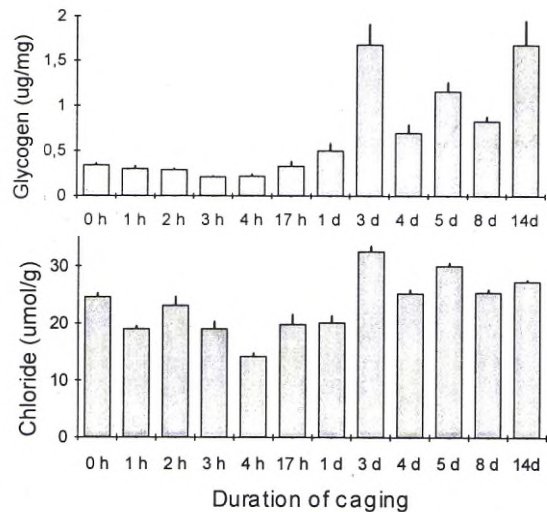

Fig. 3. Mean dorsal muscle glycogen and total fish chloride concentrations (+SE) of vendace escapees immediately after capture (0 h), and after 1 hour to 14 days caging periods.

Table 2. Mean dorsal muscle glycogen and total fish chloride concentrations of purse-seine-caught young vendace immediately after capture (0 h), and after 5 or 20 days recovery period.

Caging time	Number of fish	Glycogen (SE) µg/mg	Chloride (SE) µmol/g
0 h	29	0.40 (0.02)	26 (0.7)
5 d	10	0.64 (0.05)	32 (0.8)
20 d	10	0.45 (0.12)	32 (0.6)

The lowest chloride concentrations (14-19 µmol/g) in escapees were measured during the 1-4 post-capture hours (Fig. 3). Chloride levels began to increase after one day post-capture, and were higher (25-32 µmol/g) following 3 days of recover than immediately after the escape.

Muscle glycogen concentration of seine-caught vendace immediately after capture (0.38-0.46 µg/mg) was similar to that observed for codend escapees (Table 2). Average total fish chloride concentration (26 µmol/g) of seine-caught fish was slightly higher than that of codend escapees (compare to Fig. 3), however, the difference was not significant.

Pound-net-caught vendace had significantly higher levels of muscle glycogen (0.78 µg/mg; SE 0.13) and total chloride levels (36 µmol/g; SE 0.8) immediately after capture than trawl or seine-caught vendace.

Discussion

Vendace subjected to a trawl capture and escape process exhibited strong stress symptoms, especially during the first day after capture. In the simultaneous survival experiments, most escapee mortality occurred during the first day and often during the first hours after escape (Suuronen et al. 1995). So, the connection between secondary stress symptoms and mortality was apparent; highest mortality coincided with highest physiological stress.

One functional consequence of stress can be the activation of latent infections resulting in disease mortality (e.g. Mazeaud et al. 1977, Pickering 1981, 1992, Wedemeyer et al. 1984, 1990, Barton and Iwama 1991). However, the rapid death of escapees suggest that bacterial or viral infections were not the major cause of their death.

Judged by the decreasing chloride content during the first caging day, the osmotic balance of vendace escapees was disturbed due to the capture process. Exhaustion and stress experienced by fish may have been caused this disturbance (c.f. Borisov and Efanov 1981, Eddy 1981, Wardle 1981, Soivio et al. 1991). Moreover, skin injury suffered by the escapees (see Suuronen et al. 1995) may have markedly contributed here. It is well documented that skin and scales act as barriers against infections and also function as osmotic barriers between fish and surrounding water (e.g., VanOosten 1957, Rosseland et al. 1982, Lockwood et al. 1983, Main and Sangster 1991, Gadomski et al. 1994, Sangster and Lehman 1994). In our study fish scales were often observed by underwater video camera around the cod end during trawling. Thus, scale loss was the most general mechanical damage of the escaped vendace. On the contrary, seine-caught fish did not suffered similar descaling. However, detailed examination on skin injuries were not done.

Muscle glycogen in vendace was heavily utilized during the trawl capture process and decreased further within the first day after capture. Glycogen reserves in fish rapidly decrease when fish are subjected to strenuous exercise (e.g. Black et al. 1960, 1966, Wendt and Saunders 1973, Forsman and Virtanen 1989, Soivio et al. 1991). Although the duration of our trawl tows was only 10 minutes, a towing speed of 2 knots (1 m/s) apparently caused rapid exhaustion of small (5-10 cm) vendace. Swimming speeds of only 15-

16 cm/s for 30 minutes exceeded the aerobic capacity of 5 cm vendace (J. Karjalainen, University of Joensuu, pers. comm.). Energy reserves of fast growing young vendace probably are very limited for accomplishing extensive swimming efforts.

Differences in the levels of stress indicators between trawl- and seine-caught vendace immediately after capture were unexpectedly small. However, on average 50 per cent of the trawl-escapees died, whereas the mortality of seine-caught vendace was only 9 per cent (Suuronen et al. 1995). Nevertheless, these comparisons do not explain all the potential differences in physiological status between trawl-caught and seine-caught fish because only live trawl-caught fish were sampled. It is possible that these individuals showed less profound physiological effects than escapees which had died. It is noteworthy that vendace caught by the passive gear (pound-net) exhibited higher muscle glycogen and total fish chloride levels than trawl- and purse-seine-caught vendace. Clearly, seine capture is not an appropriate method to catch physiologically undisturbed small vendace.

Some other factors associated with the experimental procedure may have biased our results too. Sampling fish from cages may have caused acute stress in spite of rapid killing of fish (e.g. Railo et al. 1985, Wood et al. 1990, Milligan and Girard 1993, Pankhurst and Dedual 1994). This is supported by the observations that the total fish lactate concentrations of young vendace caught by trawl, seine and pound-net were at high levels throughout the recovery period (unpubl. data). Further, the exact exposure time of vendace did vary depending their arrival time in the trawl; individuals caught at the very beginning of a 10-min tow may have had a greater risk of severe exhaustion resulting in greater stress responses. This may have increased the overall variance in our data. It also might be argued that the absence of real, undisturbed controls makes it impossible to interpret our data. However, the main point in our study was not to find the absolutely resting level for vendace but rather to determine the duration and the relative changes in the levels of some basic stress indicators in order to assess the role of physiological stress in causing mortality.

In conclusion, on the basis of these results we are not able to specify any particular physiological disturbance as the dominating source of mortality in young vendace escapees. Nevertheless, it is clear that physiological disturbances caused by the trawl capture process markedly contribute to the high mortality of escapees. Mortality of escapees is likely caused by a combination of physiological (exhaustion) and physical (mechanical injury) factors.

Acknowledgements

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Fishing by Residents and Non-Residents in a Rural District in Norway: Subsistence and Sport - Conflict or Coexistence?

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Abstract

Many fish resources around the world are exploited by anglers as well as subsistence fishermen. However, when two or more types of fisheries exploit the same resource conflicts may arise. In rural Engerdal, a district in central Norway, we interviewed local subsistence and sport fishers, and non-resident anglers about their fishing behaviour and opinions toward different fishery regulations. There was a significant spatial segregation of resident and non-resident fishermen, reflecting resource and management differences in the area and varying preferences among resident and non-resident fishermen. While locals did not support increased restrictions on tourist angling, tourist anglers were in favour of more restrictions on resident gillnet fishing. This situation represents a challenge to managers since angling for brown trout and grayling probably represents a higher risk of over-exploitation in the study area than gillnetting for whitefish. Information aimed at non-resident fishermen should attempt to explain the reasons behind the extensive subsistence gillnet fishery in the area, while residents and non-residents should be informed about the current challenges confronting trout and grayling management.

Keywords: Subsistence fishing, angling, conflicts, regulations.

Introduction

Fisheries across the world are undergoing specialisation with increased segregation of angling, commercial fishing and subsistence fishing. In freshwater and along the coast, angling increases and commercial fishing has declined, while commercial open-ocean fishing is growing (Everhart and Young 1981). Subsistence fishing is declining in most areas (Glass and Muth 1989). However, many fish resources are still exploited by two or three main types of fisheries (Lackey 1979). Coexistence of traditional subsistence fishing and angling exploiting the same stocks in the same waters is common in sub-arctic areas; in Russia, Scandinavia, and North America, and in tropical areas, like Latin America, Africa and Asia. In both regions, angling tourism has developed parallel to resident subsistence fishing. Multiple use of fish resources often involves several ethnic groups.

Multiple use practices regarding fish resources are very common in Scandinavian freshwater fisheries (Sipponen 1994, Aas 1996). Rural residents with strong subsistence traditions, carry on traditional gillnet fisheries despite the decline in the economic value of this type of fishery over the last decades. However, rural people are also often anglers. A typical rural fisherman is frequently a combined gillnet fisherman and angler (Aas 1996). Tourist fishermen often maintain an interest for angling. Local fishing regulations in Norway generally restrict gillnet fishing to residents only.

Subsistence or not?

Subsistence fisheries, as originally defined (cf. Sharif 1986), are extremely unusual in the western world today. Glass et al. (1995) therefore suggested defining households which supplement their incomes from a variety of sources and di-

rect consumption of fish, wildlife and other natural resources, as subsistence households. They also emphasised the importance of recognising sociocultural and psychological benefits of subsistence lifestyle. This makes it difficult to distinguish between subsistence and sport fishing. In a managerial perspective, type of equipment used is one method for distinguishing between subsistence and sport. Gillnets are the most important subsistence fishing gear. Gillnet fishing harvests significant quantities of freshwater fish (for example the 650 resident fishermen in Engerdal caught 23,000 kg fish in 1992) and involves sharing procedures for more efficient use of the harvest (Aas 1992). On a national level, non-commercial fishing (sport and subsistence) has been estimated to harvest a total of 30,000-40,000 metric tons of saltwater and freshwater fish annually, of which freshwater fish comprise about one fourth of the catch (Aas 1993). Based on the broad definition of subsistence (Glass et al. 1995), gillnet fishing by rural residents in Norway must be considered a subsistence fishery.

Multiple use of a fish resource represents a challenge to management because of the risk of conflict (Lackey 1979, Smith 1980). Adequat planning and management are therefore important for multiple use fisheries. Combining subsistence and angling can initiate severe conflicts because the two groups may represent different value systems (Usher 1976). In order to avoid conflict and to optimize benefits from a multiple use fishery, knowledge of the types of fishery taking place and the social groups involved is imperative, in addition to biological data on fish stocks.

We investigated the fishing habits of residents and non-residents (equipment use and area use) and their opinions about fishery management and regulations in a rural area in central Norway. The following issues were investigated:
a) what characterised the fisheries carried out by residents and non-residents, with respect to equipment use and area use?
b) which fishery management actions and regulations did the two groups prefer,
c) were there any differences in their opinions?

Study area and Methods

Engerdal is a remote municipality in central Norway. There are 1,700 rural residents, living in an area of approximately 2,100 km². The municipality is rich in natural resources and contains a variety of rivers and lakes (275 km² lake area, more than 100 km of larger rivers). Forestry, tourism, agriculture and the public sector constitute the most important sources of employment (Statistical yearbook Norway 1993).

Engerdal provides diverse inland fishing opportunities. For fishing, the four most popular species are brown trout *Salmo trutta* L., Arctic charr *Salvelinus alpinus* (L.), grayling *Thymallus thymallus* (L.) and whitefish *Coregonus lavaretus* (L.). The waters of Engerdal can be roughly divided into three categories:
1. The north-eastern wilderness area, with the Femundsmarka national park offers fishing in small lakes and streams.
2. The central area, mainly with lakes of various size. The most important is Lake Femund, the third largest lake in Norway (204 km²).
3. The southern area, offers fishing in several large outlet rivers and streams.

The north-eastern and southern area historically include famous Scandinavian angling waters (Eknæs 1979), where brown trout, Arctic charr (north-east) and grayling are the most important species. The large lakes in the central area contain several fish species, but whitefish gives the highest yield (Sandlund and Næsje 1989). Annually, 10,000 fishing licences are sold in Engerdal, of which only approximately 650 are to residents. Residents almost exclusively purchase annual licenses, while non-residents buy day, week and annual licenses. Most of the waters are state owned, and incomes from licences do not directly support the local economy. However, angling tourism is important for the local economy. Licenses to non-residents are equally distributed among tourist anglers from southern Norway and Sweden (Aas and Kaltenborn 1995). Because of the low percentage of residents among licence holders, we conducted separate surveys for residents and non-residents.

An estimate for 1992 indicated that local fishermen harvested approximately 23 metric tons, of which two thirds were whitefish. Non-residents harvested approximately 25 metric tons, mostly grayling and trout; and the commercial fishery in Lake Femund caught 15 metric tons of whitefish (Aas 1994).

Non-residents were studied with an access point survey (Hayn 1991) during the fishing season, while we chose a telephone for resident fishermen conducted in September immediately after the clode of the fishing season. Both surveys related to the fishing season of 1992. Questionnaires aimed at non-resident anglers were distributed at camp sites and at the Femund ferry, which transports most of the anglers to the north-eastern fishing area. Random interviews throughout the main fishing season (20 June to 31 August) yielded 555 replies corresponding to a response rate of 87%. The data is not representative for all non-resident license holders, as sampling at the site overrepresents those staying for longer periods (Kokel et al.1991). The questionnaire was pre-tested among 50 anglers and contained, in addition to the questions presented here, questions concerning angler motivation and interest for local services (see Aas and Kaltenborn 1995 for details).

The telephone survey among residents based on structured questionnaires was conducted from 17:00 to 21:30 hours on weekday evenings. This study was part of a larger study on regional differences in angling habits in Norway (Aas 1996). The questionnaire contained a number of questions comparable to those given to non-residents. Two hundred residents were contacted on a random phonecall basis. In each household, a random member older than 16 years of age was chosen. The sample is thus representative for all citizens above 16 years of age. 111 or 56% stated that they fished in the district during the last year. Their responses were compared to those of non-resident anglers.

Differences in attitudes between the two groups were analysed using analysis of variance (ANOVA).

Table 1. Percent of resident and non-resident fishermen participating in subsistence fishing (gillnetting) and angling, and equipment use among anglers in Engerdal, Norway, during 1992.

Fishing behavior (%)		
	Residents (n=111)	Non-residents (n=555)
Subsistence and angling	57	
Only subsistence	17	
Only angling	26	100
Anglers (n=92 and 555):		
Fly only	8	24
Generalists	55	37
Spin- and bait	37	39

Results

Most resident fishermen participate in angling as well as in subsistence fishing (Table 1). Approximately one out of five used gillnets only, while 27% practised angling only. Resident's angling behaviour was as follows: 6% only participated in fly fishing, 46% used both fly and spin equipment, while 31% only used spin equipment. Non-resident anglers include a larger fraction of specialised fly fishermen. Twenty-four percent of the visitors only fished with fly, whereas 38% fished with fly and other angling equipment, and 39% used spin and bait equipment only.

Table 2. Area use among resident and non-resident fishermen in Engerdal. Per cent of each group fishing different parts of Engerdal during 1992. Sum per cent >100 because people use more than one of the areas.

	n	Northeast	Mid	Southwest
Residents	111	26.1	73	44.8
Non-residents	544	35.1	13.6	63.8

Table 3. Opinions regarding different fisheries management measures among resident and non-resident fishermen in Engerdal. (df = 1 in all cases). Response format ranged from 1, supports strongly, to 5, oppose strongly, with 3 being neutral. Ranking of different management measures among the two groups are in parentheses.

Management action	Resident	Non-resident	n	F-value	P
Reduce pollution	1.17 (1)	1.53 (1)	540	17.92	0.0000
Stocking trout fry	1.49 (2)	2.04 (2)	584	28.67	0.0000
Stocking catchable size trout in small lakes	2.44 (3)	2.19 (4)	573	3.51	0.06
Stocking catchable size trout in main rivers	2.46 (4)	2.48 (6)	540	0.01	0.92
Reduce number of whitefish	2.50 (5)	2.97 (7)	458	14.40	0.0002
Ban spring fishing	3.23 (6)	2.24 (5)	512	51.30	0.0000
Increase minimum size for brown trout	3.45 (7)	3.39 (8)	577	0.20	0.66
Increase minimum size for grayling	3.74 (8)	3.30 (9)	543	10.04	0.002
One fly only per fishing rod	3.96 (9)	3.44 (10)	561	15.41	0.0001
Restrict non-resident fishing licenses	4.14 (10)	3.61 (11)	514	20.56	0.0000
Introduce bag limit in the rivers	4.55 (11)	3.88 (12)	593	36.22	0.0000
Prohibit gillnet fishing	4.68 (12)	2.15 (3)	542	378.00	0.0000

Non-residents mainly used the southern part of the study area, while residents were more dependent on the central part of the study area, where lakes dominated (Table 2). Even if angling is permitted for non-residents in this area and the lakes are easily accessible, it is obviously not as attractive as the other areas.

Resident and non-resident opinions about fisheries management and regulations in general were similar, except for some issues (Table 3). Reducing pollution and various stocking practices were favoured by both groups. However, residents favoured stocking trout fry more than stocking catcheable sized skrout. No such priorities were observed among non-residents. Both groups opposed harvest regulations (increased minimum size for trout and grayling, bag limits in river fisheries, and one fly per rod). However, residents generally held stronger opinions (negative and positive) about the different alternatives, whereas non-residents were often more uncertain about the alternatives, resulting in non-commital answers, or they answered that they didn't know (left out from further analysis) (Table 3).

The most striking differences between the groups regarded restrictions directed toward the other group; prohibiting resident's gillnet fishing, and reducing the number of angling licenses available to non-residents. While residents strongly opposed restrictions for gillnetting, non-residents favoured these restrictions just as strongly. Less expectedly, restrictions on non-resident angling were less opposed by non-residents than by residents. Like gillnetting, fishing in the spring is an activity mainly conducted by resident anglers (taking place before the holiday season), when large trout kelts are easy to catch for skilled anglers. Because of the catch of kelts, this fishing is controversial. Residents support this type of fishery, while non-residents oppose it.

There were only small differences in preferences <u>within</u> the two sub-groups. The only significant difference between resident anglers, resident combined anglers and subsistence fishermen, and resident subsistence fishermen, was related to opinions about restricting the number of flies allowed per rod. Resident anglers opposed this regulation more than resident subsistence fishermen.

Discussion

Multiple use of a fish resource including subsistence fishing and angling is beneficial from several points of view. Firstly, multiple use principally involves broader interests groups and larger numbers of participants as compared to a single interest group. Multiple use of a fish resource theoretically produces a higher yield, since different fisheries partly supplement each other. This is particularly important for the multi-species fisheries common in Scandinavia. Benthic and riverine brown trout are very attractive for anglers, and efficiently harvested with angling gear. The pelagic, planktivorous whitefish is difficult to harvest efficiently with angling gear and consequently of less interest to anglers.

On the other hand, the large number of fishermen in Engerdal with different interests and with varying traditions, rights and cultural backgrounds, represent a considerable potential for conflict. A conflict stems from incompatibilities between the interests of one group and the behavior of another (Jacob and Schreyer 1980). Goals and behaviours may be defined as incompatible when the achievement of a goal by one person is frustrated by the behaviour of another person (Gramann and Burdge 1981). Because of the pronounced area segregation of the different user groups, conflicts in Engerdal are probably substantially reduced. Non-resident anglers mainly use the north-eastern and southern area which offer good opportunities for angling in rivers and small lakes. Resident fishermen use the central area which is easily accessible and has excellent gill-net fishing opportunities in lakes. In spite of segregation, the study uncovered several issues which are experienced as conflicts between the various user groups.

In many areas with combined subsistence and sport fishing, conflicts between those using gillnets and sport equipment are frequent. Common arguments from those fishing with gillnets are that anglers steal or destroy nets, while the angling community claims that locals using gillnets overexploit the fish stocks. However, in Engerdal residents did not advocate increased

restrictions for non-resident angling, whereas anglers were strongly in favour of restricting gillnet fishing. Residents probably do not feel that their exclusive gillnet fishing rights are threatened by tourists. In addition they understand that the community depends on income and jobs created by angling tourism. Non-residents strongly opposed resident gillnet fishery and obviously regard this as a threat to their own angling possibilities. However, the gillnet fishery probably only has minor influence on non-resident angling, because this fishery is mainly directed towards whitefish in lakes, and to a very limited extent harvest lake running trout (Sandlund and Næsje 1989). If the resident gillnet fishery stopped or was reduced the fish stocks might develop negatively with increased density of smaller whitefish, and reduced number of trout and grayling (different species composition, cf. Healey 1975, 1983, Jensen 1981). In a large number of Norwegian lakes with pelagic Arctic charr or whitefish, reductions of traditional fishing have resulted in a number of dense, low quality stocks (Amundsen 1988, Saltveit and Brabrand 1989).

Common for previous studies of behaviour and differences in attitudes among anglers (Renyard and Hilborn 1986, Teisl et al. 1993), is that fishermen oppose regulations restricting their own activity severely, while they support or accept regulations which do not interfere, or only slightly affect their own behaviour. Renyard and Hilborn (1986) studied salmon angler's attitudes towards different sport fishing regulations in British Columbia. They found that seasonal closure and a daily bag limit were generally not acceptable to anglers. Preference for other regulations depended upon frequency of fishing. Infrequent anglers preferred low annual bag, while frequent anglers preferred larger size limits and gear restrictions. Teisl et al. (1993) investigated management opinions regarding balancing open-water and ice fishing in Maine. Resident anglers favoured policies seeking even distribution between open water and ice fishing. Non-residents clearly preferred regulations favouring open water fishing. This was largely because residents were the only group who practised ice-fishing.

These results are similar to our findings, and indicate a weak attitude towards protection of fish stocks, as long as protection is incompatible with existing fishing and harvesting behaviour, and from non-residents no recognition of resident fishing practices. This pattern parallels partly Hardin's (1968) description of the "tragedy of the commons". Hardin's (1968) theory in short is that in a situation where the individual sees no or few benefits of harvest restrictions, and the costs of overharvesting are distributed among all users, this will likely lead to the destruction of a resource for a shorter or longer term. The single fisherman experience what is called the prisoner's dilemma (Ostrom 1990). Traditionally, a licensed fishery is not considered a commons resource, but these results indicate that those exploiting a inland fish resource act in accordance with Hardin's (1968) theory, within the framework of the existing regulations. If overharvesting is a problem, regulations that equally distribute the costs of reduced harvest among all users, but which do not exclude any groups, are probably a constructive solution to the situation.

Conflicts may be severe and bind management resources whether they are "real" or only perceived by one or more of the user groups involved (Jacob and Schreyer 1980). Often a lack of appropriate information keeps a conflict going for a long time. This seem to be the case also in Engerdal, as there is no biological evidence to indicate that whitefish stocks are overexploited by gillnetting. On the contrary managers and biologists worry about that a reduced harvest of whitefish can result in stunted populations of other species with less value and reduced quality (Sandlund and Næsje 1989). The strong opinion by non-resident anglers in favour of restricting subsistence fishing by residents is therefore largely based on a lack of information about subsistence gillnetting and its effects on fish stocks. Information for non-resident anglers on the species composition of catches by resident fishermen and the consequent positive effects on fish stocks would probably reduce or eliminate these conflicts. Both residents and non-residents lack information about the effects of angling on

riverine fish stocks of trout and grayling. Both angler groups strongly oppose regulations aimed at reducing the exploitation rate and changing the catch composition by applying increased minimum sizes and bag limits. This reflects the well established tradition for consumptive angling in Norway (Aas and Kaltenborn 1995). Direct restrictions on harvest opportunities in angling, like bag limits and catch-and-release, are still unfamiliar to most anglers in Scandinavia.

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Newly-emerged *Salmo trutta* Fry that Migrate to the Sea - An Alternative Choice of Feeding Habitat?

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Abstract

Traditionally, it has been assumed that fry of the anadromous brown trout, *Salmo trutta*, which migrate seawards when newly-emerged from the gravel, are the losers in an intense intra-specific competition. They are supposed to stop feeding and drift downstream and eventually die. From a field study of a small Baltic Sea population of 'sea trout' it was found that the total body length and physical condition, in terms of body-length-adjusted body-weight, body-length-adjusted mean-otolith-length and mean-otolith-length-adjusted fluctuating asymmetry of the otoliths of newly-emerged fry that migrated seawards were no different from the values for stream-dwelling fry. Although food items found in the stomachs of the two samples of fry were somewhat different, they had eaten the same amounts of food. These findings provide support for the hypothesis that the seaward migration of the fry is an adaptation to to low summer water levels, which regularly occur in many of the small streams entering the Baltic Sea.

Keywords: Anadromous brown trout, newly emerged fry, migratory strategies, physical condition, summer dry-out streams.

Introduction

Although many small streams periodically dry out during the summer, they can still provide a habitat for spawning populations of anadromous brown trout, *Salmo trutta*. For instance, anadromous trout (i.e. sea trout) have been observed in at least 14 of 20 Gothlandic streams (Sweden), which regularly dry out during the summer (Gydemo et al.1982). This is exceptional, since the sea trout are assumed to spend their first year(s) in running freshwater before smoltification and migration to the sea (for a review see Elliott 1994). In order to analyse the population dynamics of anadromous trout living in such streams, a study started in 1992 on the spawning population in and smolt migration from the River Själsöån on the Island of Gothland. The results have shown that the number of spawning fish outnumbers the number of seaward migrating smolts (Table 1). Hence, it would not seem to be a valid proposition that the spawning population is solely dependent on its smolt production.

Three alternative hypotheses to smolt production can explain the recruitment of the spawning stock: 1. Adult trout straying from other streams; 2. Adult trout spawn more than one season; 3. Homing adults have migrated to the sea as fry before the stream dries out. The first

Table 1. The number of fish caught in the fish-trap during the spawning and smolt migration seasons.

	1992/93	1993/94	1994/1995	1995/96
Main upstream migration period	12.11-17.12	27.11-06.02	06.11-21.01	17.11-19.01
Number of adult females	35	49	46	17
Number of adult males	33	42	41	41
Number of smolt	23	29	70	68

hypothesis is unlikely, because the normal frequeny of straying among the Baltic Sea trout is rather low (Alm 1936, Larsson et al. 1979, Svärdson and Fagerström 1982). The second hypothesis is unlikely as the smolt to adult survival rate to is low (about 10%) as well as the survival rate from the first-time-spawning to second-time-spawning (about 30%). Because, a pilot study showed that a large proportion of the fry from the River Själsöån migrate to the Baltic Sea and are found in shallow waters close in shore (Figure 1), we have focused this study on testing some predictions from the third hypothesis. In general, those fry that migrate downstream are regarded as losers in the intense intraspecific competition among the newly emerged fry. They are supposed to stop feeding, soon to lose weight, drift downstream and eventually die.

The survivors start to feed and either remain near the nest or migrate, usually upstream (e.g. Elliott 1989, 1990, 1994). If the second hypothesis is to be valid, then a downstream migration of newly-emerged fry should represent an adaptive response to drying-out periods and, hence, the sea-living fry should be in good physical condition.

The aim of this study was to test the prediction from the second hypothesis by analysing fry from the river, the river mouth and the sea outside the river mouth in regard to total body length, body-length-adjusted body weight, body-length-adjusted mean otolith length, mean-otolith-length-adjusted fluctuating asymmetry of the otoliths, and the content and volume of the stomach and intestine.
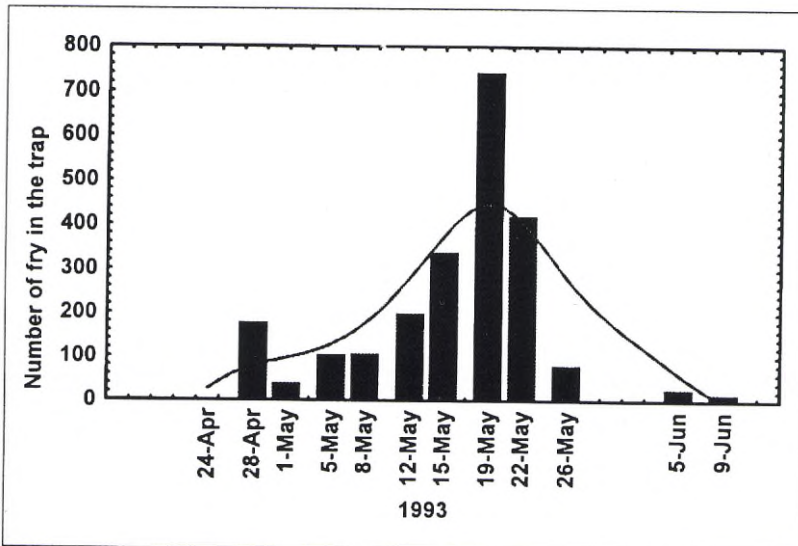

Fig. 1. The number of newly emerged fry caught in a fry-trap. The trap was mounted in 1993 in the lower part of the stream.

Material and methods

The study area

The ecological field study has been in progress, since 1992, in a small stream, the River Själsöån, on the Island of Gothland. The Island of Gothland is located almost in the middle of the Baltic Sea (58°N, 19°E) and it is the biggest island in the Baltic Sea (3,140 km²). Sea trout has been observed in at least 24 of 36 Gothlandic streams. In eight of the 24 streams, smolt production has been recorded and in 16 streams only nests or young of the year have been observed (Gydemo et al. 1982). Although 20 streams regularly dry out during the summer, nest or sea trout have been observed in 14 of those streams (Gydemo et al. 1982). Hence, it is reasonable to assume that sea trout inhabit streams which regularly dry out.

The River Själsöån basin is about 35 km². The studied area has been restricted to the initial 550 m stretch of the stream. Upstream from this point, there is a waterfall, which prevents further upstream migration of sea trout. The streambed consists mainly of calcareous gravel, which explains why the pH varies from 8.6 in the autumn and winter to 7.6 during late summer. The average width is about three metres, but it varies from one to eight metres throughout the initial 550 m stretch. However, during the summer the stream usually dries out . The upper half of the stream is usually completely dry and only some pools of water remain in the lower parts. Water-level gauge readings revealed that the water level varies from 150 mm when the stream is almost dry during the summer to 1,100 mm when there is a flood during the autumn and winter, corresponding to a water flow of about 700 Ls⁻¹. The stream banks are mainly covered by trees and bushes. The mean gradient from the river mouth to the waterfall is 2.7%. During normal water-level conditions, the stream enters the sea in a channel. However, when the water-level is low, the stream enters river mouth across a small delta. The bay is rather exposed for winds from the south and the west (Fig. 2). A trap has been operating in the stream since the autumn
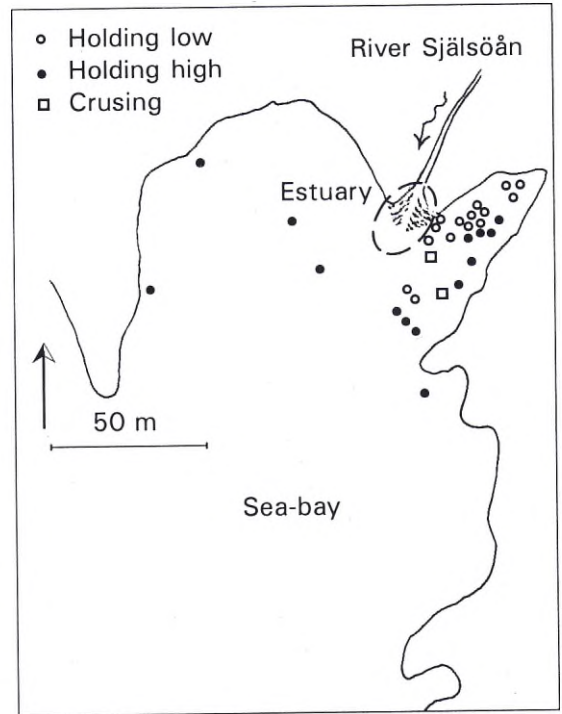

Fig. 2. A map of the bay where the River Själsö has its outlet. The symbols on the map denote where the fry were caught in the Baltic Sea. O denotes fry caught when holding a low position on the bottom; ● denotes fry caught when holding a position high up in the water mass; □ denotes fry caught cruising.

of 1992, catching the upstream and downstream migrating fish more than 100 mm in length.

The trout in the River Själsöån

When the water-flow increases during the autumn, sexually mature trout start to enter the river. The spawning migration continues to February (Table 1). The timing of the spawning period depends on the water-flow, and normally it extends over November and December, although spawning has been observed as late as February (Table 1). A pilot study made in 1993, showed that the emerging fry may appear in May and that a large number of them migrate in to the sea (Fig. 1). The numbers of one- and two years-old trout were fairly low, thus contributing a smaller number of smolt than the number of

spawning adults (Table 1). Over a four-year period, the average number of spawning individuals was 76 and the number of smolt was 48 in each year.

The field study

Field observations and capture of the fry

To find out when the fry emerged in 1995, the stream was inspected at 2-day intervals. The first fry was observed on the 18th of May and fry were caught from May 20 to May 24. Three types of capture methods were used. In the stream we used hand net and electrofishing, in the river mouth we used a hand net, small fyke nets and electrofishing and in the sea we used hand net and small fyke nets. The electrofishing gear could not be used in the sea because of the salinity. Altogether 125 fry were caught in the stream, 85 in the river mouth and 47 in the bay. Different methods were used as we were not interested (or able) to estimate the abundance of fry in all three habitats, but to catch as many fry in the bay as possible.

Before the fish were caught by hand netting in the sea-bay their positions were noted on a map together with their behaviour. Three types of behaviour were recorded, viz. fish standing on the bottom (holding low), standing high in the water (holding high) and cruising in the sea. In Fig. 2 the positions of the fish caught are recorded on a map.

Treatment of the fry

After capture, each fry was placed in a tube containing 96% alcohol, for conservation and subsequent assessment of total body length, body weight, length of each sagittal otolith and its stomach and intestine contents. Thirty-two of the fry were directly weighed and total body length measured. These data were to assess of the loss due to the preservation method.

To minimize the effect of storage time on the variation in dehydration due to conservation, the weights and lengths were recorded in the laboratory about 30 weeks after the capture. Each fry was decapitated and both sagittal otoliths

were collected. They were mounted on microscope slides in clear nail polish and total length immediately measured under a stereo-microscope to the nearest 0.01 mm. The remainder of the body was replaced in the tube for later dissection of the stomach and intestine.

The stomach and the intestine were removed under a stereomicroscope at the laboratory and separated near the pyloric sphincter. The stomach and intestinal contents were then adjudged according to four categories; empty, almost empty, half full or full. The Taxon of each food item in the sample was then, if possible, identified and its predominance (%) in the gut sample was recorded, using the percentage by volume method (Hansson 1980).

Calculation of parameters and statistical analyses

An analysis of the effect of dehydration due to preservation showed that 96% of the variation in "preserved total body length (pbl)" was explained by "field total body length (fbl)" and 99% of the variation in "preserved body weight (pbw)" was explained by "field weight (fbw)" (Fig. 3,4). The total body length was assessed by the regression equation;

$$pbl = 0.741 + 0.897 \cdot fbl,$$
$$r = 0.98, \ t = 26.3, \ df = 29, \ P < 0.00001$$

and the body weight was assessed by the regression equation;

$$pbw = -5.357 + 0.619 \cdot fbw,$$
$$r = 0.99, \ t = 59.5, \ df = 29, \ P < 0.00001$$

Both dominance status and otolith size at first feeding were good predictors for body size three-month later (Metcalfe et al. 1992). Although, the fry in this study have started to feed, the otolith total length was used as such a predictor. In order to remove the effect of body length (pbl) from mean otolith length (mol) we used the residuals from the regression equation;

$$ln(mol) = 0.154 + 0.916 \cdot ln(pbl),$$
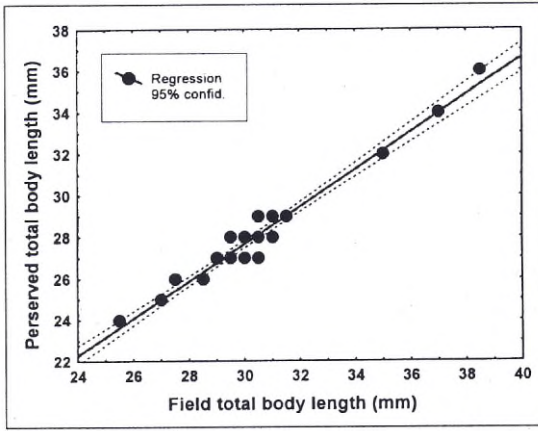$$r = 0.78, \ t = 12.8, \ df = 107, \ P < 0.00001$$

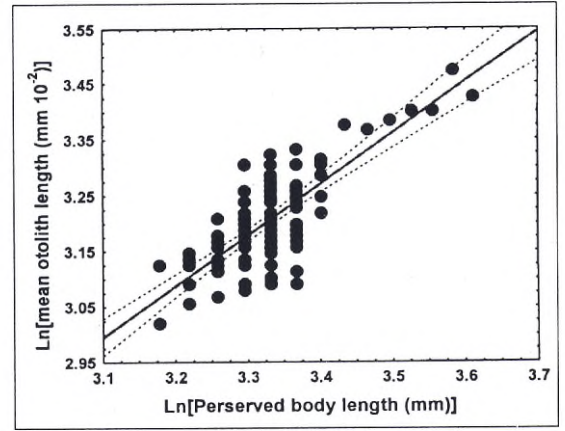Fig. 3. The correlation between field - and perserved total body length.

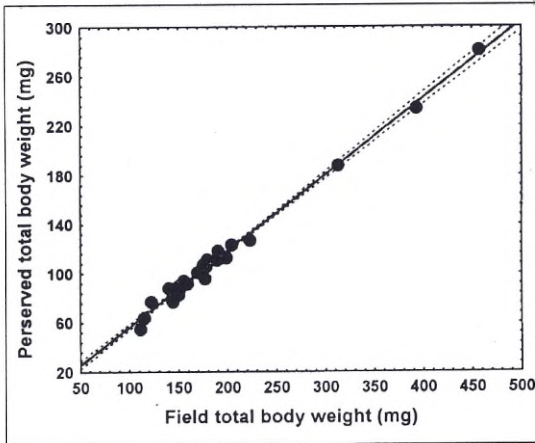Fig. 5. The correlation between the logaritmic values of perserved body length and mean otolith length.

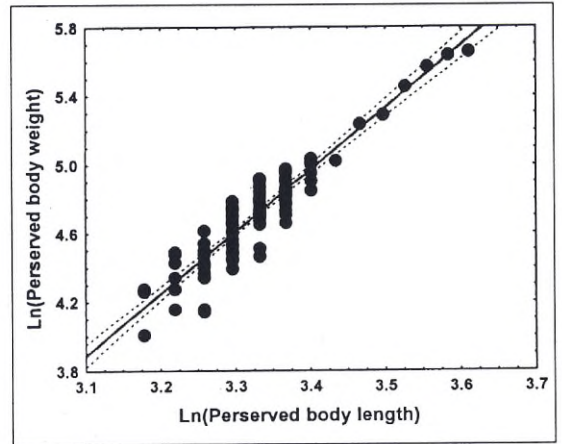Fig 4. The correlation between field - and perserved total body weight.

Fig. 6. The correlation between the logaritmic values of perserved body length and body weight.

as an assessment of body-length-adjusted mean otolith length and, hence, dominance status of the fry (Fig. 5).

In order to assess the relative physical fitness of the fry we used the residuals from the calculated regression shown in Fig. 6.

$$ln(pbw) = -8.191 + 3.881 \cdot ln(pbl),$$
$$r = 0.93, \; t = 41.4, \; df = 255, \; P < 0.00001$$

A perfect bilateral symmetry is regarded to be the ideal outcome of development in pair wise morphological traits. Fluctuating asymmetry is the measure of deviation from this ideal (van Valen 1962, Palmer and Strobeck 1986, Leary and Allendorf 1989, Parsons 1990). The view that such fluctuating asymmetry could reflect environmental heterogeneity, or stress, during ontogeny has been supported by the results of studies on fish (e.g. Valentine et. al. 1973, Ames et al. 1979). Downhower et al. (1990) showed that the asymmetry between the left and right sagittal otoliths reflects the condition during early development. Hence, it is reasonable to

assume that "losers" during early development should exhibit a more pronounced asymmetry between their left (*lol*) and right (*rol*) otoliths, compared to "winners". In this study, the asymmetry (*as*) between total length of the left and right Sagitta otolith was assessed as;

$$as = Abs|lol-rol| \cdot mol^{-1}$$

Because there is a correlation between mean otolith length (*mol*) and asymmetry, the residuals from the regression equation;

$$as=0.155-0.005 \cdot mol,$$
$$r=-0.27, t=-2.88, df=107, P<0.01$$

were used in order to remove the effect of otolith size *per se* (Fig. 7)

In order to reveal any differences between capture site (viz. stream, river mouth, bay) in regard to body length, body weight, condition factor, otolith size and asymmetry, a general ANOVA procedure was used. The difference in the mean distances from the river mouth at which the fry were performing a 'holding low' or a 'holding high' behaviour were tested by using an ANOVA procedure. When an 'all effect' was revealed, a Scheffe's test was used for *post hoc* comparisons. In order to assess any difference
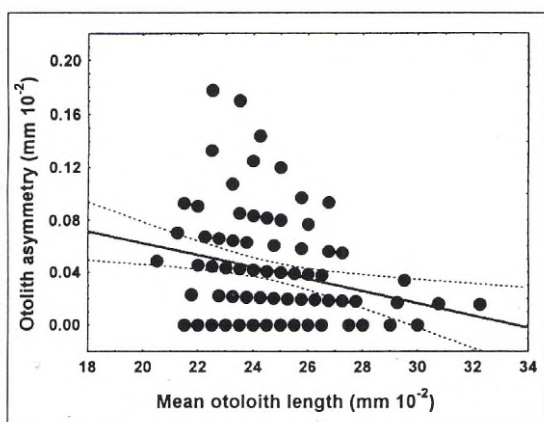

Fig. 7. The correlation between the asymmetry of left and right sagittal otolith length and mean otolith length.

between sites in regard to the volume and nature of the contents of the stomach and intestine, a non-parametric Kruskal-Wallis ANOVA test was used.

The correlation between total body length, body-length-adjusted body weight, body-length-adjusted mean otolith length and mean-otolith-length-adjusted fluctuating asymmetry of the otoliths with the current amount of food in the stomach, and intestine respectively, were calculated with help of a forward stepwise multiple regression.

Two types of Ho hypotheses were analysed in a stepwise multiple regression, viz. *Ho: R=0* for the overall effect and $Ho:\beta_j=0$ for each partial regression coefficient (*j*). Furthermore, in the ANOVA and Kruskal-Wallis ANOVA tests the *Ho* hypothesis was postulated as $Ho:\mu_1 =\mu_2=\mu_3$. The level of significance was set at *P<0.05*.

Results

The summated effect of all parameters on the volume of food in the stomach was significant (*R=0.44*, *F(4:81)=4.87*, *P<0.01*). The only significant individual factors were the total body length and the body-length-adjusted body weight (i.e. condition factor) on stomach fullness (Table 2A). Corresponding analyses for the intestine contents revealed a significant overall effect (*R=0.40*, *F(3:82)=5.07*, *P<0.01*), but individually only the body-lenght-adjusted otolith length and mean-otolith-length-adjusted fluctuating asymmetry of the otoliths showed significant correlation (Table 2B).

A Kruskal-Wallis test showed that those fry caught in the river mouth had less food in their stomachs than either those caught in the stream or in the bay (Fig. 8). A corresponding analysis revealed that there was no overall significant difference in the volumes of food in the intestines of fry caught in all three habitats (Fig. 9). An analyses of the type of food eaten showed that the major food items were Chironomidae larvae and subimagoes. In the stomachs of the fry caught in the bay, the proportion of Chironomidae subimagoes was significantly

Table 2. A stepwise regression showing the relationship between the volume of food in the stomach **(A)** and the intestine **(B)** with total body length, residual body weight, residual mean otolith length, residual otolith asymmetry. Only total body length and residual body weight significantly explained some of the variation in the volume of food in the stomach, and only the residual mean otolith length and residual otolith asymmetry were significantly related to the volume of food in the intestine.

(A) Regression analysis summary: $N=86$, $R=0.44$, $F(4:81)=4.87$, $P<0.01$

Variables	BETA	$t(81)$	P
Body length	0.31	3.03	0.004
Residual body weight	0.27	2.36	0.02
Residual otolith length	0.10	0.88	0.38
Residual otolith asymmetry	-0.14	-1.40	0.17

(B) Regression analysis summary: $N=86$, $R=0.40$, $F(3:82)=5.07$, $P<0.01$

Variables	BETA	$t(81)$	P
Residual otolith asymmetry	-0.27	-2.66	0.009
Residual otolith length	0.24	2.37	0.02
Body length	0.17	1.68	0.10

higher than in those caught in the river mouth and the stream (Table 3). Furthermore, the proportion of Chironomidae larvae was significantly higher in the fry caught in the bay compared to those caught in the stream as was the proportion of Plecoptera (Table 3) Some evertebrate groups, such as Oligochaete, Simuliidae, Psylloidea and Ceratopogonidae, were only eaten by fry in the stream; others such as Collembola were only found in the stomachs of fry caught in the bay and such as Tipulidae only in the river mouth (Table 3).
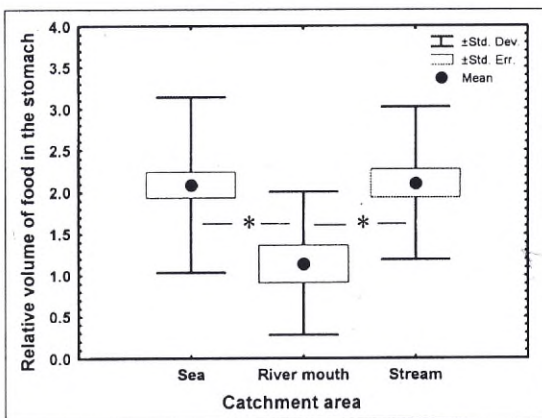

Fig. 8. Difference in the average volume of food in the stomach of fry caught in the stream, the river mouth and the bay (Kruskal-Wallis ANOVA by ranks; $H(2:100)=10.5$; $P<0.01$).
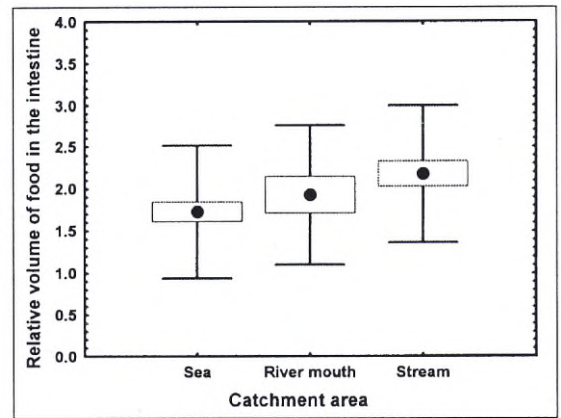

Fig. 9. Difference in the average volume of food in the intestine of fry caught in the stream, the river mouth and the bay (Kruskal-Wallis ANOVA by ranks; $H(2:86)=5.8$; $P>0.05$).

Table 3. The proportions of different groups of food species found in the stomach of the fry (Kruskal-Wallis ANOVA).

Group of species	Sea Mean% $N=44$	River mouth Mean% $N=14$	Stream Mean% $N=28$	K-W-ANOVA Over all P	Sea vs. stream P
Chironomidae subimagos	34.1	10.4	18.8	0.06	0.03
Chironomidae larvae	39.6	48.2	50.9	0.36	0.16
Chironomidae imagos	0.7	0	2.7	0.41	0.53
Copepoda	8.3	3.9	3.3	0.41	0.22
Plecoptera	1.4	0	10.7	0.003	0.03
Gammarus	2.4	7.1	0.7	0.94	0.73
Oligochaeta	0	0	0.4	0.12	0.14
Simuliidae	0	0	6.1	0.04	0.07
Psylloidea	0	0	0.5	0.36	0.31
Collembola	0.1	0	0	0.62	0.33
Tipulidae	0	6.8	0	0.08	0.30
Ceratopogonidae larvae	0	0	0.2	0.36	0.31
Detritus	2.1	9.3	2.2	0.48	0.64

An ANOVA test revealed that there was no significant difference in total body length between the fry caught in the stream, the river mouth and the sea (Fig. 10). However, a corresponding analysis of the residual body weight showed a significant main effect (Fig. 11). The

Scheffe *post hoc* test revealed that the total-body-length-adjusted body weight was significantly lower for fry caught in the river mouth compared to those caught in both the stream and the bay (Fig. 11). There was no significant difference in the main effect between the habitat factors in
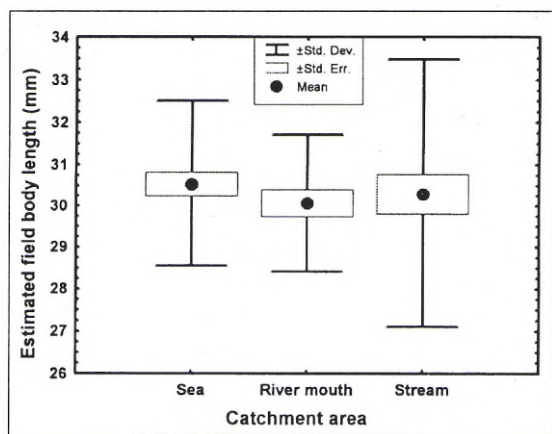

Fig. 10. Difference in estimated mean total body length of fry caught in the stream, the river mouth and the sea (ANOVA:$F(2:106)=0.3$; $P>0.05$).
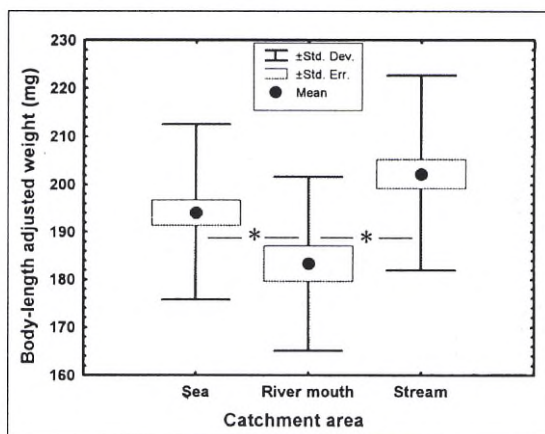

Fig. 11. Difference in mean residual body weights (condition index) of fry caught in the stream, the river mouth and the bay (ANOVA: $F(2:106)=5.2$; $P<0.01$).

regard to either body-length-adjusted otolith length or mean-otolith-length-adjusted fluctuating asymmetry of the otoliths (Fig. 12, 13).

The behavioural study of the fry after they had entered the sea-bay revealed that the change their behaviour depended on how close they were to the stream mouth. 'Low holding' fry were caught significantly closer to the river mouth than 'high holding' fry (Fig. 14).

Fig. 14. Difference in the mean distances from the river moutn at which the fry were caught a holding low or high in the sea (ANOVA: $F(1:27)=9.4$; $P<0.01$).
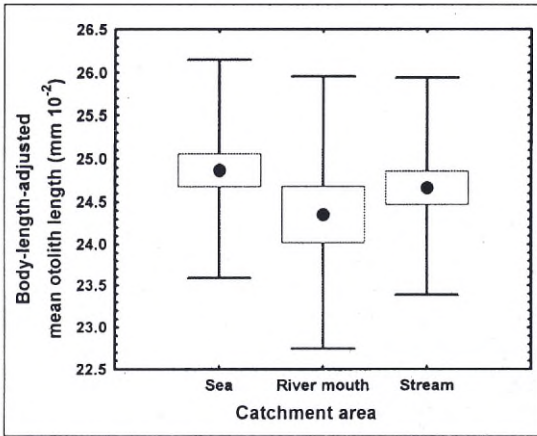

Fig. 12. Difference in residual mean otolith lengths of fry caught in the stream, the river mouth and the bay (ANOVA: $F(2:106)=1.2$; $P>0.05$).
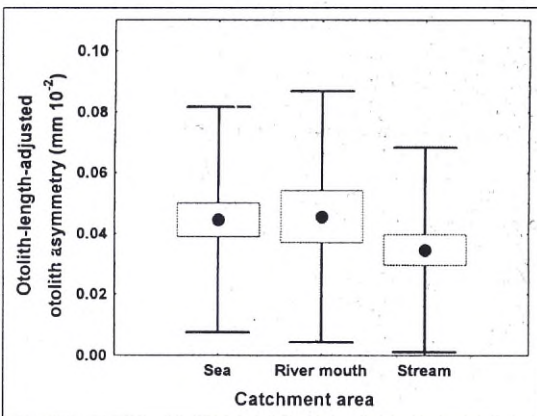

Fig. 13. Difference in residual mean otolith asymmetry of fry caught in the stream, the river mouth and the bay (ANOVA: $F(2:106)=1.0$; $P>0.05$).
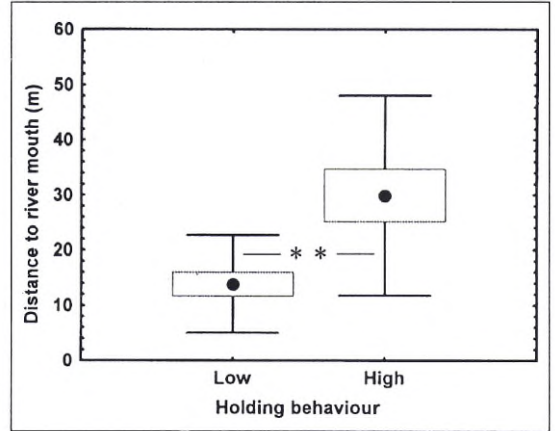
Discussion

Assessment of physical condition

One of the most noticeable responses of fish to any form of environmental stress is to cease feeding (for a review see Jobling 1994). This cessation of feeding may affect many different biological parameters. For example, both the body size and otolith size of anadromous salmonids are believed to be associated with starvation and a reduction of physical fitness (Metcalfe et al. 1992). However, other factors such as fluctuating bilateral asymmetry of the otoliths (Downhower et al. 1990) and condition factor (Pedersen and Jobling 1989), may reflect the physical fitness of a fish as well. In this study, total body length and condition factor were correlated with the amount of food in the stomach. Mean otolith length adjusted for body length and otolith asymmetry adjusted for mean otolith length were associated with the amount of food in the intestine. Hence, it is reasonable to assume that those variables are true predictors of the individuals' physical fitness.

Habitat choice, feeding and morphological parameters

The chances of an individual fry surviving during its initial feeding period is heavily dependent on its ability to compete for resources such as food and space within its natal stream (e.g. Elliott 1989, Metcalfe et al. 1992). Those which fail to become established in the stream are supposed to drift downstream, lose weight and eventually die (Elliott 1989, Titus and Mosegaard 1990). Thus, the fry in the river mouth and those in the sea would be supposed to have less food in their stomach and intestine and, in consequence, be smaller, have a lower condition index, have a smaller mean otolith size at first feeding and a greater degree of otolith asymmetry. However, if the native stream regularly dries out, then it is obvious that evolution should favour a migratory strategy involving migration of the fry into the sea. If this hypothesis is valid, then these fry should have the same physical condition as their conspecifics in the stream. The results of the present study clearly show that the latter hypothesis can not be rejected out of hand. The fry caught in the bay were as similar in body size and had a similar physical condition, in terms of condition index, mean otolith size and fluctuation asymmetry of the otoliths as the fry caught in the stream. Furthermore, they had about the same amounts of food in their stomachs. That the fry is foraging during their seaward migration is supported by differences in the food items taken in the stream, the river mouth and the bay. However, since the fry caught in the river mouth had less food in their stomachs and a lower condition factor, it would seem that the fry lose in physical condition during the migration but recover when they reach the sea. Further support for that conclusion is the fact that the fry change their behaviour when in the sea. Close to the river mouth they perform a typical stress-induced behaviour pattern by 'holding low' on the bottom, whereas further out they adopt an ordinary stream-dwelling behaviour pattern, such as 'holding high' and including attacks on food items.

For an individual fish the drive to migrate from one habitat to another changes with time, either due to changes in the habitat conditions or in the requirements of the individual (Baker 1978). Within the genera *Salmo* and *Oncorhynchus*, the migratory drive to change the habitat from running freshwater to the sea may be treated like a habitat selection problem, with a trade off between the size-specific mortality risk and the expected size-specific growth rates in the two habitats (for theory of the principles see Bennett and Houston 1989). In general, the sea habitat is more productive than the freshwater one (Gross et al. 1988), wherefore the expected growth rate and the predation rate are higher in the sea. For the anadromous species of *Salmo* and *Oncorhynchus,* the fry usually stay in the river for a certain period of time after emergence from the gravel nest, before they migrate to the sea (for a review see McDowall 1988 and Mills 1989). The time the juveniles spend in freshwater varies between both species and stocks. For example, fry of the pink salmon, *O. gorbuscha*, migrate to sea soon after emergence from the gravel (Hoar 1956), whereas those of the Atlantic salmo, *S. salar*, usually stay in the river for one to six years before metamorphosing to become smolts and thereafter migrating to the sea. Due to the seasonal dry periods in the River Själsöån, the fry there are subjected to a high average mortality rate in the stream if they stay in the stream to smolt age. Hence, fry that migrate straightway seawards may gain in Darwinian fitness. However, it was beyond the scope of this study to find out whether or not both migratory strategies do in fact contribute to the stock recruitment.

To conclude, because the data obtained indicate that the fry in the sea are in as good physical condition as the fry in the stream, we cannot at present reject the hypothesis that fry migrate to the sea as an adaptation to seasonal dry periods.

Acknowledgements

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Plasticity in Growth of Indoor Reared European Eel

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Abstract

Elvers, *Anguilla anguilla* (L.), were fed in excess for 137 weeks at constant water temperatures. Six populations (initially 1,300 elvers/tank) were monitored and size graded every fifth or sixth week. The biomass increased between gradings with 4.6 ± 0.2, 7.5 ± 0.3 and 10.0 ± 0.3%/week (mean+SE, N=46), at 17, 20 and 26 °C, respectively. At 50-70 g body weight, the specific growth rate of tagged individuals was positively related to temperature, but independent of sex and of age, except for a positive trend with age at 26 °C. After 95 weeks, 164-278 individuals remained in four original tanks at 20 and 26 °C. During the 42 following weeks, the numbers were reduced by removal of eels $\geq$60 g. The growth of untagged eels could be estimated from the progression of cumulative weight distributions. For eels remaining in the original tanks in week 137, the specific growth rates were estimated at 0.5-3%/week until week 95. During week 95-137, the specific growth rate was further depressed in low ranked eels, while it increased in individuals of higher weight rank. These results show that eels, with depressed growth for more than two years, have potential for faster growth at higher age and size. The plastic response to water temperature is most purely expressed in tagged eels, above a body weight when the future growth is independent of age.

Keywords: *Anguilla anguilla*, plasticity, growth potential, temperature, age.

Introduction

The Atlantic eel species, *Anguilla anguilla* (L.) and *A. rostrata* (LeSueur), are regarded as two separate panmictic populations with wide geographic distributions of juveniles (McCleave et al. 1987). Both species show great variability in growth, both between and within local stocks (Helfman et al. 1987, Moriarty 1987, Vøllestad 1992), and it has been argued that random mating within each species would produce individuals genetically prepared for most habitat types (Helfman et al. 1987). In other terms, many characters might have low heritability, but show plastic reaction norms (Stearns 1992). Eels have a complex life cycle (reviewed by Fontaine and Dufour 1991), including extremely delayed sexual maturation. Mature gametes have only been observed after artificial maturation by hor-

mone treatment. It has still not been possible to examine inheritance of growth potential in groups of siblings.

In general models of organism growth, the specific growth rate decrease with increased body size (Ricker 1979). Biological explanations rely on the observed allometry of metabolic components in relation to body weight (Peters 1983, Reiss 1989). Within limits set by the genotype, individual growth is more or less plastic. Fish growth is influenced by both abiotic and biotic factors, e.g. temperature, light, salinity, oxygen, food availability, competition and social status (Brett 1979).

Young fish of normally distributed size often develop into skewed or even bimodal size distributions (Thorpe 1977, Shelton et al. 1979, DeAngelis and Coutant 1982, Yamamoto and Nakano 1996). Disproportional food aquisition

can sometimes outweigh genetic differences as mechanism responsible for the size hierarchy effect on growth (Koebele 1985). When larger fish show higher specific growth rates than smaller ones, it has been concluded that the smaller individuals are suppressed below their potential maximum (Jobling and Wandsvik 1983). Also in laboratory reared elvers, some initial fastgrowers make use of favourable conditions, while others display no obvious growth (Kuhlmann 1979, Holmgren et al. 1992, Holmgren 1996). Social interactions, as dominance and avoidance (Knights 1987), might further impede the growth of the smaller eels. Pair-wise battles induced changes in the gastrointestinal tract of the subordinate eel, but not in the dominant one (Peters 1982). Size culling tend to increase the specific growth rate of small elvers (Wickins 1987). Similar results were not documented for larger and older eels (Kamstra 1993).

This study relies on data from an indoor rearing experiment, which was specifically designed for studies on sex ratios (Holmgren 1996) and on sex related growth patterns (Holmgren and Mosegaard 1996). The idea that the eel has a plastic growth potential of low heritability can not readily be tested. Instead, it was hypothesized that the expressed individual growth reflects the individual growth potential. In a specified environment, e.g. at constant water temperature, initial slow growers should always be relatively slow growing. At approximately equal size (50-70 g body weight), the specific growth rates of individually tagged eels were expected to decrease with age or time taken to attain this size. Within individuals the specific growth rate should decrease with increasing size. The specific growth rate of eels too small to be tagged, was explored by the progression of cumulative weight distributions, ranging from 0.2 g to more than 100 g body weight.

Material and methods

Fish and rearing conditions

The origin of the eels, the rearing conditions and the handling procedures have been described previously (Holmgren and Wickström 1996,

Holmgren 1996). Elvers from the River Severn (England) were first kept in quarantine (3-5 °C) for eight weeks and then weaned at 17 °C for five weeks. In week 0, eels of 0.1-0.5 g body weight (mean=0.2 g) and 5.9-8.0 cm total length (mean=6.9 cm) were distributed into six 'original' tanks (about 1,300 eels/2.25 m² tank). Water temperature was set at 17, 20 or 26 °C, using two tanks per temperature. The eels were fed in excess for 137 weeks, by hourly rations of dry feed of various sizes. Oxygen levels were usually above 85% saturation, and the observed ammonium levels never exceeded 1 ppm. The populations were monitored and size graded every fifth to sixth week. The larger eels were reared in a third 'reserve' tank at each temperature. The lower limit for moving eels was increased from 3 to 60 g, as the experiment proceeded (Holmgren 1996). The number and sizes of dying eels was monitored on a daily basis. Population growth rate (PGR,%/week) was computed by $100 \cdot \ln(B_{(t+w)} / B_{(t)})/w$, where $B_{(t+d)}$ and $B_{(t)}$ is biomass before present grading and after preceding grading, respectively, and w is number of weeks between gradings. Whenever dead eels where observed since preceding grading, their weights were included in the biomass before present grading.

Individually tagged eels

At a minimum body weight of 10 g, 1,758 specimens of variable age (week 36-131, Holmgren 1996) were tagged with Passive Integrated Transponders (PIT, Prentice et al. 1990). Individual measurements of length and weight were taken on ordinary monitoring occasions. The eels were killed and sexed when they attained 150 g (38-45 cm length), or if they ceased growing as silver eels of lower weight. The individual weight curves were inspected visually (e.g. Fig. 1). The most homogenous growth, within temperatures, was found at approximately 60 g. For testing the effect of age on specific growth rate ($SGR = 100 \cdot \ln (W_{age+t} / W_{age}) / t$, where $t = 5$ or 6 weeks), observations of W_{age}=50-70 g were selected (not more than one observation per individual).
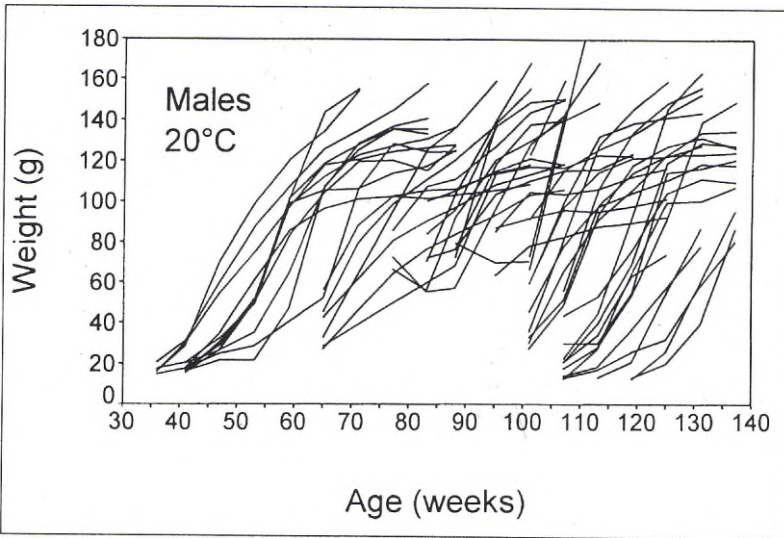
Fig. 1. An example of individual weight curves, showing every tenth tagged male reared at 20 °C.

Weight distributions in original tanks

After the gradings made in week 95, 164-278 individuals of less than 60 g remained in the four original tanks at 20 and 26 °C (Table 1). During 42 following weeks (seven six-weeks-periods), numbers were further reduced by removal of eels $\geq$60 g. Only a few eels died between measurements (0-3% of remaining numbers), and total losses were less than 6%. The growth of untagged eels could thereby be estimated from the progression of cumulative weight distributions. On each occasion, individual weights were sorted and ranked from smallest to largest. Relative ranks were set as (individual rank)/(total number in week 95). Within ranks, specific growth rates were calculated for different periods of growth.

Data analysis

Data were examined within the programmes Excel 5.0 and SPSS for Windows, Release 6.0, including statistical tests such as Spearman rank correlation, *t*-tests and linear regressions. Only two-tailed tests were performed, and the level of significance was set at $P=0.05$.

Results

Population growth rate

Population growth was low or negative during weeks 0-5. During 23 growth periods from week 5 to week 137, the level of *PGR* did not decrease, although median and maximum weight increased (Table 2). It remained constant in original tanks at 17 and 20 °C (Spearman rank correlation, $P>>0.05$), while it slightly increased in both tanks at 26 °C. *PGR* did not differ between tanks within temperatures (Table 2, *t*-tests, $P>>0.05$), and the pooled mean values and standard errors were 4.6 ± 0.2, 7.5 ± 0.3 and 10.0 ± 0.3%/week ($N=46$), at 17, 20 and 26 °C, respectively.

Table 1. Water temperature (temp,°C) and numbers of eels <60 g in four original tanks in week 95. Percentages are given for eels remaining in original tanks in week 137, for removed eels $\geq$60 g, and for lost eels during week 95-137, respectively.

Tank	temp	week 95	week 137	$\geq$60 g	lost eels
4	20	278	50.4%	45.3%	4.3%
5	20	256	47.3%	46.9%	5.9%
2	26	164	61.6%	37.8%	0.6%
3	26	198	52.6%	44.4%	3.0%

5

Table 2. Water temperature (temp, °C) and population growth rate (*PGR* in %/week, mean±SE) in six original tanks. *N*=23 growth periods between weeks 5-137. Weight (g) distributions in week 5 and in the beginning of the last period (week 131) are indicated by median (Md), minimum (min) and maximum (max) values.

Tank	temp	PGR	week 5			week 131		
			Md	min	max	Md	min	max
7	17	4.62±0.24	0.27	0.11	0.55	2.99	0.46	45.7
8	17	4.61±0.29	0.31	0.13	0.63	2.58	0.45	43.7
4	20	7.45±0.33	0.26	0.05	0.55	3.43	0.49	54.7
5	20	7.56±0.39	0.29	0.12	0.85	3.37	0.37	58.2
2	26	9.93±0.39	0.27	0.11	0.69	2.47	0.50	35.8
3	26	10.07±0.52	0.33	0.10	1.14	1.90	0.47	59.6

Individually tagged eels

Within each temperature, there was no significant difference between sexes in *SGR* at W_{age}=50-70 g (Table 3). At each temperature the level of *SGR* was similar to that of *PGR* of smaller eels in the original tanks (Table 2). The highest values of *SGR* were actually observed in males of W_{age}=10-40 g, with maximum values of 14.8, 20.1 and 25.9%/week at 17, 20 and 26 °C, respectively. In the selected weight interval, *SGR* did not decrease with increasing age (Fig. 2).

Table 3. Specific growth rate (*SGR* in %/week, mean±SE) at W_{age}=50-70 g, shown separately for males (M) and females (F) at each temperature (temp, °C). The numbers of observations are given within parentheses. * The two-tailed *t*-test (between sexes) was performed with unequal variances at 17 °C.

temp	Sex	SGR	*t*-test
17	M	5.80±0.25 (191)	*P*=0.086
	F	4.76±0.53 (25)	
20	M	7.24±0.23 (241)	*P*=0.911
	F	7.17±0.52 (34)	
26	M	9.58±0.26 (161)	*P*=0.289
	F	8.99±0.49 (45)	

Linear regressions of *SGR* with age were not significant at 17 and 20 °C. At 26 °C, relatively slow growth of eels with W_{age}=50-70 g before week 50, gave rise to a significant positive regression (r^2=0.099, *P*<0.001).

Cumulative weight distributions

Weight in relation to relative rank is best illustrated on a logarithmic weight scale (Fig. 3). For a given relative rank, the vertical distances between curves of different weeks are directly proportional to the specific growth rates. Increasing distances with time indicate increasing *SGR* between subsequent growth periods. Whenever *SGR* within ranks decrease with age, subsequent weight distributions will come closer and closer on the weight axis. In the two tanks at 20 °C, the distances between curves increased with relative rank, indicating higher *SGR* with higher relative rank (Fig. 3). The within rank distances were rather constant in tank 4, while long and short distances were alternating within intermediate ranks in tank 5. A different pattern appeared at 26 °C (Fig. 4). All distances were short within low relative ranks (below 0.3-0.4) and they were long within high ranks (above 0.7-0.8). Within intermediate ranks, the distances increased abruptly at 3-5 g body weight.
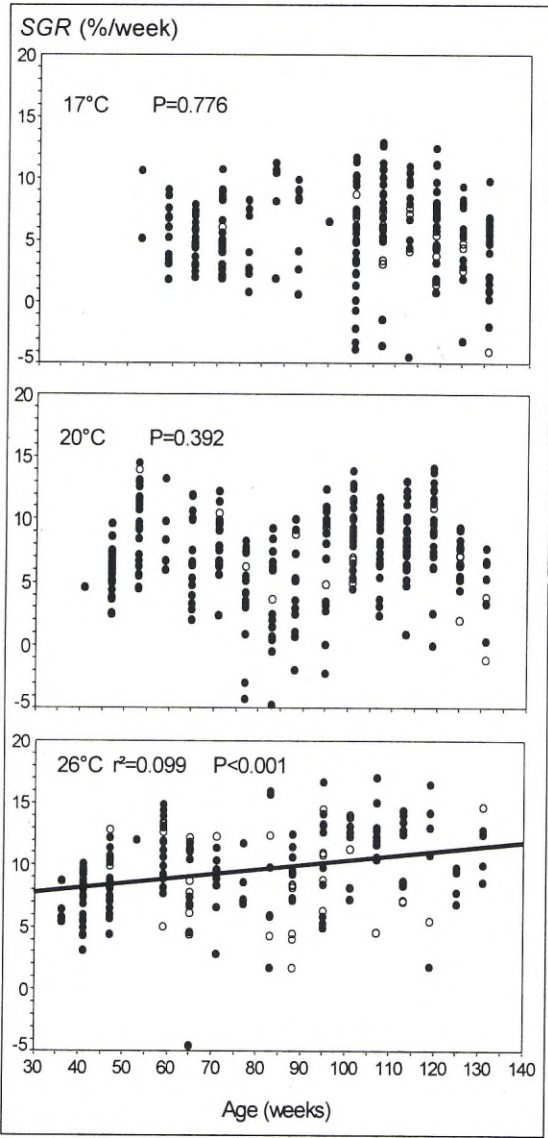
Fig. 2. Specific growth rate (*SGR* at W_{age}=50-70 g,%/ week) in relation to age, i.e. weeks reared at each temperature. Males and females are represented by filled and unfilled circles. The numbers of observations are 216, 275 and 206, at 17, 20 and 26 °C, respectively. r^2- and *P*-values refer to linear regressions.
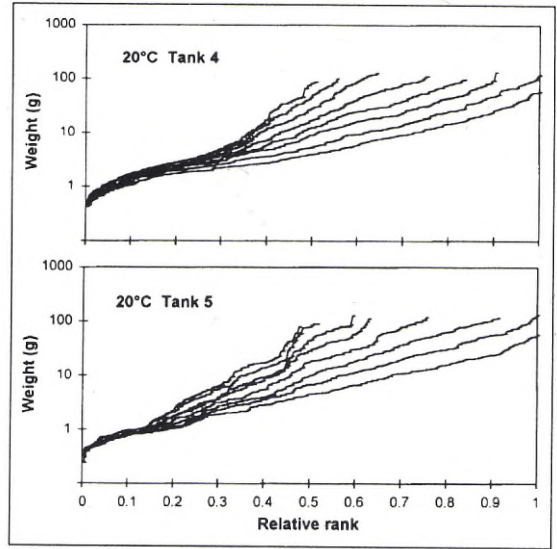

Fig. 3. Cumulative weight distributions in two tanks at 20 °C. The curves represent eight occasions from week 95 (lower right) to week 137 (upper left).
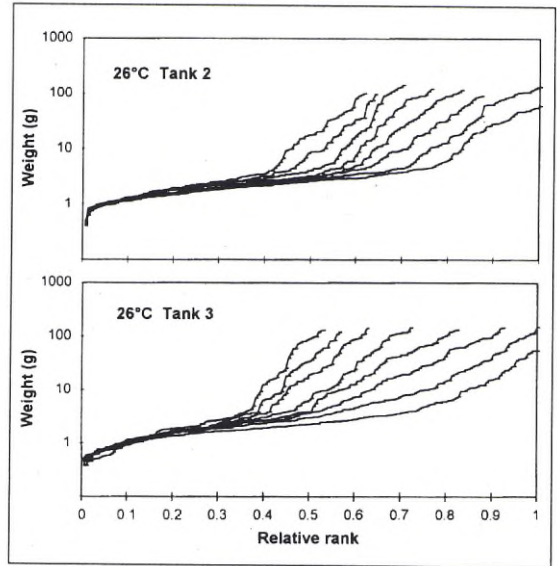

Fig. 4. Cumulative weight distributions in two tanks at 26 °C. The curves represent eight occasions from week 95 (lower right) to week 137 (upper left).
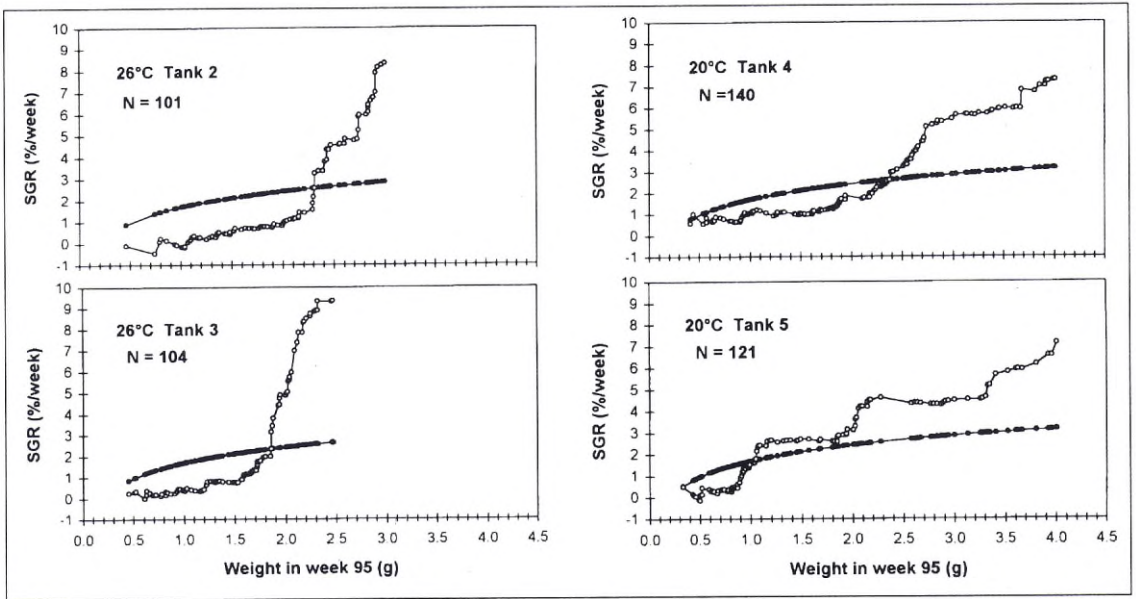
Fig. 5. Rank-specific *SGR* (%/week) in relation to weight in week 95, for two periods, week 0-95 (filled circles) and week 95-137 (unfilled circles), respectively. *N* = numbers of eels left in each tank.

In week 137, 101-140 eels remained in the original tanks. According to their ranks, individual weights had been ≤3 g (26 °C) or ≤4 g (20 °C) in week 95. Their specific growth rates during weeks 0-95 were estimated at 0.5-3%/week, by assuming initial weights of 0.2 g each. During week 95-137, the specific growth rate was further depressed in low ranked eels, while it increased in individuals of higher weight rank (Fig. 5).

Discussion

The present eel populations were reared at 17, 20 and 26 °C, where the latter level was intended to give optimum eel growth (Kuhlmann 1979, Dosoretz and Degani 1987, Seymour 1989). Both the population growth rate (*PGR*) in original tanks and the specific growth rate (*SGR*) of tagged individuals increased with temperature, just as expected. Temperature dependent growth rate is one of the most widely accepted plastic responses to environmental change, both in fish

(Brett 1979) and in other poikilothermic organisms (Peters 1983, Atkinson 1994). The expected effect of temperature was however not found in a previous rearing experiment (Holmgren et al. 1992). Those eel populations were not systematically graded, and population growth rates declined to almost zero as mean weight approached 100 g. The size distributions became bimodal, with peaks of small, growth depressed individuals and of larger silver males.

Without social interactions, the specific growth rate should decrease with increasing body size (Brett 1979). In the original tanks *PGR* did not decrease with increasing median weight, but of course, *SGR* decreased within tagged individuals of larger size. In males even the absolute growth rates decreased (Fig. 1), and many males stopped growing at less than 150 g. In a previous analysis, males of less than 40-60 g displayed higher growth rates than females, while the opposite relationship was found above 80-100 g (Holmgren and Mosegaard 1996). It was suggested that growth rate of undifferentiated eels might influence the differentiation into male or

female. At W_{age}=50-70 g there was no significant difference in *SGR* between sexes.

Some early fastgrowers at 26 °C, attained 50-70 g within 36 weeks. Initially slower growing eels were regularly recruited to this weight interval, and *SGR* of equally sized eels did not decrease with age. Individuals could obviously maintain a high growth potential, while being temporarily suppressed by faster growing eels. Further support was given by the progression of weight distributions in original tanks at 20 and 26 °C. Eels of intermediate ranks in week 95, showed increasing growth rates during week 95-137. At 26 °C, this appeared clearly from raw weight data (Fig. 4). It was less pronounced at 20 °C, although it was evident from comparisons of rank-specific *SGR* between week 0-95 and week 95-137. The use of specific growth rate is only recommended for short time intervals, because fish growth is not supposed to be exponential for extended periods. As the increasing growth rates were apparent even on a logarithmic scale, there is no doubt that many growth depressed individuals maintained a considerable growth potential.

In some previous studies on individual growth variation, the elvers were newly caught and/or the controlled experiments were run for less than 20 weeks. Wickins (1985, 1987) performed a series of experiments with newly caught elvers, which were reared at 23-25 °C either in isolation or in groups. He concluded that the expression of growth was not related to size or previous hierarchical position, but may be governed by behavioural and physiological responses to handling and to changed social environment. For example, some stunted individuals, which lost weight when reared in large groups for 30 days, grew extremely well (>6.5%/day) during 21 days in isolation (Wickins 1985). Kamstra (1993) obtained eels from a commercial eel farm. Initial individual weights were mainly within 5-60 g. The eels were first reared in unsorted groups for 50 days and then in sorted or unsorted groups

for 82 days. When results from groups of small and large eels were combined, neither the increase in total biomass nor the weight-frequency distribution differed from the unsorted groups. Furthermore, the distribution of specific growth rates, of marked individuals, was not affected by sorting. The author concluded that slow growth rates of stunted individuals were governed by physiological responses rather than by social interactions. The present experiment was not designed for testing whether or not grading affected individual growth. However, some eels of less than 4 g, after 95 weeks at high constant temperature, could obviously grow faster at higher age and size.

Moriarty (1987) suggested that the success of catadromous eels is partly based on avoidance of marine predators. By migration into freshwater they often have to survive during suboptimal conditions for growth. In a Norwegian river system, 16-50% of ascending elvers survived to the silver eel stage (Vøllestad and Jonsson 1988), and in some Finnish lakes 56% of stocked elvers were recaptured as yellow or silver eels (Tulonen and Pursiainen 1992). Otoliths from a slow growing eel population displayed an irregular pattern of broad and thin annual increments (Poole and Reynolds 1996 a, b), which might reflect high variation in body growth between years. Provided that small, slow growing eels can survive during temperate winters, the present results indicate that at least some individuals have physiological capacity for increasing growth rates. Whether all eels have similar capacity for compensatory growth, still remains to be discovered.

Acknowledgments

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Otolith Growth Scaling of the Eel, *Anguilla anguilla* (L.), and Back-calculation Errors Revealed from Alizarin Labelled Otoliths

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Abstract

The otoliths of individually tagged eels were labelled with alizarin complexone, and otolith length and body length were measured for individuals on three sample dates over a 16-week period. All eels, including some nongrowing specimens, showed measurable otolith growth. The otolith to body length ratio (otolith scaling) changed inversely with body growth rate. The otolith increment per body length increase (otolith growth scaling) was not significantly different between two subsequent growth periods. Back-calculations based on constant otolith scaling produced significant bias, especially in fast growing eels. When constant otolith growth scaling was assumed, the means of back-calculated data were generally not biased, but this method produced wider error distributions. By any method, the deviation of back-calculated from observed body length was with few exceptions within ±15%. In the most slow growing eels, the error of back-calculated body growth could well exceed ±100% of observed values.

Keywords: otolith growth, body growth, back-calculation, *Anguilla anguilla* (L.), alizarin.

Introduction

Annual or daily increments of sagittal otoliths are most often used for age determination and back-calculation of growth of anguillid eels (Vøllestad et al. 1988, Tsukamoto 1989, Lecomte-Finiger 1992). Several authors have reported linear regressions of otolith length, or radius, with eel body length (Peňáz and Tesch 1970, Rossi and Villani 1980, Dekker 1986, Vøllestad and Jonsson 1986, Paulovitz and Biro 1986, Fernandez-Delgado et al. 1989, Nagiec and Bahnsawy 1990). Others have made the general assumption of a linear proportionality, before they back-calculated previous body length, or growth, from the relative width of increments between otolith annuli (Moriarty 1983, Berg 1985, Poole et al. 1992, Poole and Reynolds 1996).

Two common back-calculation methods are based on linear proportionality within individuals (see review by Francis 1990). The Dahl-Lea-equation simply states a constant ratio between otolith length and body length, while a constant otolith increment per unit body length increase is described by the Frazer-Lee-equation. The latter equation may have an intercept different from zero, empirically found or estimated by linear regression.

Back-calculated data have indicated that female eels are larger than males at similar age (Rossi and Villani 1980, Vøllestad and Jonsson 1986), but the sources of variation in the otolith/somatic growth relation were not examined. Panfili et al. (1994) found larger otolith increments in females than in males, which they interpreted to represent a sex-related difference in body growth. In only two eel studies, attempts

have been made to quantify back-calculation errors. Back-calculated data were biased compared to observed values, by using either the Dahl-Lea method (Dekker 1986) or the Frazer-Lee method (Moriarty 1983). Holmgren (1996a) examined the residuals of the otolith/body length relationship in eels reared under controlled conditions. The residuals increased with water temperature and age. They also varied inversely with recent growth rate in individually tagged eels, indicating continued otolith growth during periods with no body growth. The results were in accordance with the view that otolith growth reflects metabolic activity, which is not always coupled to somatic growth rate (Mosegaard et al. 1988, Wright 1991, Bradford and Geen 1992).

In this study, use of individual tagging and otolith labelling provided tools for repeated measurements of both otolith length and body length. The experimental eels had been raised under controlled conditions since the elver stage, and some information on past otolith and body growth history was available. These data were used to test the hypothesis that the otolith to body length ratio (otolith scaling) or otolith increment per body length increase (otolith growth scaling) is constant within individuals. Both Dahl-Lea and Frazer-Lee methods were applied to get error distributions of back-calculated body length and body length increase.

Material and methods

History of population studied

The eels selected for this study originated from a previous experiment (Holmgren 1996b). They had been reared at 17 °C from the elver stage. The eels were always fed in excess (according to Seymour 1989) by hourly rations of commercial dry feed (EWOS, different sizes of granulate and pellets). By continous aeration and water renewal, oxygen saturation was usually above 85% (Oxyguard) and observed ammonium levels never exceeded 1 ppm (Aquamerck 1,158). A constant light regime (9 h light : 15 h dark) was maintained in the experimental hall. The eels recieved some diffuse light, although the rearing tanks were covered with Styrofoam plates.

After a weaning period of five weeks, each of two tanks (area 2.25 m²) were stocked with 1,300 individuals. Biomass and size distributions (length and weight) were monitored every fifth or sixth week. Some random otolith samples were taken before the populations were first graded (Holmgren and Wickström 1996, Table 1). Later on, the largest eels were regularly transferred from the original tanks.

After 150 weeks, 487 eels from two tanks were still smaller than 10 g (80-210 mm body length). Otoliths were then sampled from the entire size distribution (Holmgren 1996a). Furthermore, the largest eels were removed for separate purposes. In the remaining group, the largest 60 eels were within 130-160 mm body length, and they were reared together with smaller eels in one of the original tanks. After 29 additional weeks, 55 individuals (body size: 197-282 mm, 10-34 g) were selected for the present study.

Present experiment

The selected individuals were individually tagged with Passive Integrated Transponders (PIT, Prentice et al. 1990). Before measurement and tagging, the eels were anaesthesized using 0.12 g benzocaine/L of rearing water. The eels

Table 1. Body length and otolith length in random samples taken before the first grading (Holmgren and Wickström 1996).

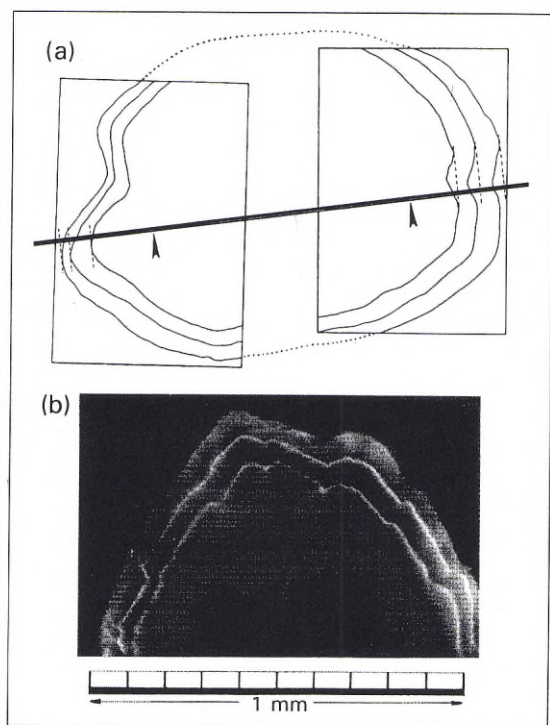| Sample	Weeks at 17 °C	N	Body length (mm)			Otolith length (mm)		
			mean	min.	max.	mean	min.	max.
1	<1	77	70.1	62	82	0.338	0.29	0.38
2	11	20	70.6	61	79	0.472	0.44	0.53

Fig. 1. (a) Sketch of two photos prepared for measurement of otolith increments along the total length axis. (b) Caudal portion of the otolith of an eel of 279 mm body length, showing two fluorescing alizarin marks. A distance of 1 mm is indicated between arrows in (a) and by the total length of the scale bar in (b).

were also immersed for 24 hours in an aerated solution of alizarin complexone (alizarin-3-methylamine-N,N-diacetic acid, 50 mg/L of rearing water at 17 °C), in order to get simultaneous fluorescent marks in the otoliths. After eight weeks, the individuals were identified and body lengths and weights were measured, before performing a second treatment with alizarin. Another eight weeks later, the individuals were finally identified and measured, and their sagittal otoliths were collected. Between the handling occasions, the eels were reared at the same conditions as before.

The right sagitta was mounted in clear nail polish, with sulcus side up, on a microscope slide. The final otolith length was defined as the maximum length parallel to the sulcus. It was measured with the resolution of 0.01 mm, by use of an ocular micrometer in a stereo microscope. The same whole otolith preparation was later illuminated by a "Nikon super high pressure mercury lamp" (Model HB-10101 AF), and the red fluorescence was filtered through. Both alizarin marks were identified in all except for one eel, which was evidently not included in the second alizarin treatment. As the scale of the ocular micrometer could hardly be distinguished in the fluorescent light, two photos of each otolith were taken at 100 times magnification, showing the oral and caudal parts, respectively. Paper copies were mounted as to get a scale-corrected view of the original otolith shape and its length axis (Fig. 1a). Otolith increments, between the intense red marks and the diffusely fluorescent otolith edge (Fig. 1b), were measured on the photos, with a resolution of 0.5 mm (representing 0.007 mm of otolith increment).

Calculations and variable definitions

Otolith length on each marking occasion ($OL1$ and $OL2$) was calculated by subtracting the sum of oral and caudal increments from the final otolith length (OLfin). The repeated measurements of body length, were also distinguished by different variable names, $BL1$, $BL2$ and BLfin. Body growth and otolith growth were consequently calculated as;

$BG1 = BL2 - BL1$ $OG1 = OL2 - OL1$
$BG2 = BL$fin$ - BL2$ $OG2 = OL$fin$ - OL2$
BGtot$ = BLfin - BL1$ OGtot$ = OLfin - OL1$

The term otolith scaling was used for the ratio between otolith and body length, while the otolith/body growth ratio was termed otolith growth scaling. The following variables were calculated for the test of constant otolith scaling;

OLratio$=100 \cdot OL1/OL$fin, and BLratio$=100 \cdot BL1/BL$fin.

Back-calculations were performed in the following ways (notice that Dahl-Lea 2 differs from

Dahl-Lea 1, simply by use of intermediate instead of final values of body length and otolith length):

Dahl-Lea 1: estimated $BL1=OL1 \cdot BLfin/OLfin$
Dahl-Lea 2: estimated $BL1=OL1 \cdot BL2/OL2$,
    and estimated $BG1=BL2$ - estimated $BL1$
Frazer-Lee: estimated $BG1=OG1 \cdot BG2/OG2$
    and estimated $BL1=BL2$ - estimated $BG1$

The relative back-calculation error, using each of the three methods, was expressed as absolute deviation from observed value in per cent of observed value.

Graphical and statistical procedures

All computations, plots and statistical procedures, e.g. Spearman rank correlation, linear and polynomial regressions and paired samples *t*-test, were run within the program package "SPSS for Windows, Release 6.0". Residual trends were graphically illustrated by the lowess smoothing procedure.

Before comparing individual performance between two growth periods, the eels were divided in three equally sized groups with respect to total body growth (18 or 19 eels/group). Effects of total body growth (BGtot) on relative back-calculation errors, were explored by plotting 95% confidence intervals of mean error for slow, intermediate and fast growing eels, respectively.

Results

Body growth

There was a slight correlation between total body growth (BGtot) and initial body length ($BL1$) (Spearman rank correlation, $r_s=0.336$, $P=0.012$, Fig. 2). Some eels, independent of $BL1$, grew more than 100 mm (and more than 50 g) within 16 weeks, but slow growing individuals were most frequent at low $BL1$. Nine eels with BGtot less than 10 mm, grew less than 2.5 g in body weight, with a mean value of 0.0 g.
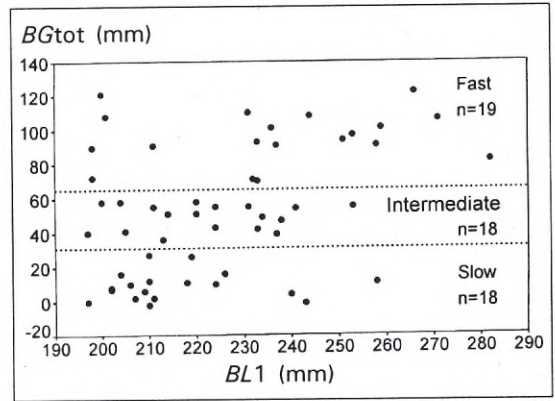

Fig. 2. Total body growth (BGtot) in relation to initial body length ($BL1$). *n*= number of slow, intermediate or fastgrowing eels.

Otolith growth scaling

Individual trajectories of otolith length and body length were mostly linear (Fig. 3), but trajectories from the nongrowing or shrinking individuals were vertical or had negative slopes. In the intermediate and in the fast growing eels, paired sample *t*-tests revealed that body growth, otolith growth, and otolith growth scaling (i.e. slopes in Fig. 3), were not significantly different between the two eight weeks periods ($P>0.1$ in each
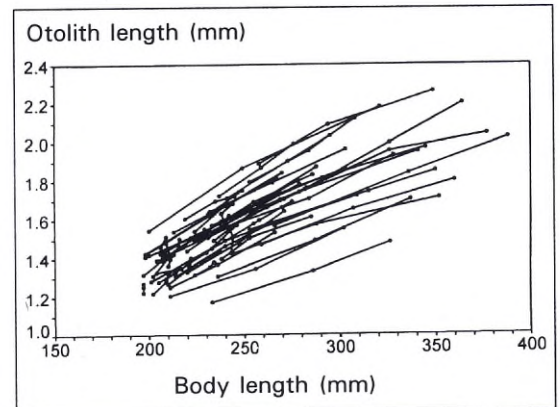

Fig. 3. Individual trajectories of otolith length versus body length in 55 individuals. Observations (dots) from each of three sample dates are linked with straight solid lines.
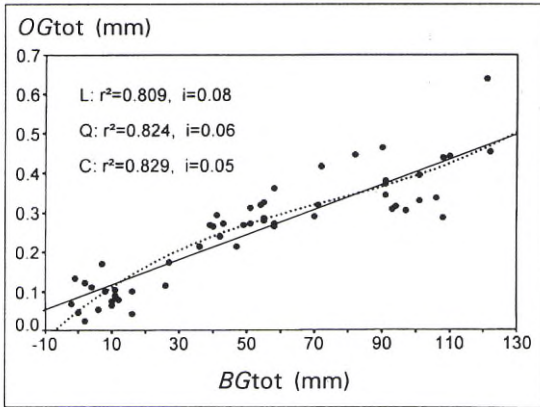
Fig. 4. Total otolith growth (*OG*tot) in relation to total body growth (*BG*tot). r^2-values and intercepts (i) are derived from linear (L), quadratic (Q) and cubic (C) regressions. The linear and cubic fits are shown by the solid and dotted lines, respectively.

Fig. 5. Otolith length ratio (*OL*ratio) in relation to body length ratio (*BL*ratio). The expected relationship (*OL*ratio = *BL*ratio) is indicated by the solid line, and the dashed line is the observed linear regression (*OL*ratio = 0.57 *BL*ratio + 38.80, r^2=0.855, n=55).

of six tests). Slow growing eels showed significantly lower *BG*2 than *BG*1 ($P<0.05$) and lower *OG*2 than *OG*1 ($P<0.001$), but mean otolith growth scaling did not change significantly ($P>0.1$).

Among individuals, total otolith growth (*OG*tot) increased with *BG*tot, but data indicated a nonlinear relation (Fig. 4). Quadratic and cubic regressions explained slightly more of the variation (82.4 and 82.9%, respectively) than did a linear regression (80.9%). All intercepts were greater than zero, as all nongrowing individuals showed measurable otolith growth.

Otolith scaling

Based on the above results, data from the total growth period were used to test the hypothesis of constant otolith scaling. Observed data were fitted to the following regression, *OL*ratio = 0.57 (±0.06) *BL*ratio + 38.80 (±5.37) (Fig. 5), where values in brackets are 95% confidence limits of the estimates. Both the slope and the intercept differed significantly (*t*-tests, $P<0.0001$) from expected values (slope=1, intercept=0). Paired sample *t*-tests showed that otolith scaling increased during 16 weeks in slow growing eels ($P=0.020$), while it decreased in intermediate ($P=0.001$) and in fast growing eels ($P<0.001$).

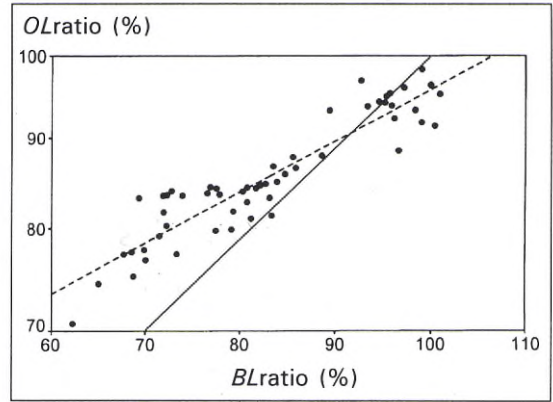## Back-calculation errors

Back-calculated initial body length (*BL*1) was, on average, overestimated by use of individual final otolith scaling (Dahl-Lea 1), with a tendency for increased relative errors at higher observed *BL*1 (Fig. 6a). The bias was smaller, but still apparent, during the first eight week period (Dahl-Lea 2, Fig 6b). By use of final otolith growth scaling (Frazer-Lee) the error distribution was skewed towards underestimation of *BL*1 (Fig. 6c). Back-calculated *BL*1, by any method, was usually within $\pm15\%$ of the observed value. Back-calculated body growth during the first eight weeks period (*BG*1) gave higher relative errors (Fig. 7a, b), ranging from -2,180 to +1,247% of observed *BG*1. By exclusion of individuals with total body growth less than 10 mm, the relative errors were usually within $\pm100\%$ of observed values.

The relative bias of back-calculated body length (*BL*1) was slight or insignificant in slow and intermediate growing eels (Fig. 8), and it hardly differed between calculation methods. In fast growing eels, all methods gave results significantly different from each other, and both methods based on constant otolith scaling significantly overestimated *BL*1. Relative errors of
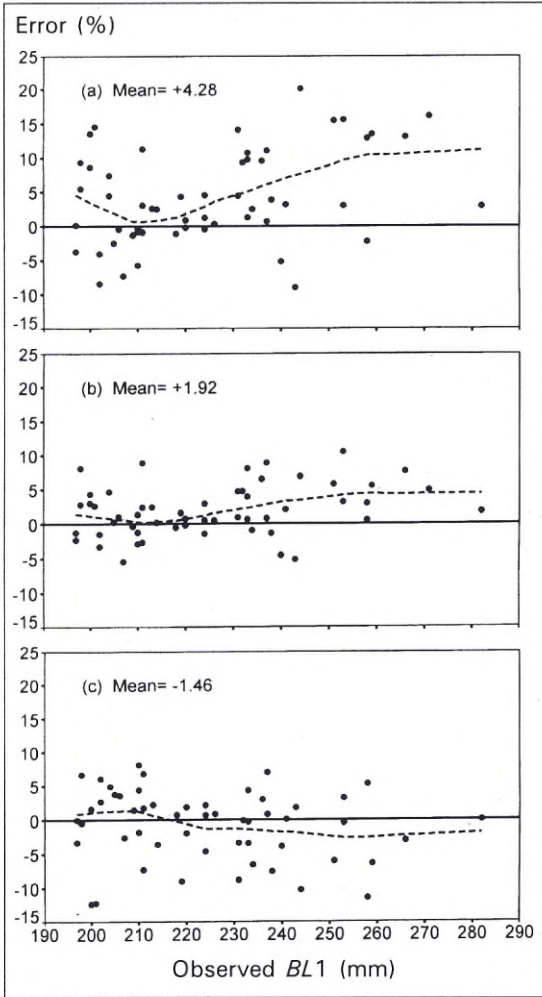
Fig. 6. Back-calculation of initial body length (*BL*1). Relative error in relation to observed *BL*1. Both the expected reference lines (solid), the residual trends (dashed lines) and the mean relative errors are given. Calculations were made by; (a) the Dahl-Lea 1 (*n*=55), (b) the Dahl-Lea 2 (*n*=54), and (c) the Frazer-Lee method (*n*=54, one omitted outlier with error = -33.8% is included in the mean).

Fig. 7. Back-calculation of body growth (*BG*1) of 45 eels with total body growth greater than 10 mm. Relative error in relation to observed *BG*1. Both the expected reference lines (solid), the residual trends (dashed lines) and the mean relative errors are given. Calculations were made by; (a) the Dahl-Lea 2, and (b) the Frazer-Lee method.

Fig. 8. Back-calculation of initial body length (*BL*1) in slow, intermediate and fast growing eels. 95% confidence interval of mean relative error, by each of three methods as indicated in the legend.

back-calculated body growth (*BG*1) were not significantly biased in eels of slow or intermediate growth (Fig. 9). Again, the estimated growth of fast growing eels was biased from the expected mean value, negatively (Dahl-Lea 2) or positively, but not significantly (Frazer-Lee).
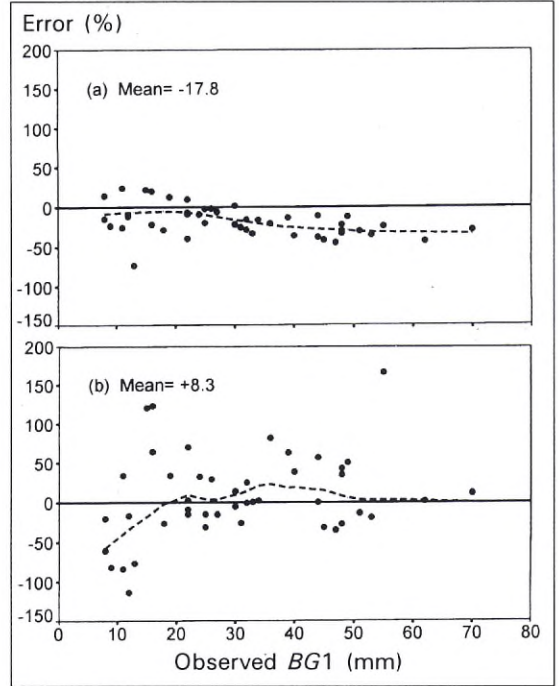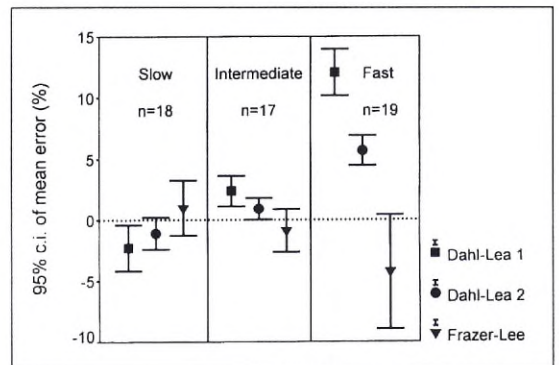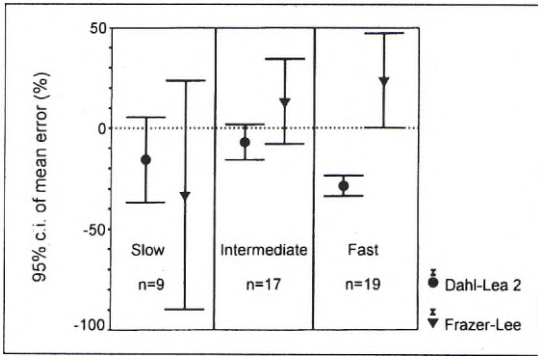
Fig. 9. Back-calculation of body growth (*BG*1) in slow, intermediate and fast growing eels. 95% confidence interval of mean relative error, by each of two methods as indicated in the legend. Eels with total body growth less than 10 mm are excluded.

Discussion

The relationship between otolith length and body length is not always isometric. Rijnsdorp et al. (1990) found a slightly curvilinear relationship between otolith width and body length of growth of the plaice, *Pleuronectes platessa*. By use of log-transformed variables they found an inherent proportionality within individuals, and they could perform back-calculation without significant bias. However, previous authors have used linear models, based on either the Dahl-Lea or the Frazer-Lee equation, to back-calculate eel growth (Peňáz and Tesch 1970, Rossi and Villani 1980, Moriarty 1983, Berg 1985, Dekker 1986, Vøllestad and Jonsson 1986, Paulovitz and Biro 1986, Fernandez-Delgado et al. 1989, Nagiec and Bahnsawy 1990, Poole et al. 1992). In the present study, otolith growth scaling within individuals was not significantly different between two subsequent growth periods. The Frazer-Lee method thereby produced unbiased results, although of low precision.

The observed regression of *OL*ratio with *BL*ratio indicated that the general assumptions for using the linear Dahl-Lea equation were indeed violated. A slope less than one and an intercept greater than zero, indicate that the individual otolith scaling changes with size or with changed somatic growth rate. The effect of body growth was further indicated from the relationship between otolith growth and body growth among individuals. This relationship had an intercept greater than zero, and it was better fitted to polynomial regressions (quadratic and cubic) than to a linear regression. All eels used in the present study had been extremely slow growing during 150 weeks, in spite of excess feeding and constant water temperature. They lived together with larger, previously faster growing eels, which were continuously removed from the population (Holmgren 1996b). Later on, when larger competitors were absent, the selected eels grew considerably faster than before. During the 29 weeks before individual tagging, the body length range increased from approximately 130-160 mm to 197-282 mm. The most extreme range of individual body length increase was 40-150 mm, or 22-83 mm if recalculated to a 16 weeks period and assuming constant growth rates. All individuals with total body growth (*BG*tot) beyond the limits of this range (i.e. most of the eels in the slow and fast growing groups) had changed their absolute growth rates, just before or during the present experiment.

Whenever individuals grow continuously according to the von Bertalanffy function or to any other described growth model (Ricker 1979, Schnute 1981), a continous allometric relationship between otolith and body size might also be expected. In practice, such an assumption can be violated for different reasons, e.g. Rijnsdorp et al. (1990) found that body size of plaice, relative to otolith size, first increased and then decreased during each growing season. In temperate habitats, there is a seasonal variation in fish body growth as well as in water temperature and food availability. More or less synchronized interruptions in otolith growth and somatic growth form the basis for using annual or biannual ring patterns in age determination, but otolith and somatic growth rate can respond differently to water temperature (Mosegaard et al. 1988). There are also several reports on otolith growth in starving fish (Campana 1983, Wright et al. 1990, Sogard 1991). A gradual decline in otolith

growth might reflect the exhaustion of energy reserves (Molony and Choat 1990). The otolith growth in slow or nongrowing eels decreased during the second growth period, which might indicate a time-lag before a decrease in overall metabolic rate.

Panfili et al. (1994) were aware of published evidence of short term uncoupling between otolith and somatic growth, but without validation they argued that it would not occur on a seasonal scale. Moriarty (1983) back-calculated length at tagging of three Floy-tagged and re-captured eels. As he used the naturally formed otolith annuli, a time-lag between annulus formation and tagging might have caused some bias. By marking the otoliths with fluorenscent dyes, e.g. tetracycline, oxyteracycline, calcein or alizarin complexone, the otolith marks can refer to an exact date (Geffen 1992). Anyway, back-calculated length at marking was underestimated in some recaptured eels labelled with oxytetracycline (Dekker 1986). In this study, two subsequent alizarin marks were applied, each of them followed by a period of known body growth. Back-calculation errors could thereby be measured. As there was no significant difference in individual otolith growth scaling between two growth periods, the Frazer-Lee method generally estimated initial body length or growth with insignificant bias. Whenever the otolith growth scaling changes, a simultaneous change in otolith scaling will produce bias in results derived from Dahl-Lea methods. The time-lag before significant bias occurs, decreases with the absolute change, which was demonstrated by a lower bias when using otolith scaling after eight weeks (Dahl-Lea 2) instead of final otolith scaling (Dahl-Lea 1).

One general assumption in back-calculation models is that the family of individual trajectories of otolith scaling really includes the population trajectory and is of similar mathematical form (Francis 1995). A large and random sample, including all ages and sizes from the elver stage, would admit estimation of a specific linear or curvilinear population trajectory. Still, the present exercise showed that inherent proportionality (linear or nonlinear) in individual otolith size/growth scaling should not be assumed without some knowledge of early growth history variation. In indoor reared eels, otolith scaling increased both in nongrowing elvers (Holmgren and Wickström 1996, Table 1) and in PIT-tagged eels with insignificant growth (this study). Hypothetically, repeated periods with no body growth might have caused discrete steps or oscillations in individual trajectories of otolith length in relation to body length. Winter survival of elver sized eels has not as yet been reported from natural temperate habitats, but in this unnatural environment small nongrowing eels survived for several years. During periods when otoliths grow in nongrowing individuals, any back-calculation will give positive values of body growth.

In all comparative studies, some estimate of the error distribution is even more essential than support for using the best back-calculation model. In small lakes or ponds, release and recapture of marked eels (individually tagged and otolith labelled) would provide data for estimation of errors. In this special case, the deviation of back-calculated from observed body length was usually within $\pm 15\%$, while the error of back-calculated body growth during short periods could exceed $\pm 100\%$ of observed values.

Acknowledgments

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The Effect of Size, Antennal Injury, Ownership, and Ownership Duration on Fighting Success in Male Signal Crayfish, *Pacifastacus leniusculus* (Dana)

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Abstract

When resources are limited, aggressive interactions may decide who gets access to a limited resource. It is important to win these interactions since the loser usually not obtain any or only a small part of the contested resource when competition takes the form of direct interference. This will decrease the chances of future survival, growth and reproduction. In order to reveal which external and internal factors affect competitive ability, a series of paired confrontations between adult signal crayfish males were staged in aquaria. As expected larger crayfish won most of their fights, but relatively larger claws and undamaged antennae also increased the chances of winning a fight. The larger males usually initiated the contests. When smaller crayfish were given access to a shelter during the acclimatization period, before the actual contest, their behaviour changed and they became more inclined to initiate interactions. In addition, when smaller crayfish were given access to a shelter for a longer period prior to the contest, this also affected the final outcome of the fight and they were able to win fights over larger opponents. Thus, when crayfish compete for a limited resource, both morphological characters and an individual's motivation to fight are important for the outcome of a fight, when crayfish compete for resources.

Keywords: Competitive ability, behaviour, motivation, morphology, signal crayfish, *Pacifastacus leniusculus*.

Introduction

When animals compete for access to resources they sometimes fight. The ultimate goal of these fights is that the winner takes possession of the resource, but since fighting entails costs such as energy expenditure, risk of injury and risk of predation, it is in the mutual interest of opponents to settle the disputes as non-violently and quickly as possible. It is however important to win these interactions since, when competition takes the form of direct interaction, the loser does not usually obtain any or only a small part of the contested resource (Lomnicki 1988). This will decrease his chances of future survival, growth and reproduction.

Several factors have been shown to affect fighting success or resource holding potential (RHP; Parker 1974). These factors can be roughly divided into two categories. Correlated asymmetries, such as size, weight, fighting skill or weapons, are directly connected to fighting ability. Uncorrelated asymmetries are seemingly irrelevant asymmetries, uncorrelated with relative fighting ability, such as owner-intruder roles or reproductive status. Uncorrelated asymmetries are thought to reflect the internal state or motivation of the individual (Maynard Smith and Parker 1976).

Body size is usually a good indicator of RHP in crustaceans (Salmon and Hyatt 1983, Smith et al. 1994), including crayfish (Bovbjerg 1953,

1956, Lowe 1956, Rabeni 1985, Momot and Leering 1986, Ranta and Lindström 1992, 1993, Pavey and Fielder 1996). Apart from body size, the size of weapons used in fights like the claws in crayfish may also be important (Stein 1976, Berrill and Arsenault 1984, Snedden 1990, Rutherford et al. 1995). In dense crayfish populations it is common to find individuals with damaged, or missing, claws, walking legs or antennae, also in the absence of predators (Abrahamsson 1966). These injuries are thus probably the results of intraspecific interactions and are likely to have a negative effect on fighting ability. In addition, fighting ability may also be heritable as found in lobster juveniles (Finlay and Haley 1983), or fighting skill may be acquired by experience and learning during the course of an individuals life.

In other studies, uncorrelated asymmetries like sex, previous experience and burrow ownership were found to be important for the outcome of fights (Hazlett 1966, Rubenstein and Hazlett 1974, Hyatt and Salmon 1978, Momot and Leering 1986, Evans and Shehadi-Moacdieh 1988, Figler et al. 1995). When the owner is more aggressive and wins, regardless of being smaller, this may reflect that the contested resource is more valuable to the owner, or that the owner is better informed about the actual value of the resource. The owner is thus willing to take a higher cost and invest more in the ensuing fight.

To investigate the effect of several measures of body and claw size, and the level of injuries to legs and antennae, on the competitive ability of adult signal crayfish, a series of staged contests between adult males was set up. We also examined the effect of duration of ownership by allowing one of the competitors a shelter for different periods of time prior to the contest.

Materials and methods

Study objects

In the experiments we used male signal crayfish (*Pacifastacus leniusculus*) originating from Lake Skillötsjön, 50 km southwest of Stockholm. The crayfish were kept in mixed sex groups in tanks (bottom surface: 0.9 x 2.5 m) at densities of 15 crayfish/m². The tanks were furnished with 2.5 shelters/crayfish. All shelters in the study consisted of terracotta bricks with holes measuring 50 x 40 x 130 mm. Computer controlled 60 W bulbs were used to simulate outdoor light conditions. All water used in the experiments was pumped from Lake Mälaren, filtered through a dynamic sand filter and aerated. The inlet and outlet were situated in opposite ends of the tank. The crayfish were fed ad libitum three times a week with corn, green peas and fish pellets.

Three days before a contest, experimental crayfish were weighed and a number of size measures taken. We measured total length (from the tip of the rostrum to the end of the telson), carapace length (from the tip of the rostrum to the posterior end of the carapace), claw length (from the carpal joint to the tip of the propodus), claw width and claw depth (at widest and deepest point of the propodus). Number of intact walking legs and injuries to antennae (assessed on a scale from 0 to 1 for each antenna) was also noted. The characteristics of the males taking part in the contests are shown in Table 1. Eightyfive out of the total of 100 males had all legs intact, but only 23 males possessed antennae without any injuries. Minor injuries to the body exoskeleton and to the propodus and dactylus of walking legs were also noted, in order to identify injuries obtained during the contests. Males

Table 1. Morphometric measurements and damage to walking legs and antennae, for the crayfish males taking part in the staged contests. *N*=100.

	x̄ ±SD	Range
weight (g)	45.3±14.7	17.7-72.5
length (mm)	106.6±10.6	84-125
carapace length (mm)	53.1±5.7	40.5-63.8
claw length (mm)	45.5±7.5	27.9-59.1
claw width (mm)	19.5±3.5	11.4-26.3
claw depth (mm)	10.7±2.0	5.4-14.9
intact walking legs	7.8±0.5	6-8
antennae	1.58±0.48	0.2-2.0

were individually marked on the carapace with typewriter correction fluid.

The males were separated and acclimatized for three days in 17 l plastic tanks with a water temperature of 15 °C, and given a new light regime, 12 h light : 12 h dark, with light gradually switched on at 15:00 h. Each tank had one shelter and food was provided ad lib. The day before a contest, males were randomly assigned as opponents in a dyad, and 2 males were transferred to each of the 2 compartments of the test aquarium. The light and temperature conditions in the test room were the same as in the acclimatization room.

Experimental setup

The contests aquaria measured 470 x 360 x 300 mm. The bottom of the aquarium had a thin layer of sand glued on to it, to ensure a firm substrate for the crayfish. The aquarium was divided into two equally sized compartments by an opaque plastic plate. The partition was fitted into cords of U-shaped rubber profiles glued to the sides and to the bottom of the aquaria. The rubber seals were coated with a thin layer of silicon grease. There was no exchange of water between the two compartments when the plate was in place, since one compartment could be filled with water without any leaking into the other. Thus the crayfish were both visually and chemically isolated from each other when the partition was in place. The silicon grease also acted as a lubricant so that the partition could easily slide up and down. The plate was connected through a nylon cord to a small electrical engine. The engine was manoeuvred by remote control from an adjacent observation room. The partition could thus be removed without disturbing the crayfish. Each compartment was supplied with heated and filtered lake water from Lake Mälaren at the rate of 400 ml/min. Each compartment also had an outlet in the middle of the back wall keeping the water level in the aquarium to 190 mm from the bottom. The mean water temperature during the contests was 14.8 °C. In all the contests the partition was removed and the contests were started from 09:00 to 12:00.

Contests

Fifty contests were run under three different conditions. In a first series of 20 contests there was only an asymmetry in size between crayfish. In these contests the males only competed for space. The larger male in a dyad was on average 18% heavier than his opponent. In a second series of 18 contests, the smaller male of each dyad had a shelter placed in his compartment of the test aquarium during the 24 hours prior to the start of the contest. The larger crayfish in a dyad was on average 12% heavier than the shelter owner. The compartment that should contain the shelter was decided by the flip of a coin. Finally, in a third series of 12 contests, the smaller male was again given a shelter in his compartment prior to contests. However, both males spent 72 hours in the test aquarium. This way we wanted to test if the time as shelter owner would influence a males motivation to fight and the chances of winning. The larger male was on average 24% heavier than the shelter owner.

Immediately after the termination of a contest males were weighed on a Mettler scale and this weight was later used for the analyses. Males were also inspected for injuries obtained during the fights.

The contests were conducted during the period from May to October 1991, at the Institute of Freshwater Research in Drottningholm. We only used hard shelled crayfish that were not close to moulting.

Behavioural observations

The contests were recorded in the dark under infra-red illumination, using an infra-red video camera. The camera was connected to a video recorder and a monitor in an adjacent room. The contests could be started by removing the partition when males were positioned at equal distance from the centre of the aquarium. The males were filmed and observed for one hour. In five contests, with a size asymmetry only, the males were filmed for 24 hours after removal of the partition, to see if the initial dominance pattern was stable over a longer time period.

A fight consisted of several bouts or interactions. An interaction was defined as a situation when one crayfish approached the other within the distance of one crayfish length. We noted which individual initiated each interaction. Each interaction was ended when one of the competitors walked or swam away more than one crayfish length from his competitor. The male remaining was scored winner of the interaction. The interactions were classified into three different categories representing increasing levels of escalation. This classification is based on the assumption that the highest level signifies the highest cost in terms of energy expenditure and/or risk of being injured. Non-aggressive interactions consisted of the displacement of one male by his competitor, without any apparent aggression or displays. In interactions with aggressive displays males employed threatening postures. A male walked towards the opponent, with the abdomen in an upright U-shaped posture, on fully extended legs, with chelae outstretched and raised and antennae pointing upwards. Interactions with overt aggression included actual fighting with physical contact such as chelae strikes and opponents locking claws, pushing each other and trying to flip each other over. For details on the behaviour patterns used by crayfish in agonistic situation, see studies by Bovbjerg (1953, 1956), Rubenstein and Hazlett (1974) and Bruski and Dunham (1987). In their studies on Orconectid species, the crayfish use behaviour patterns almost identical to the ones we observed in our study (unpubl. data).

The male that won the majority of the interactions was considered winner of the whole contest. The male that was scored winner based on this criteria, was also always the winner of the last interaction.

Results

Outcome of contests

In 85% (17 cases of the total of 20 fights of this type) of the fights without shelter the heavier male won (Fig. 1). Thus, there was a significant effect of body weight on fighting ability ($P<0.01$,
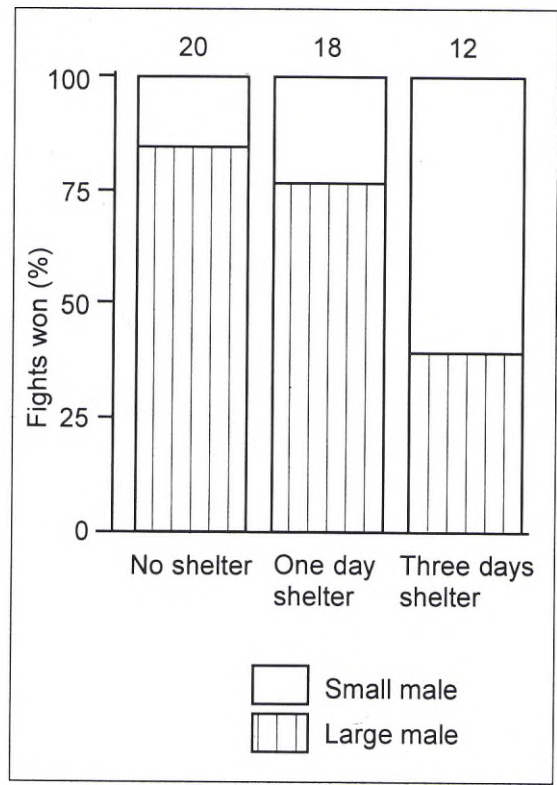

Fig. 1. The proportion of contests won by larger and smaller males, depending on the three types of experimental conditions. Numbers indicate the number of contests of each category.

Binomial test). Body length was closely correlated to body weight (total length: $r=0.95$; carapace length: $r=0.97$; $P<0.001$ in both cases; all values log transformed), and in most cases the heaviest crayfish was also the longest (17/20 considering total length; 16/20 considering carapace length). However, when using body length as an indicator of size, slightly fewer of the outcomes of fights could be predicted (15/20 for both total and carapace length). Thus, weight was the best measure to use when assessing the effect of body size on competitive ability. In the three fights where the smaller male won, his competitor was on average 6% heavier. In the fights where the smaller male lost, his competitor was on average 20% heavier (Table 2).

6*

Table 2. Average percentage size difference (*N*) between the two contestants in the three different types of fights, depending on if the smaller male won or lost. The differences between won and lost fights were evaluated by Mann-Whitney *U*-test.

Type of fight	Small male wins	Small male loses	All fights	*P*
Size asymmetry only	6% (3)	20% (17)	18% (20)	>0.20
Size and ownership (1 day) asymmetry	4% (4)	14% (14)	12% (18)	<0.05
Size and ownership (3 days) asymmetry	13% (7)	40% (5)	24% (12)	<0.05

Most of the length and weight measurements in this study are heavily intercorrelated. Therefore, the relative importance of these characters, and the level of injuries to legs and antennae for a males fighting ability, was evaluated by a stepwise multiple regression analysis. For this analysis all measurements were log transformed before calculating the differences between opponents. Relative claw size was calculated as an index, combining all three claw size measures and adjusting for body length ([length x width x depth]/body length^3). The absolute size and weight of males, calculated as the average size and weight of the two competitors in a contest, were also included as independent variables. The outcome of fights was the dependent variable.

Relative antenna injury was entered into the regression model in the first step and explained 30% of the variance in outcome of fights (*P*<0.01). The difference in body weight entered in the second step and accounted for 16% of the additional variation (*P*<0.05). The claw size difference between opponents entered in the final step and explained 10% of the additional variation when entered into the regression (*P*<0.05). Relative body weight, claw size and status of antenna thus had a combined effect on the fighting success of a male, together explaining 56% of the variation in outcome of fights. Differences in total length, carapace length, leg injuries or the absolute length, weight and claw size of the males, had no significant additional effect.

In 78% (14/18) of the fights were the smaller male had access to a shelter 1 day prior to the contest, the heavier male won (Fig. 1). Body weight was still decisive for who won (*P*<0.05). There was also no difference in the outcome of these fights compared to fights with no shelter present (*P*>0.6, Fisher exact test). In the four fights where the shelter owner won his competitor was on average 4% heavier. In the fights where the shelter owner lost, his competitor was on average 14% heavier (Table 2). The weight difference was significantly larger when the smaller shelter owner lost (*P*<0.05, Mann-Whitney *U*-test).

In 41% (5/12) of the fights were the smaller male had access to a shelter 3 days prior to the contest, the heavier male won (Fig 1). Thus, compared to contests without shelter, three days in possession of a shelter significantly increased the chances for a smaller crayfish of winning a contest (*P*<0.05, Fisher exact test). Increasing the shelter access for the smaller male from one to three days had an effect on the fighting success of the shelter owner. The effect was however not statistically significant (*P*=0.06, Fisher exact test). In the seven fights where the smaller male won his opponent was on average 13% heavier. In the fights where he lost, the opponent was on average 40% heavier (Table2). The weight difference was larger when the smaller shelter owner lost (*P*<0.05, Mann-Whitney *U*-test).
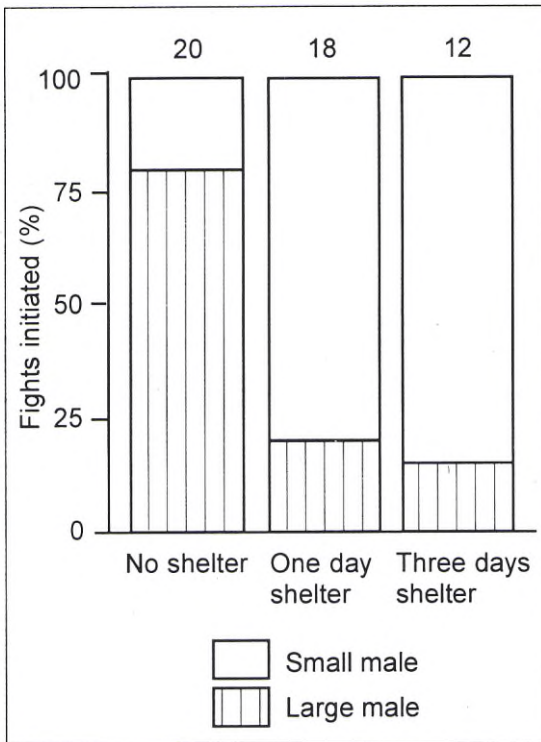
Fig. 2. The proportion of contests initiated by larger and smaller males, depending on the three types of experimental conditions. Numbers indicate the number of contests of each category.

In the 30 fights with a shelter present, the smaller male had a advantage of larger claws in 7 fights and an advantage of less injuried antennae in 11 fights. Of the 11 fights where the smaller male won, he had a claw advantage in 27% (3/11), and an advantage of less injuried antennae in 36% (4/11) of the fights. In the 19 fights where the smaller male lost, he had a claw advantage in 21% (4/19), and an advantage of less injuried antennae in 37% (6/19) of the fights. There were no significant differences between proportion of fights with advantages, comparing fights lost or won by the smaller males (*P*>0.7 in both cases, Fisher exact test). Claw or antennae advantages to the smaler male could thus not explain the outcome of the contests with a shelter present.

The initiation of contests

The smaller male initiated in only 20% (4/20) of the fights without shelter (Fig. 2). Thus, the relatively larger male in a dyad was more inclined to take the first step in a contest (*P*<0.01, Binomial test). This was not found in the fights with shelter present. Instead, in 78% (one day shelter) and 83% (three days shelter) of these fights, the smaller shelter owner initiated the contest (Fig. 2). Thus, possession of a shelter made the owner more inclined to take the first step, despite being smaller (*P*<0.001 in both cases, Fisher exact test). In all the 11 fights when smaller shelter owners finally won, they had initiated the contests.

Discussion

Morphology

Body size is generally thought to be the most important indicator of resource holding potential in animals (Huntingford and Turner 1987, Archer 1988). As expected (Ranta and Lindström 1993), body size turned out to be a good predictor of fighting ability, also for the signal crayfish in this study. Body weight rather than the two measures of body length was better in predicting the outcome of a fight. This is expected, since weight should be more closely correlated to factors like condition and muscle mass. These factors are most relevant to an individuals actual fighting ability.

The magnitude of the size difference also had an effect on the outcome of the fights. The size asymmetry was smaller in fights where the smaller shelter owner succeeded in winning, compared to fights where he did not win. Due to the experimental setup, where the smaller male was given the shelter, the effects of size and ownership were counteracting each other in these fights. When the size asymmetry was small, the internal state of the smaller crayfish decided the outcome but when the asymmetry got larger the size effect took precedence and the larger male won.

Claw size also affected competitive ability, so that relatively larger claws increased the chances of winning a fight. This agrees with studies on other crayfish species where large claws confer a competitive advantage (Stein 1976, Berrill and Arsenault 1984, Snedden 1990, Rutherford et al. 1995). The claws are used extensively in agonistic situations and are the only "weapons" that can inflict damage to a crayfish in the intermoult stage. In addition, males have larger claws than females in most crayfish species (e.g. *Astacus*, Lindqvist and Lahti 1983, *Pacifastacus*, Ranta and Lindström 1993). This sexual dimorphism is likely to have evolved as a consequence of the impact of the claws in aggressive interactions between males.

Less expected was the strong effect of antennal injuries on fighting ability. In the multiple regression model it even explained a larger part of the variance than relative weight. Males that had lost a larger part of their antenna were apparently handicapped and experienced lowered competitive ability. However, apart from visual signals, tactile signals are important in agonistic communication and antennal waving increases as light levels decrease (Bruski and Dunham 1987, Bruski and Dunham 1990). Antennae also have their main function as mechanoreceptors (Bush and Laverick 1985). Heckenlively (1970) found a correlation between antennal position and the intensity of agonistic disputes. He suggested that upright position of the antenna constitute a visual threat display. By losing parts of the antenna a male may thus lose the ability to deliver and receive tactile information and/or to display efficiently. Since the fights in this study were conducted in the dark it is likely that the loss of tactile ability had the strongest effect.

Motivation

In the dyads with no shelter present the larger crayfish initiated the majority of fights. However, when the smaller male possessed a shelter, he initiated most fights. Apparently, a male in possession of a resource was more prone to take the risk of a fight. This has also been found in other studies of crustaceans (Hyatt and Salmon 1978, Evans and Shehadi-Moacdieh 1988, Ranta and Lindström 1993).

The motivation to persist in fights was however dependent on the length of the time period as owner. After one day with shelter, the smaller owners initiated most fights but were not successful in finally winning them. After being shelter owner for three days, smaller males again initiated fights against larger competitors and this time they were also able to persist and win the fight. This shows that ownership affects the internal state and increases the competitive ability of the crayfish males. It also shows that in signal crayfish males the motivation to fight increases gradually the longer an individual remains resident. It further suggests that site defence or territoriality may form an important part of the spacing pattern in signal crayfish.

Acknowledgements

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NOTES AND COMMENTS

Gram Negative Bacteria in the Hemolymph of Noble Crayfish *Astacus astacus*, in an Intensive Crayfish Culture System

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Introduction

Freshwater crayfish are reported to have bacterial, fungal, protozoan and metazoan diseases but as Alderman and Polglase (1988) pointed out, the knowledge of European crayfish diseases has been overshadowed by crayfish plague (*Aphanomyces astacii*) and bacterial diseases of crayfish are virtually unknown (Thune 1994). Relatively few crayfish diseases have been confirmed to be of bacterial origin (Smith and Söderhäll 1986).

Bacterium do account for some disfiguring epibiotic and systemic infections in freshwater crustaceans and they could have caused losses in hatcheries or holding tanks (Smith and Söderhäll 1986). The stressful conditions (e.g., high densities, feeding rates, and water temperature) may lower the resistance of host crustaceans and encourage growth and the spread of opportunistic bacteria (Vey 1977). Bacterial infections have in these conditions caused mortalities (Alderman and Polglase 1988). Furthermore, gram negative bacterium, because of their cell wall structure (Lehninger 1982), are less sensitive to drugs and more difficult to control in the culture system than gram positive bacterium.

In this study we isolated and identified gram negative bacteria from the hemolymph of noble crayfish (*Astacus astacus*) reared in an intensive crayfish culture system (ICCS). Knowledge on the hemolymph bacteria may help to clarify their role in causing diseases and stress in crayfish.

Methods and Material

Crayfish originated from Lake Suur-Lauas, Valkeinen and Valkealampi in Kuopio Province in Central Finland. They were reared communally in Kuopio University Fish Farm for a period of 1 year before starting the experiment. During the experiment crayfish were reared in PVC-tanks in individual cages (8•23•13 cm) with tubes as hids. Two separate, identical systems were used each with 50 adult (CL 34-56 mm) noble crayfish (*A. astacus*) males. Water was recirculated (400 L, flow 2 L min^{-1}) and 10 ml min^{-1} of tap water was added to culture system to compensate evaporation, and splash. Culture conditions were: 14-21 °C, pH 6.9-7.8, DO 4.4-6.5 mg L^{-1}, and 14D:10N. One system was treated once a week with formalin (8 mg L^{-1}) and methylen blue (25 mg L^{-1}) and the other used as control. Tanks were cleaned once a week. Crayfish were fed with slightly cooked potatoes, frozen peas and frozen fish (*Rutilus rutilus*) three times a week ad libidum and leftovers were removed after 24 hours. The experiment lasted 22 weeks.

Hemolymph samples were taken from all crayfish in the beginning of the experiment, after 8

weeks and after 16 weeks from crayfish ventral abdominal artery with syringe and 24G needle. Tail surface was disinfected with 96% ethanol prior inserting syringe. Hemolymph (about 0.1 ml) was spread on bovine blood agar. Plates were incubated at room temperature (20-25 °C) in aerobic conditions for 7-14 days. Representative colonies were reisolated for characterization (GSP, MERCK® and McConkey -agar) and identified with standard bacteriological methods (Baron and Finegold 1990) with the API 20E and API 20NE test kits (Analylab Products). API-test instructions were followed with one exception: incubation temperature was +20 °C instead of +37 °C for three days. API test results were processed with APILAB Plus V3.2.2B. GSP-agar plates (MERCK®, *Aeromonas* and *Pseudomonas* sp. selective agar) were used for the genera *Aeromonas* and *Pseudomonas* identifications (Kielwein 1971). The APILAB Plus shows the percentage of identification (%ID): acceptable %ID >80.0, good %ID >90.0, very good %ID ≥99.0 and excellent %ID ≥99.9. APILAB Plus produced also a *T*-value, which estimates how closely the profile corresponds to the most typical set of reactions for each taxon (0≤T≥1).

Results and Discussion

Samples taken after 0, 8 and 16 weeks showed 41%, 46% and 79% infestation rate in gram negative bacteria, respectively.

Almost half of the different isolated colonies were gram negative rods. The genera *Pseudomonas, Comamonas, Sphingomonas, Sphingobacterium, Aeromonas, Pasteurella,* and *Acinetobacter* were identified from the isolated colonies (Table 1). Among gram negative bacteria family Pseudomonadaceae was most frequently encountered in the hemolymph of *A. astacus* with *Pseudomonas* being the most common genus in the family. Hemolymph samples from two dying crayfish developed large number of colonies of solely *Pseudomonas* sp.

Some *Aeromonas* colonies showed negative reactions for assimilation of mannitol in the API-tests and could not be identified by the APILAB

Table 1. Gram negative bacteria from the hemolymph of noble crayfish *A. astacus* identified with API-tests. The %ID = the percentage of identification - estimates how closely the profile corresponds to the taxon relative to all other taxa in the data base; *T*-value = profile correspondance.

Taxa	%ID	*T*-value
Pseudomonadaceae		
Pseudomonas fluorescens	96.9	1.00
P. putida	99.7	0.96
P. cepacia	98.1	0.43
P. vesicularis	99.6	0.90
Comamonas acidovorans[1]	99.7	1.00
Sphingomonas paucimobilis[1]	97.0	0.51
Neissericeae		
Acinetobacter sp.[2]		
Vibrionaceae		
Aeromonas sp.[3]	99.0	0.67
Pastereurellaceae		
Pasteurella spp.	97.2	0.70
Sphingobactererium sp.[4]		

[1] = synonym to *Pseudomonas*
[2] = API -tests show good identification
[3] = identified with complementary tests as *A. hydrophila* or *A. caviae*
[4] = synonym to Flavobacterium, has not been assigned to any family (Krieg and Holt 1984)

Plus to species level. According to test results these colonies are either *A. hydrophila* or *A. caviae*. Eleven isolated colonies could be identified only to genus, and eight were *Pseudomonads*, two others belong to *Pasteurella, Sphingobacterium,* and *Acinetobacter* (Table 1).

Mortality during the experiment was 30 per cent. Causes of death other than mentioned above were not examined.

This study showed that various gram negative bacteria exist in the hemolymph of healthy crayfish and that infestation rate of intensively reared crayfish increased in time. Bang (1970) reported that the hemolymph of healthy crustaceans is free of bacteria, however, various studies have isolated several genera of bacteria could be isolated from the hemolymph of healthy crustaceans (Cornick and Stewart 1966, Amborski

and Amborski 1974, Haskell et al. 1975). Scott and Thune (1986) also isolated significant levels of bacteria from the hemolymph of pond cultured crayfish (*Acinetobacter, Aeromonas, Arthrobacter, Vibrio, Bacillus, Corynebacterium, Pseudomonas*).

Pseudomonads are very common in nature and can be isolated from variety of natural materials (O'Leary 1989). Mickeniene (1983) has noted that *Pseudomonas fluorescens* and other Pseudomonads are part of the normal gut flora of *A. astacus*. Pseudomonad colonies were numerous in the hemolymph sample of dying crayfish that could be an implication of its potential pathogenity (Amborski et al. 1974, Krieg and Holt 1984, Alderman and Polglase 1988).

Aeromonas sp. is one of the most common aquatic bacteria (cf. Rhodes and Kator 1994) and its presence in hemolymph could be expected. Normally, *Aeromonas* is not pathogenic to crayfish, but mass infections may cause crayfish deaths (Amborski et al. 1974). *Acinetobacter, Sphingobacterium*, and *Pasteurella* have been reported as potential pathogens of fish and crayfish (Amborski et al. 1974, Thune 1994).

Cultural conditions could have an impact on bacterial flora of crayfish hemolymph, due to different infection routes (crayfish stock and eggs, water supply, fodder fish, equipment and supplies, visitors, and wild animal; Nylund and Westman 1992). In this indoor crayfish culture system, there are two main sources of bacterial contamination: the crayfish and diet.

This study showed that healthy noble crayfish were carrying bacteria in their hemolymph. Some of the genera isolated could cause severe losses in the cultured crayfish.

Acknowledgments

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Keep them short.

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

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

Prefixes

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

Time and Temperature

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

Spell out year, month, and week.

In Table and Fig.:

year	yr
month	mo
week	wk

Weights and Measures

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

Spell out hectare and tonne.

Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations

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

probability of type II error (false acceptance of null hypothesis)	$P\beta$			

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

Physics and Chemistry

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

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

General (some are restricted)

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

Word List

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

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

CONTENTS