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Survival and growth of sea-ranched Atlantic salmon, *Salmo salar* L., treated against sea lice before release

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Cultured Atlantic salmon smolts were treated with Slice®, orally administered emamectin benzoate, before release in the Dale River, western Norway, to study the potential effects of sea lice during the early stages of their marine phase. In all, 10 470 treated and untreated (control) fish from ten family groups were adipose fin-clipped, coded-wire tagged, and released on three different dates in 2002 (11 May, 25 May, and 7 June), which coincided with the natural smolt run. The percentage of released smolts recaptured as one-sea-winter salmon in 2003 did not differ between the treated and untreated groups released on the two dates in May 2002, but the recapture rate of fish from the treated group released on 7 June 2002 was almost twice that of the controls. The weights of the recaptured one-sea-winter salmon tended to decline from the first to the third release date, and one-sea-winter salmon from the treated groups were approximately 15% heavier than the controls. The difference in recapture rate between the treated and untreated groups increased after inclusion of the two-sea-winter and three-sea-winter salmon recaptured in 2004 and 2005, respectively. We conclude that the infestation level of salmon lice changed from non-lethal to lethal levels during the period of the smolt migration in 2002 and that non-lethal infestation levels may adversely affect Atlantic salmon populations by reducing the growth rate of fish and, consequently, their size at spawning.

Keywords: Atlantic salmon, emamectin benzoate, growth, salmon lice, survival.

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Introduction

Because of the large number of available hosts, even very low infestation rates of sea lice on farmed salmon can result in large numbers of sea lice nauplii (*Lepeophtheirus salmonis* and *Caligus elongatus*) being released into coastal waters. In Norway, sea lice from fish farms are thought to pose a serious threat to wild salmonids (Heuch *et al.*, 2005). During the 1990s, heavy infestations of sea lice on wild sea trout, *Salmo trutta*, were observed in regions with high densities of salmon farms (Birkeland and Jakobsen, 1997; Tully *et al.*, 1999; Bjørn *et al.*, 2001), and it has been shown that wild salmon smolts can be heavily infested with sea lice and that the lice can have serious physiological effects (Grimnes and Jakobsen, 1996; Finstad *et al.*, 2000; Tully and Nolan, 2002). Although it has been generally assumed that sea lice have a negative impact on salmon smolts migrating to sea from rivers in Norway, few published studies have documented the relationship between sea lice and the marine survival of salmon. Most of the monitoring data have appeared in annual reports. An overview of these data is provided by Heuch *et al.* (2005), who reviewed the Norwegian "National Action Plan against Salmon Lice on Salmonids" and proposed that release experiments should be performed to investigate the effects of sea lice on the survival of salmonids at sea.

Simultaneously releasing groups of smolts, both untreated and treated, is a relatively simple method of estimating the effect of sea lice during the migration of smolts to the sea. Emamectin benzoate (Slice®, Schering-Plough Animal Health) administered in feed has been used as a preventative treatment against infestations of sea lice and has been shown to prevent or markedly reduce the level of infestation following transfer to seawater (Stone *et al.*, 2002).

However, the probability of wild smolts being infested varies during their migration to sea, both within a region and over time. Several biological factors influence the degree to which sea lice copepodites infect wild salmon

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(Heuch *et al.*, 2005). Moreover, the copepodites are transported by the prevailing currents and may not be distributed evenly in the sea. Consequently, a single-release experiment is a simplified way of describing a fluctuating environment. If the intention is to monitor sea lice–salmon dynamics during one season, repeated releases are preferable. Release dates should also be timed to coincide with the natural smolt migration period.

There is evidence of a genetic component in the susceptibility of Atlantic salmon to sea lice at the family level (Glover *et al.*, 2005) and possibly also among stocks (Glover *et al.*, 2004). Family variation may mask the effect of sea louse treatment in release experiments if the genetic composition of the release groups is not taken into account. The need for family controls is further highlighted by the findings of Jonasson *et al.* (1997), who demonstrated that the return rate varied between families of sea-ranched Atlantic salmon.

The total production of farmed salmon and rainbow trout in Hordaland County, in mid-western Norway, amounted to 96 000 t in 2002 (K. Johnsen, pers. comm.). In a comparative study conducted between 1993 and 2000, marine survival rates of salmon stocks from Hordaland County were estimated to be lower than those from other regions of western Norway (Skurdal *et al.*, 2001). Krkošek *et al.* (2005) estimated that sea louse infestation pressure on Pacific salmon juveniles increased by several orders of magnitude as they migrated past a single salmon farm.

The advantage of using cultured smolts for release experiments is that it is possible to achieve a level of standardization desirable for comparisons of releases within and between years. The numbers of smolts released, their treatment, the time of release, and their genetic background may be controlled to reduce variability in such experiments.

The aim of the present study was to test the null hypothesis that there is no difference in marine survival between groups of untreated control fish and salmon smolts treated with Slice®, using fish of known family background and releasing them at different dates in a region in Norway characterized by a high level of fish farming activity (>200 farms; Figure 1).

Material and methods

Fish material

The salmon smolts released in this experiment were derived from wild salmon broodstock collected from the Dale River. Eggs from each of five two-sea-winter female salmon were divided into two batches. A large adult male salmon was used to fertilize one batch of eggs from each female, while a mature male parr was used to fertilize the other batch of eggs from each female, thus producing five pairs of maternal half-sib groups.

All eggs were fertilized on 27 October 2000. The ten family groups of alevins were transferred to, and mixed together, in five 1×1-m indoor tanks for first-feeding on 15 May 2001 under continuous light. On 29 November, the fish were transferred to four 2-m diameter circular tanks under natural photoperiod, permitted by a translucent roof above the tanks. The fish were mixed by placing a quarter of the contents of the five 1×1-m tanks into the four 2-m diameter tanks.

To estimate the contribution from each family to the group of 1-year-old+ smolts and to check the mixing of families among the tanks, 94 fish from the four tanks (376 fish in all) were sampled for family identification on 5 and 6 March 2002. The contribution from each family to the total number of smolts varied from 4.5% to 13.8%. The difference in contribution between the five pairs of half-sib groups was less than 2%. There was no reason to believe that the ten family groups had not been randomly distributed among the four tanks (10×4 G-test, $p = 0.4$).

On 12 March 2002, all fish were anaesthetized, and the mature male parr were identified, adipose fin-clipped, and returned to their respective tanks.

Group treatment and tagging

To ensure thorough mixing of the fish before release, each release group was composed of approximately equal numbers of fish from each of the rearing tanks. Fish were anaesthetized (Benzocaine), adipose fin-clipped, and tagged with sequentially numbered Decimal Coded Wire tags™ (Northwest Marine Technology™, Seattle, WA). On the three release dates in 2002 (11 May, 25 May, and 7 June), there was one control group and one group treated with Slice® before release (see Table 1). Slice® fed to fish is absorbed from the gut and distributed throughout the tissue of the fish and, when sea lice feed on treated fish, emamectin benzoate is taken up in the tissue of the lice and binds to ion channels of nerve cells disrupting transmission of impulses, causing paralysis and the death of the lice. Slice® can prevent sea lice larvae from developing on treated fish for several weeks post-treatment. Salmon smolts in the treated groups were fed with feed containing Slice® for eight days before their release.

Two further release groups, treatment and control, consisting of previously mature male parr, were coded-wire tagged and included in the last release. These fish, which had been adipose fin-clipped in March, were chosen for the experiment if they were larger than 12 cm and appeared to have smolted, i.e. silvery scales, slender body shape, dark fin margins, and parr marks faint or absent.

A fykenet was installed in the river during the last week of April 2002 to record the timing of the migration of wild smolts. This net was checked daily until 17 June 2002. All groups of smolts were released in the river close to the hatchery, 3 km upstream from the estuary of the Dale River, to coincide with the wild smolt run, which peaked in mid-May and lasted until the end of the first week in June 2002 (Figure 2).

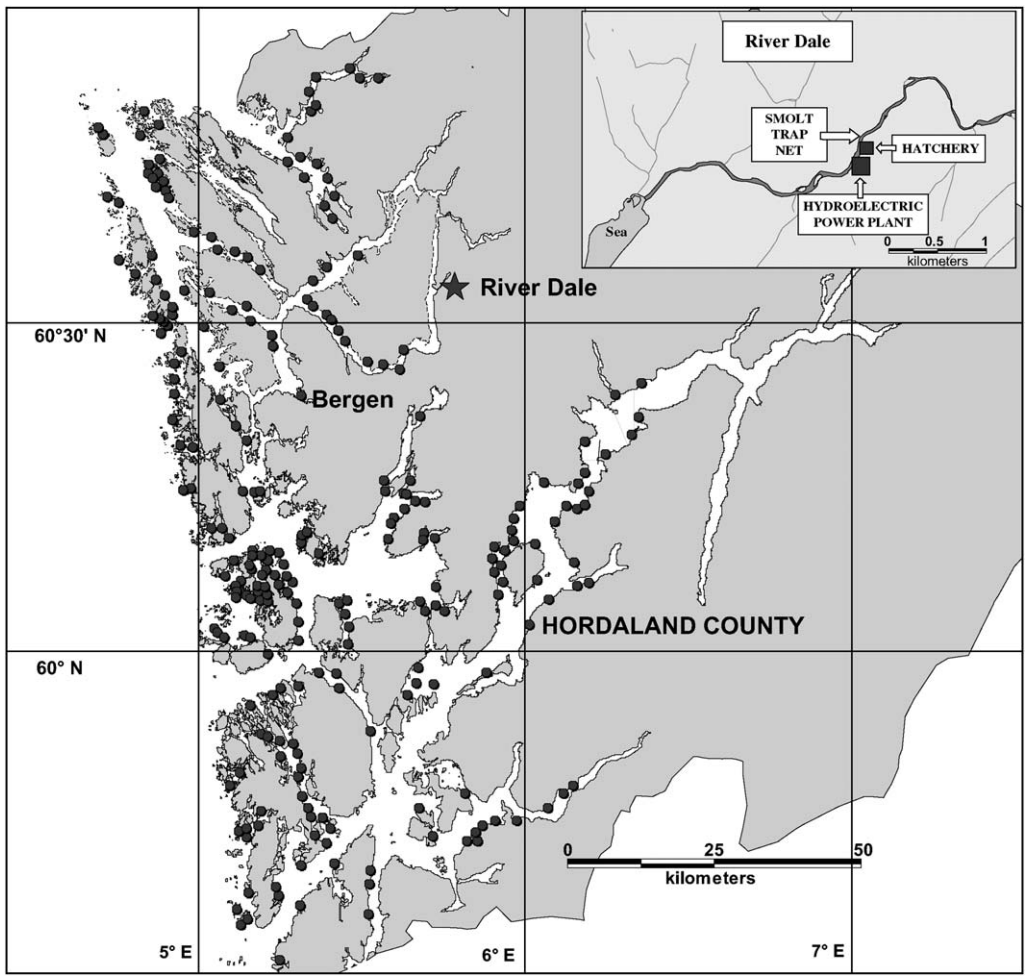

Figure 1. The location of the Dale River in Hordaland County, western Norway. The sites of rainbow trout and salmon farms are also shown (filled circles).

Table 1. The number of fish in each release group and dates in 2002 of tagging, treatment, and release of smolts and previously mature male parr (PMM; see text for explanation). The average fork length and weight of fish in three samples consisted of a mixture of treated and untreated fish, and the numbers of fish in these samples (*n*), are also shown.

			Average size at tagging				
Release group	Number of fish	Tagging date	Fork length (cm)	Weight (g)	*n*	Treatment period	Release date
Treatment 1	1 836	23 April	15.8	45.4	80	2–10 May	11 May
Control 1	1 698	23 April					11 May
Treatment 2	1 771	14 May				15–24 May	25 May
Control 2	1 761	13 May					25 May
Treatment 3	1 479	15 May	16.4	53.3	62	29 May–6 June	7 June
Control 3	1 400	15 May					7 June
PMM treated	276	16 May	14.8	36.6	44	29 May–6 June	7 June
PMM control	250	16 May					7 June

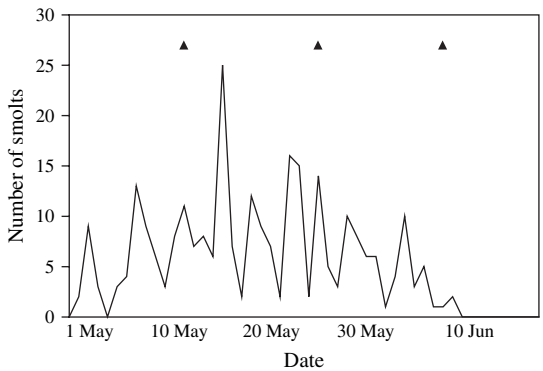

Figure 2. Daily catches of wild smolts in the fykenet in the Dale River in 2002. The dates of the releases of cultured smolts are shown by black triangles.

Collection of data from returning adults

Data from returning adult salmon were derived mainly from angling catches in the Dale River. Posters were distributed to advise the anglers of the tagged and fin-clipped fish that had been released and the purpose of the experiment. A reward of NOK 50 (approximately £4 GBP) was paid to anglers who assisted the project by providing scale samples and the upper jaw (containing the coded-wire tag) from adipose fin-clipped salmon. A freezer for storing samples was installed in a room open to the public in the hatchery, which is located close to the most productive angling sites. Twenty per cent of the adult salmon were caught after the fishing season ended during the collection of broodfish, and 5% were caught in a bag net in the fjord, approximately 11 km from the estuary of the Dale River. Recapture rate was defined as the percentage of released smolts subsequently recaptured as coded-wire tagged adults.

The Rådgivende Biologer consultancy examined the scales of the adult samples to estimate individual smolt length as part of a regional salmon monitoring programme.

Microsatellite analysis for family identification

Tissue samples were collected from all the broodfish used in the experiment to facilitate the genetic identification of their offspring. In the hatchery, a sample of pelvic fin tissue from the progeny of the broodfish was used for family identification. All recaptured tagged adults were also tested for parentage.

DNA was extracted from approximately 40−50 mg of tissue using a Qiagen DNeasy kit, following the manufacturer's instructions. Four microsatellite loci were amplified: *Ssa85*, *Ssa197*, *Ssa202* (O'Reilly *et al.*, 1996), and *SsOSL85* (Slettan *et al.*, 1995). Polymerase Chain Reactions (PCR) were performed in 96-well plates with a total reaction volume of 12 µl on an Applied Biosystems GeneAmp 9700 thermal cycler. Each reaction consisted of 50 ng genomic DNA, 1.5 mM $MgCl_2$ (2.5 mM for *SsOSL85*, *Ssa171*, and *SsOSL438*), 0.2 µl of forward and reverse primers (Applied Biosystems, fluorescently labelled), 0.2 mM dNTPs, and 0.5 U Taq polymerase (Promega). The following programme was used for PCR: initial denaturation at 94°C for 5 min, 30 (35 for *Ssa197* and *SsOSL85*) cycles of 94°C for 50 s, 40 s at locus-specific annealing temperature, 50 s at 72°C, followed by a final extension at 72°C for 10 min. The annealing temperatures used for the different loci were as follows: 55°C for *SsOSL85*, *Ssa85*, and *Ssa202*, and 56°C for *Ssa197*. The PCR products were diluted to between 1:20 and 1:50 with deionized water and, to each well in Applied Biosystems Optical Well 96-well trays, 2 µl diluted product was added to 8 µl formamide and 10 µl Genescan™ Liz-500 size standard. Three to four different PCR products mixed together were run on an Applied Biosystems ABI 3100 Genetic Analyzer. Alleles were scored using Genotyper Analysis Software version 3.7, with manual control of the automatically scored peaks.

Parentage was determined by matching progeny multilocus genotypes to those of the known parental crosses, using exclusion-based software (Family Assignment Program; J. Taggart, unpublished data).

Statistical analysis

The hypothesis that the family groups were evenly distributed in the tanks was tested using the *G*-test (Sokal and Rohlf, 1981). The General Linear Models (GLM) package of Statistica (StatSoft, 2005) was used for analysis of covariance to examine differences in size of one-sea-winter salmon. The LOGISTIC Procedure of the SAS Software Package version 9.1 (SAS Institute, Cary, NC) was used to fit a Generalized Linear Model (GLM) (McCullagh and Nelder, 1989) with a logistic link function to test for differences in the numbers of salmon recaptured (binomial response) with release date, family, and treatment:

$$\log\left(p/(1-p)\right) = I + A_F + B_T + C_R,$$

where p is the probability of recapture, I is the intercept, and A_F, B_T, and C_R are the parameter estimates for the effects of family, treatment, and release date, respectively.

Results

Recaptures of treated and control groups

In all, 105 coded-wire tagged one-sea-winter salmon were recaptured (Table 2). There were no differences in recapture rates for smolt to one-sea-winter salmon between the treated and control groups released on 11 May and 25 May, but the recapture rate of one-sea-winter salmon derived from treated smolts released on 7 June 2002 was more than twice that of the control group (Table 2, Figure 3). The recapture rates were significantly influenced by the variability in recapture rates between the families

Table 2. The number of coded-wire tagged and released smolts, and the number of salmon caught and the recapture rate for one-sea-winter (1SW), two-sea-winter (2SW), and three-sea-winter (3SW) salmon. Recaptures were from angling in the Dale River (Angling), catches during the fishery for broodfish in the Dale River (Broodfish), catches in a bag net in the fjord (Bag net), and reports by fishers elsewhere (Other). The recapture for the treated groups and the control groups released on three dates in spring 2002 are shown separately, together with the recapture of tagged previously mature male parr (PMM).

	Release date								
	11 June 2002		25 May 2002		7 June 2002		7 June PMM		
	Treated	Control	Treated	Control	Treated	Control	Treated	Control	Sum
No. of smolts	1 836	1 698	1 771	1 761	1 479	1 400	276	250	10 471
Recapture 1SW salmon									
Angling	13	12	9	8	18	9	4	2	75
Broodfish	2	1	2	5	6	3	1	1	21
Bag net	2	0	0	2	4	0	1	0	9
Sum 1-SW	17	13	11	15	28	12	6	3	105
Recapture rate (%)	0.93	0.76	0.62	0.85	1.89	0.86	2.17	1.20	1.00
Recapture 2SW salmon									
Angling	5	1	1	1	4	0	0	0	12
Broodfish	1	0	1	3	4	0	0	0	9
Bag net	2	2	0	2	1	0	0	0	7
Other	0	0	0	1	4	0	0	0	5
Sum 2-SW	8	3	2	7	13	0	0	0	33
Recapture rate (%)	0.44	0.18	0.11	0.40	0.88	0	0	0	0.32
Recapture 3SW salmon									
Angling	3	0	1	0	2	0	0	0	6
Broodfish	1	0	1	0	0	0	0	0	2
Sum 3-SW	4	0	2	0	2	0	0	0	8
Recapture rate (%)	0.22	0	0.11	0	0.14	0	0	0	0.08
Sum 1−3-SW	29	16	15	22	43	12	6	3	146
Total recapture rate (%)	1.58	0.94	0.85	1.25	2.91	0.86	2.17	1.20	1.39

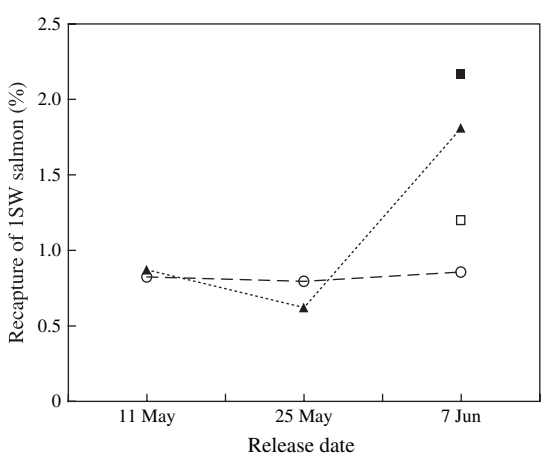

Figure 3. Recapture rates (%) of treated (filled triangles) and untreated (open circles) groups of smolts as one-sea-winter salmon in 2003 for the different release dates in 2002. Recapture rates of treated (filled square) and untreated (open square) groups of previously mature male parr released on 7 June are also shown.

and by the release dates (GLM binomial response model: $p_{\text{family}} < 0.05$, $p_{\text{release date}} < 0.05$), but not by the treatment. However, a significant contribution from treatment, and not family ($p_{\text{family}} = 0.82$), was seen when fitting a binomial response model exclusively to the return of one-sea-winter salmon from the last release date ($p_{\text{treatment}} < 0.05$).

A similar difference between treated and control fish was seen among the previously mature male parr that returned as one-sea-winter salmon (Table 2, Figure 3), but the numbers were too small to obtain significance.

The differences between the treated and control groups increased when the recaptures of multi-sea-winter salmon were included in the analysis (Table 2, Figure 4). Twenty-three of the 33 two-sea-winter salmon and all eight recaptured three-sea-winter salmon were from the treated groups. The effect of Slice® treatment, release date, and family background were all significant parameters in the binomial model when the total recaptures of one-, two-, and three-sea-winter salmon were included (GLM: $p_{\text{treatment}} < 0.05$, $p_{\text{family}} < 0.05$, $p_{\text{release date}} < 0.05$). The significant contribution from

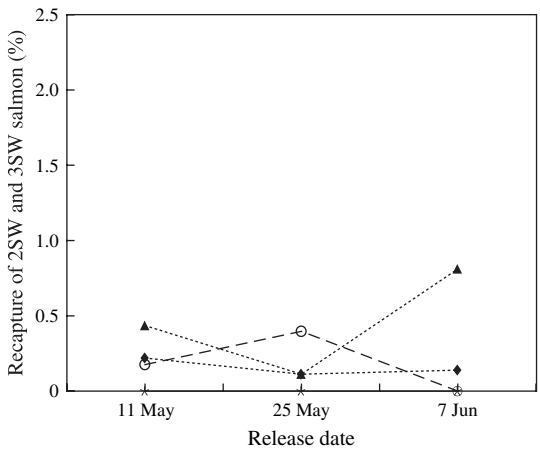

Figure 4. Recapture rates (%) of treated smolts as two-sea-winter salmon (2SW) (filled triangle) and three-sea-winter salmon (3SW) (filled diamond), and of control groups recaptured as 2SW salmon (open circle) and 3SW salmon (asterisk) for the different release dates in 2002.

family was probably a consequence of the wide variability in their recapture rates, which varied between 0% and 1.7% for one-sea-winter salmon and from 0% to 2.4% for one- and multi-sea-winter salmon combined (Figure 5). A highly significant effect of the treatment was found for the last releases on 7 June (GLM: $p_{\text{treatment}} < 0.001$). The total recaptures differed between the families from 0% to 4.2% (Figure 6), but family origin was not a significant parameter for fish released on 7 June ($p_{\text{family}} = 0.36$). Although the lack of significance may be related to the low recaptures in several of the families (Figure 6), the results also indicate that the effect of the treatment was independent of, or did not depend strongly on, family background.

Growth in the sea

The smolt sizes from the control groups that returned as adults were not statistically different from the treated fish on any of the three release dates (Table 3).

Smolts in the treatment groups grew faster in the sea than the untreated fish, and the weight of one-sea-winter salmon tended to fall the later the release date (Figure 7). The combined effect of release date and treatment significantly affected the size of the one-sea-winter salmon (analysis of covariance: $p_{\text{model}} < 0.05$, $p_{\text{release date}} < 0.05$, $p_{\text{treatment}} < 0.05$). A similar trend was observed for length (Figure 8), but it was not significant (analysis of covariance, $p = 0.12$), probably the result of higher individual variation in length. If the increase in length from smolt stage to return as one-sea-winter salmon, i.e. the length of one-sea-winter salmon minus smolt length, was substituted for one-sea-winter salmon length, the negative effect of a later release date on length was significant ($p < 0.05$). The condition factor of one-sea-winter salmon from treated groups was slightly higher than for fish from control groups (0.91 vs. 0.89, $p = 0.16$, t-test) because of their greater weight at length.

Discussion

This study found differences in recapture rates and growth in the sea between cultured smolts treated with Slice® and untreated control groups. The disadvantage of using cultured smolts to study processes in the wild is that it is not known if the performance of cultured smolts is similar to that of wild smolts. Important traits such as feeding behaviour, predator recognition and avoidance, and migratory behaviour differ in cultured smolts owing to their previous experience in the hatchery environment, and the survival of wild smolts is normally greater than that of cultured smolts

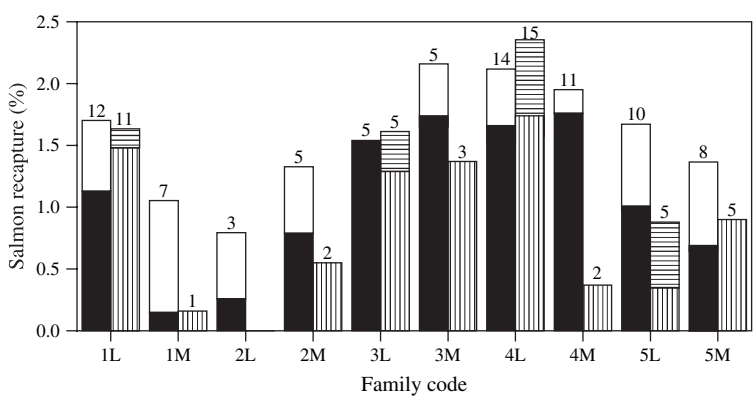

Figure 5. Recapture rates (%) of adult salmon from the ten family groups divided into the two treatment groups: treated and untreated smolts released on 11 May, 25 May, and 7 June. One-sea-winter (solid filled bars) and multi-sea-winter salmon (open bars) derived from treated groups, and one-sea-winter salmon (vertical hatching) and multi-sea-winter salmon (horizontal hatching) derived from untreated groups are shown separately. The numerals 1−5 in the ten family codes refer to the five female broodfish, while the letters L and M denote the half-sib offspring groups of the large male and the mature male parr, respectively.

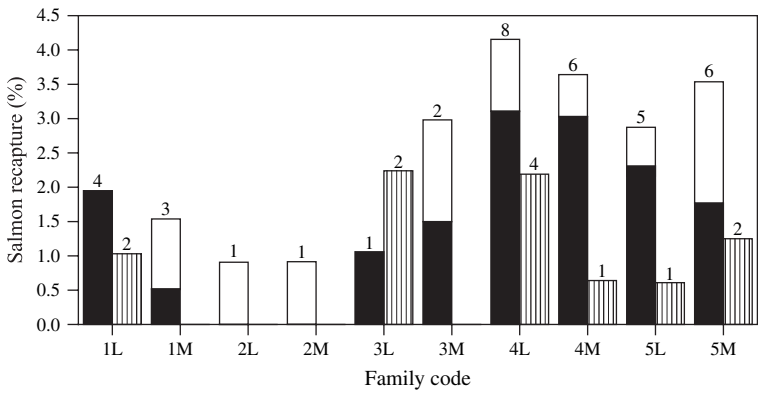

Figure 6. Recapture rates of adult salmon from the ten family groups divided into the two treatment groups: treated and untreated smolts released on 7 June 2002. One-sea-winter (solid filled bars) and multi-sea-winter salmon (open bars) derived from treated groups and one-sea-winter salmon (vertical hatching) derived from untreated groups are shown separately. The numerals 1−5 in the ten family codes refer to the five female broodfish, while the letters L and M denote the half-sib offspring groups of the large male and the mature male parr, respectively.

(Jonsson *et al.*, 2003). However, the larger size and greater energy reserves of cultured smolts may affect their ability to tolerate infestations of sea lice. These uncertainties are inherent in release experiments using cultured smolts, but it is assumed that the differences in recapture rate and growth among groups of treated and untreated cultured smolts would also apply to wild smolts.

The experimental design was intended to reduce environmental (tank) effects and biological variation among the release groups. The fish, therefore, were mixed three times from first-feeding to tagging, and previously mature males were tagged separately. Although the number recaptured was too low to permit full statistical testing of variability between families and interactions between release dates, families, and the effect of the treatment, significant effects of the treatment were found. We interpret the observed differences in recapture rate and growth between the treated and control groups as indicative of a higher rate of sea louse infestation in the untreated control fish.

This study is the first to document sublethal effects of sea lice on cultured salmon released into the wild. The recapture rate of the one-sea-winter salmon released as smolts in May was not significantly affected by treatment with Slice®, but the control group smolts probably suffered levels of sea louse infestation that were high enough to reduce growth rates. Sea lice may cause physiological stress, reduced appetite, and behavioural changes in salmonids (Grimnes and Jakobsen, 1996; Dawson *et al.*, 1999; Finstad *et al.*, 2000). In tank experiments, Wagner *et al.* (2003) found a negative relationship between the number of sea lice on Atlantic salmon and critical swimming speed, and a positive relationship between number of lice and chloride levels in the fish. Those authors concluded that sublethal infestation by sea lice may compromise the overall fitness of salmon and expressed concern about the health and fitness of wild Atlantic salmon in areas of high sea louse abundance.

Table 3. Mean total length (cm) of smolts (s.d.) estimated from the reading of scales taken from one-sea-winter salmon and the results of *t*-tests comparing the smolt length of treated and untreated fish.

	Treated		Control		
Release date	Length (s.d.) (cm)	*n*	Length (s.d.) (cm)	n	*t*-Test
11 May 2002	16.7 (2.1)	13	17.9 (2.2)	11	n.s.
25 May 2002	17.8 (1.4)	9	17.6 (1.8)	10	n.s.
7 June 2002	18.2 (1.9)	18	18.4 (1.4)	8	n.s.

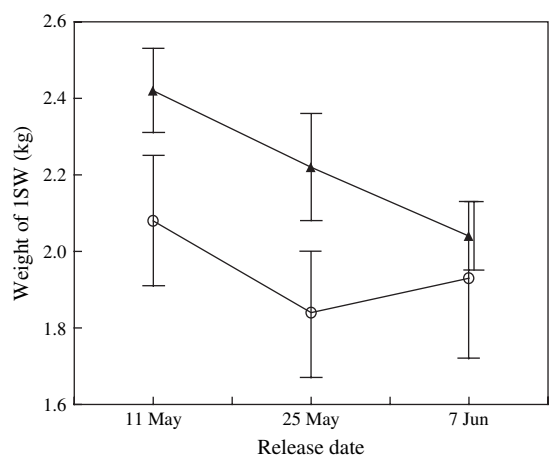

Figure 7. Mean weights and the standard error of the means (vertical bars) for one-sea-winter salmon (1-SW) recaptured in 2003 that were released as treated (solid triangle) and untreated (open circle) smolts on the different release dates in 2002.

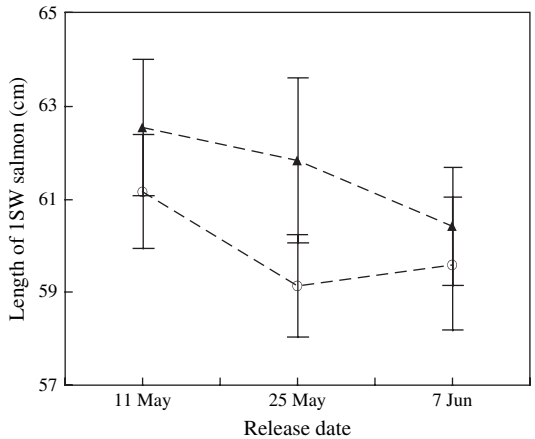

Figure 8. Mean lengths and standard error of the means (vertical bars) of one-sea-winter salmon recaptured in 2003 that were released as treated (solid triangle) and untreated (open circle) smolts on the different release dates in 2002.

The impacts of sea lice on marine aquaculture are poorly documented, but include economic losses resulting from a reduction in the growth of the cultured fish (Johnson *et al.*, 2004). Stone *et al.* (2000b) observed faster growth in salmon treated with emamectin benzoate but were unable to detect statistically significant differences owing to the small number of fish used in the trials. In a tank experiment, Dawson *et al.* (1999) observed changes in the feeding behaviour of salmon post-smolts infected with sea lice. However, the fish were able to recover, and no effects on growth rate and condition could be detected among those fish that survived beyond the pre-adult louse stage.

The early marine phase of salmon smolts is normally characterized by fast growth in an environment with high feed availability. The difference in weight between treated and control fish suggests that the untreated smolts were disadvantaged during this important period. The smaller size of the one-sea-winter salmon derived from smolts released late in the season may indicate that these fish entered the marine environment at a time when conditions were suboptimal for growth because, for example, the availability, density, or quality of food organisms were reduced later in the season or because they experienced a shorter growing season in the sea.

Sevatdal *et al.* (2005) detected emamectin benzoate in the mucus of treated, cage-reared Atlantic salmon post-smolts for up to 77 days post-treatment, and no sea lice were found on the treated fish before day 123 post-treatment. Challenging treated fish with sea lice copepodites indicated that the protective effect of treatment with Slice® is high for approximately 50–70 days and moderate from approximately 70–110 days post-treatment, possibly depending on temperature (Stone *et al.*, 2000a, 2002).

If the smolts in this experiment migrated downriver rapidly after their release and migrated to sea at a speed comparable to that of tracked hatchery-reared smolts in the Romsdalsfjord system in western Norway (Finstad *et al.*, 2005), they should have reached the open sea within a few weeks, well within the expected period of protection from sea lice conferred by the treatment with Slice®.

Reasons for the higher recapture rate of the treated fish released in June compared with releases in May are unknown. The timing of the later releases may have coincided with the development of migratory motivation, which previous release experiments have shown increases from May to June in one-year-old smolts (Skilbrei *et al.*, 1994a, b). Thus, a larger proportion of the fish released later may have departed from inshore areas than the proportion of fish released in May.

The significantly higher recapture rates of the treated fish from the last release date strongly suggest that the infestation rate increased from May to June 2002 and that the sea lice load became high enough to result in greater mortality among the untreated fish. It is not known if the mortality of untreated smolts was size-selective. However, greater mortality among smaller fish is one possible explanation for the lack of returns of two- and three-sea-winter salmon from the untreated control group and for the reduced difference in size between one-sea-winter salmon derived from the treated and control groups from the last release. In culture, the largest smolts within a family have a greater probability of maturing as one-sea-winter salmon (Skilbrei, 1989), implying that greater mortality among smaller smolts may reduce the multi-sea-winter component. Further studies are needed to examine the potential influences of sea louse infestations on the age and size composition of salmon stocks.

A crucial question in studies of animal diseases is whether parasites influence the population dynamics of their hosts or only act in a compensatory manner, affecting only those individuals in a population with lowered fitness as a result of other regulatory forces (Tompkins and Begon, 1999). Our findings strongly suggest that the effect of sea lice on the survival and growth of Atlantic salmon is additive. If this is so, salmon farming may have serious consequences for local stocks of wild Atlantic salmon if effective pest management strategies are not implemented.

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