Liming restores Atlantic salmon (*Salmo salar*) populations in acidified Norwegian rivers

Trygve Hesthagen, Bjørn M. Larsen, and Peder Fiske

Abstract: Acidification has exterminated or seriously reduced Atlantic salmon (*Salmo salar*) populations in 40–45 Norwegian rivers. As this problem still exists, liming to restore salmon has been necessary, which now involves 21 of these rivers. Thirteen rivers were electrofished 1 year before liming and again 1–12 years later. There was a significant effect both of time after liming and status (e.g., formerly lost and reduced stocks) on the densities of both fry (age 0+) and parr (age ≥ 1+). However, the rate of increase in densities of young salmon in these two status categories was not significantly different in either age group. The development in parr densities suggests that more than 20 years of liming is required to restore salmon in rivers with lost native populations. Stocked rivers and rivers unaltered by hydropower developments generally had higher fry densities and faster increase in parr densities. Annual rod catches of adult salmon increased significantly after liming started, reaching about 45 t after 10 years of treatment. This is 11%–12% of the current total catch of Atlantic salmon in all Norwegian rivers. Liming thus makes an important contribution to the restoration of salmon in formerly acidified rivers.

Résumé : L’acidification a éliminé ou considérablement réduit les populations de saumons atlantiques (*Salmo salar*) dans 40–45 rivières de Norvège. Comme le problème persiste, le chaulage reste nécessaire pour restaurer le saumon et implique actuellement 21 de ces rivières. Nous avons fait de la pêche électrique dans 13 rivières, 1 année avant le chaulage et de nouveau 1–2 années après. Il y a un effet significatif à la fois du temps depuis le chaulage et du statut (par ex., un stock perdu ou réduit antérieurement) sur la densité des alevins (âge 0+) et des tacons (âge ≥ 1+). Cependant, le taux d’augmentation des densités des jeunes saumons dans ces deux catégories de statut n’est pas significativement différent dans les deux groupes d’âge. L’évolution des densités des tacons indique que plus de 20 ans de chaulage sont nécessaires pour restaurer le saumon dans les rivières qui ont perdu leur population indigène de saumons. Les rivières empoissonnées et celles non modifiées par le développement d’installations hydroélectriques ont généralement des densités plus élevées d’alevins et une augmentation plus rapide des densités de tacons. Les captures annuelles de saumons adultes à la ligne ont augmenté de façon significative après le début du chaulage, atteignant environ 45 t après 10 années de traitement. Cela représente 11–12 % des captures totales actuelles de saumons atlantiques dans toutes les rivières de Norvège. Le chaulage apporte donc une importante contribution à la restauration des saumons dans les rivières acidifiées antérieurement.

[Traduit par la Rédaction]

Introduction

Anthropogenic disturbances of natural populations commonly entail a reduction in abundance, and salmonids are no exception (e.g., Einum et al. 2008). There has been particular concern about the recent extinction and population reductions in Atlantic salmon (*Salmo salar*), which are of high commercial and recreational value (International Council for the Exploration of the Sea 2000). Wild Atlantic salmon are under threat and have disappeared from several European countries during recent decades, and they also teeter on the brink of extinction in the United States and parts of southern Canada (Parrish et al. 1998; Friedland et al. 2003; International Council for the Exploration of the Sea 2007). Much of the decline has been ascribed to degradation of breeding habitats, water quality deterioration, excessive rates of exploitation, genetic deterioration due to escaped farmed fish, and the introduction of fish parasites such as *Gyrodactylus salaris* and salmon lice (*Lepeophtheirus salmonis*) (Johnsen and Jensen 2003; McGinnity et al. 2004; Finstad et al. 2007). However, most factors affecting salmon numbers do not act in isolation, but rather in concert (Parrish et al. 1998).

Atlantic salmon are extremely sensitive to acidification, i.e., to low pHs and high concentrations of inorganic aluminum (Rosseland et al. 1986). In southern Norway, water quality deterioration through acidification is a major threat. Populations of Atlantic salmon either have been exterminated or became seriously reduced in about 40–45 rivers. The acidification-driven decline in Atlantic salmon stocks started as early as the 19th century, and by 1970 virtually all stocks in the affected area had been lost (Hesthagen and Hansen 1991). The pH of these rivers was typically 4.4–5.3, and concentrations of inorganic aluminum lay between 70 and 160 $\mu g \cdot L^{-1}$. In Norway, since the 1980s, attempts to restore fish populations in formerly acidified rivers and lakes have been based on systematic liming (Sandøy and Ro-

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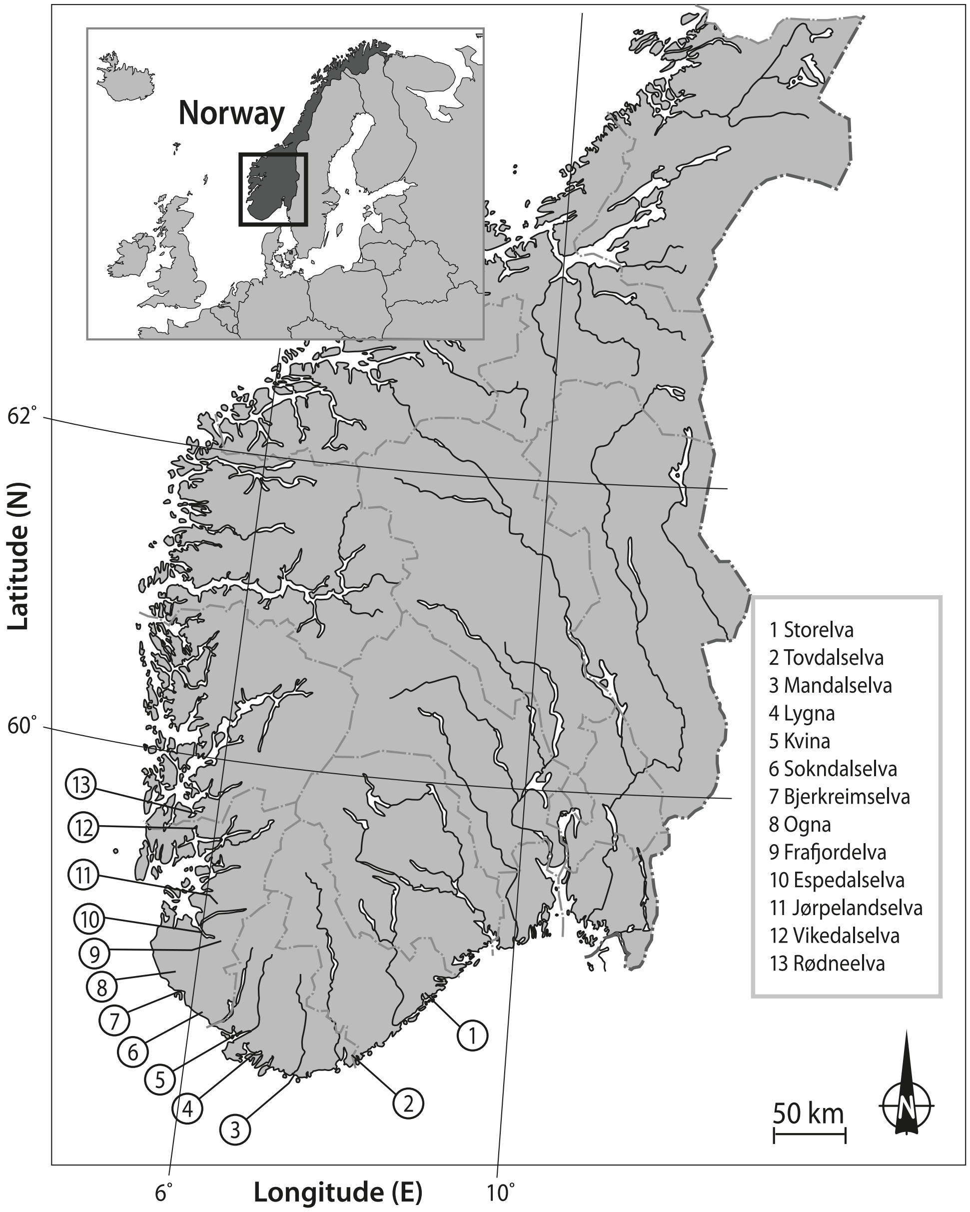
Fig. 1. Locations of limed Atlantic salmon rivers in the present study. Corresponding numbers for the rivers are shown in Table 1.



mundstad 1995). Full-scale liming of salmon rivers was initiated in 1985 with River Audna, while 21 rivers were included in the program from 1987 to 2005 (cf. Hesthagen and Larsen 2003). Ten of these rivers had entirely lost their native Atlantic salmon stocks, while the populations were at various stages of reduction in the remaining 12 rivers.

This paper provides the first extensive report on the effect of liming on densities of young Atlantic salmon, based on data from 13 rivers in southern Norway from the first 12 years of liming. We analyzed that if their densities rise in a linear fashion, then it will appear to reflect increasing input of gametes by a growing population of adults, judged from catch records. We used mean juvenile salmon densities for all rivers as a predictive variable, which may be somewhat biased, as spatial (between-river) variation exists. However, any model of biological systems necessarily involves the use of simplifying assumptions (Einum et al. 2008).

Materials and methods

The study rivers are located in the counties of Aust-Agder, Vest-Agder, and Rogaland in southern Norway (Fig. 1; Table 1). Two rivers, e.g., Mandalselva and Kvina, are severely affected by hydroelectric power generation by the creation of obstacles to adult migration through stretches of low water flow and passage through dams, reduced rearing areas for younger fish, fluctuating water levels, and the descent of smolts through tunnels in which turbines have been installed. The rivers Storelva, Tovdalselva, and Jørpelandselva are also affected to some extent by hydroelectric power generation. In most cases, Atlantic salmon and brown trout (*Salmo trutta*) were the only two species caught in the study rivers. Eels (*Anguilla anguilla*) occur in all rivers, but their numbers were low. Lampreys (*Lampetra planeri*), threespine sticklebacks (*Gasterosteus aculeatus*), ninespine

Table 1. Data for the limed rivers in this study.

River	Status	Year	N1	N2	Fish sampled (*n*)		Stocking	Stocking period	No. of stocked fish			Strain
					Fry (0+)	Parr (≥1+)			Roe	Fry	Smolt	
1. Storelva	1	1996	9	8–10	3520	595	Yes	2000–2005	66 500	19 000		Local
2. Tovdalselva	0	1996	9	14	1967	462	Yes	1997, 2000–2005	1 553 200	6 750[a]		Storelva
3. Mandalselva	0	1997	8	18	4651	1425	Yes	1996–2005	689 500	702 913	31 123	Local and Bjerkreimselva
4. Lygna	0	1991	12	9–10	2099	394	No					
5. Kvina	0	1994	11	10	2738	685	No					
6. Sokndalselva	0	1989[b]	12	9–16	6185	1817	No					
7. Bjerkreimselva	1	1996	9	18–20	8703	3024	Yes	1995–2005		1 945 000		Local
8. Ogna	1	1991	12	8–16	9290	2923	No					
9. Frafjordelva	0	1993	12	10–12	4178	2112	Yes	1993–2005		596 500		Local
10. Espedalselva	1	1995	10	8–11	3150	2174	Yes	1995–2005		605 000		Local
11. Jørpelandselva	1	1995[b]	10	6–8	829	333	Yes	1994–2005		489 000		Local
12. Vikedalselva	1	1987	12	9–17	6437	2771	No					
13. Rødneelva	1	1996	9	7–12	2325	1617	Yes[c]	1995–1996, 1998		16 500		Local

Note: River numbers refer to locations in Fig. 1. N1 and N2 are number of sampling years and numbers of sampling sites, respectively. For status: 0 = lost and 1 = reduced stock.

[a] Lake liming only.

[b] Stocking of fry only in 1997.

[c] Stocking above salmon ascending stretch only.

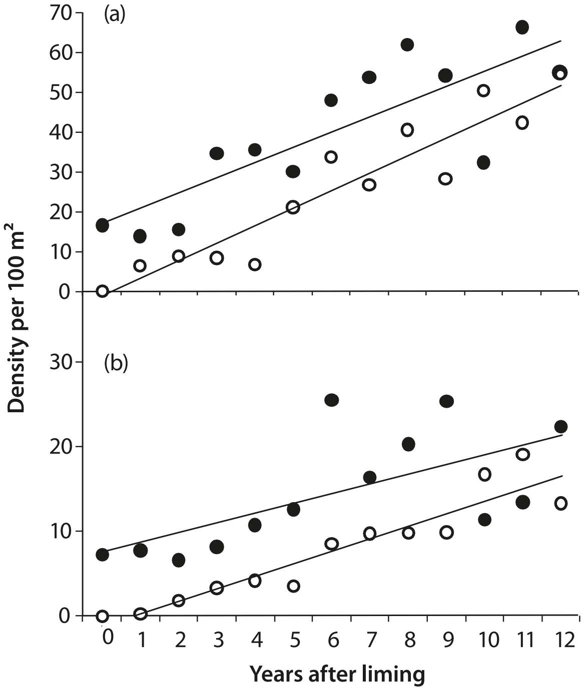


Fig. 2. Annual mean densities of Atlantic salmon fry (*a*) and parr (*b*) in limed rivers with formerly reduced (solid circles) and formerly lost (open circles) salmon stocks, 1 year prior to liming and 12 years after liming. Equations: fry, reduced = 3.82 years + 13.30; fry, lost = 4.43 years – 5.52; parr, reduced = 1.17 years + 6.31; parr, lost = 1.49 years – 2.67.

sticklebacks (*Pungitius pungitius*), brook trout (*Salvelinus fontinalis*), and European flounders (*Platichthys flesus*) were occasionally caught in some of the rivers.

Eleven of the study rivers are limed continually with limestone powder from dosers that are controlled by water flow and pH below the liming sites (e.g., Clair and Hindar 2005). In the remaining two river systems, the liming is carried out by lake treatment (Table 1). The liming has usually produced a satisfactory water quality in all rivers, with annual mean values ± standard deviation (SD) of pH (6.33 ± 0.14; $n = 34$) and concentrations of inorganic toxic aluminum (7 ± 4 μg·L^{-1}; $n = 34$), based on data from the three last years of the study period, i.e., from 2003 to 2005 (cf. Anonymous 2004, 2005, 2006).

Seven of the study rivers have been regularly stocked with Atlantic salmon since liming commenced, including rivers with either reduced ($n = 4$) or lost stocks ($n = 3$) (Table 1). In one river, stocking was only carried out above the salmon ascent stretch. Stockings mainly involved fry, which were unfed except in Mandalselva. Roe have been planted on a large scale in Tovdalselva and Mandalselva, while smolts have been stocked only in the latter river. Stocking involved the offspring of local strains, except in Tovdalselva and Mandalselva.

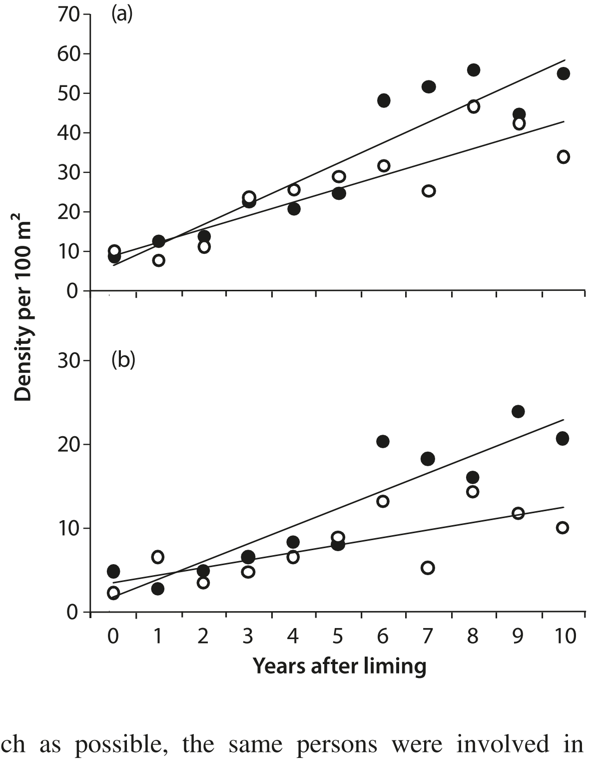
Between 1987 and 2005, young Atlantic salmon and brown trout were sampled annually using a portable backpack electrofishing apparatus (1600 V, DC). With few exceptions, sampling was performed in August to provide comparable data related to the effects of water temperature and water flow on the catchability of young salmon. As

Table 2. Annual mean densities ± standard error (SE) of Atlantic salmon fry and parr in limed rivers with formerly lost and reduced stocks, 1 year prior to liming and 1–12 years after liming.

	Fry (age 0+)		Parr (age ≥ 1+)	
Years after liming	Lost	Reduced	Lost	Reduced
0	0.2±0.2 (6)	16.8±4.6 (7)	0.0±0.0 (6)	7.3±2.0 (7)
1	6.6±1.8 (6)	14.1±5.4 (7)	0.3±0.3 (6)	7.8±2.6 (7)
2	9.2±3.9 (6)	15.7±2.2 (7)	1.9±0.7 (6)	6.7±1.7 (7)
3	8.7±2.3 (6)	34.9±10.6 (7)	3.4±0.9 (6)	8.2±1.7 (7)
4	7.0±2.2 (6)	35.7±7.4 (7)	4.2±1.9 (6)	10.8±2.1 (7)
5	21.4±8.3 (6)	30.3±6.6 (7)	3.6±1.2 (6)	12.6±2.4 (7)
6	33.9±9.0 (6)	48.3±8.8 (7)	8.5±2.6 (6)	25.5±10.2 (7)
7	26.9±6.0 (6)	53.8±12.6 (7)	9.8±3.4 (6)	16.4±4.2 (7)
8	40.8±5.5 (6)	62.1±10.6 (7)	9.8±2.7 (6)	20.4±4.4 (7)
9	28.5±5.6 (5)	54.4±7.3 (7)	9.9±3.0 (5)	25.4±6.2 (7)
10	50.7±20.4 (4)	32.6±13.0 (4)	16.8±8.3 (4)	11.5±3.7 (4)
11	42.6±2.2 (4)	66.6±24.0 (2)	19.2±10.3 (4)	13.5±7.1 (2)
12	54.8±7.2 (3)	55.2±1.9 (2)	13.3±5.5 (3)	22.4±1.4 (2)

Note: Number of rivers sampled is given in parentheses.

Fig. 3. Annual mean densities of Atlantic salmon fry (*a*) and parr (*b*) in limed rivers with formerly reduced and lost salmon stocks, 1 year prior to liming and 10 years after liming. Solid circles represent rivers with hatchery stocking; open circles represent rivers without hatchery stocking. Equations: fry with stocking = 3.39 years + 5.63; fry without stocking = 5.20 years + 1.31; parr with stocking = 2.12 years – 0.38; parr without stocking = 0.91 years – 2.59.



much as possible, the same persons were involved in the sampling throughout the study period. Between 6 and 20 sampling stations were established in each river, in which sampling areas were usually about 100–150 m^2. Each station was fished in an upstream direction in three successive runs. After each run, the fish were measured for total length to the nearest millimetre and kept in cages for release after the final run. Some specimens were retained for age analysis. The fish were classified as either fry (age 0+) or older parr (age ≥ 1+) on the basis of the length–frequency distribution and age analysis. The dominant lengths in these two age groups usually ranged between 50–65 mm and 75–130 mm, respectively. In each river, we estimated separate probabilities of capture for each age group by compiling the catch data from all stations for each run. This is recommended when the total catch on each station is fewer than 35 specimens (Bohlin et al. 1989), as was largely the case in the study rivers. Finally, we estimated annual mean densities per 100 m^2 for all rivers during the study period and separated them into those with formerly lost or reduced stocks. We used data on density from 1 year before liming and 8–12 years after liming started (Table 1). A total of 56 072 fry (age 0+) and 20 332 older parr (age ≥ 1+) were caught during the study period. We performed analysis of covariance (ANCOVA) to reveal relationships between salmon densities and time after liming (years) and population status (seriously reduced or exterminated), as well as for potential effects of hatchery stocking and hydro development.

The annual official rod catch statistics of Atlantic salmon were taken to indicate adult salmon abundance in the study rivers. These data have been available for Norwegian salmon rivers since 1876 (Hansen 1986; L'Abée-Lund et al. 2006; Vøllestad et al. 2009). The data were used to evaluate the development of adult salmon stocks in the study rivers and to compare them with total catches of Atlantic salmon in all Norwegian rivers.

Results and discussion

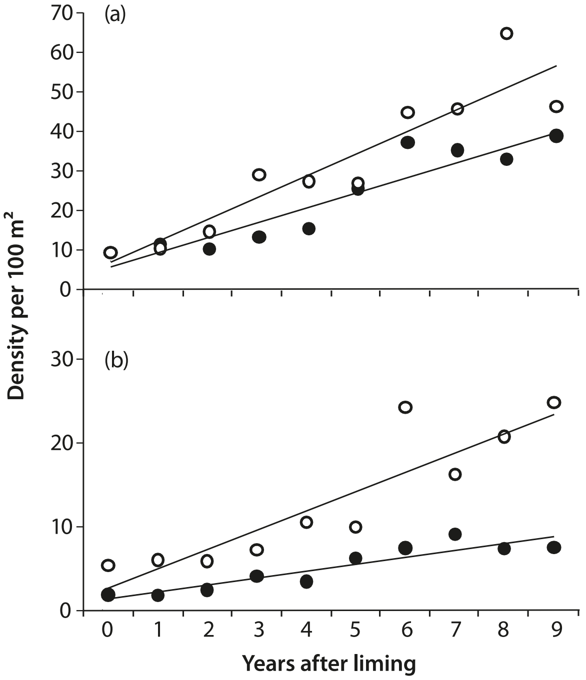
No salmon fry were caught during the electrofishing surveys in the study rivers where populations had been reported to be extinct before liming, apart from three individuals in Mandalselva. These specimens were all obtained at a single station, where some limestone had been added a few years earlier. It is thus evident that the native salmon stocks in all

Table 3. Annual mean densities ± standard error (SE) of Atlantic salmon fry and parr in limed rivers with formerly lost and reduced stocks, with and without stocking, related to years after liming.

	Fry (age 0+)		Parr (age ≥ 1+)	
Years after liming	With stocking	Without stocking	With stocking	Without stocking
0	8.6±4.1 (8)	10.0±6.4 (5)	4.9±2.3 (8)	2.4±1.5 (5)
1	12.5±4.9 (8)	7.6±2.3 (5)	2.9±1.0 (8)	6.6±4.3 (5)
2	13.7±2.3 (8)	11.1±4.9 (5)	5.0±1.6 (8)	3.6±1.7 (5)
3	23.5±16.3 (5)	23.5±7.3 (5)	6.6±1.7 (8)	4.9±1.4 (5)
4	20.6±5.0 (8)	25.5±13.5 (5)	8.4±2.0 (8)	6.7±3.1 (5)
5	24.6±6.5 (8)	28.8±9.3 (5)	8.1±1.8 (8)	9.0±4.2 (5)
6	48.0±7.3 (8)	31.5±11.3 (5)	20.4±9.0 (8)	13.3±6.2 (5)
7	51.6±11.2 (8)	25.2±7.0 (5)	18.3±3.5 (8)	5.4±1.3 (5)
8	55.9±10.2 (8)	46.5±7.1 (5)	16.2±3.9 (8)	14.4±5.0 (5)
9	44.5±7.0 (7)	42.2±11.9 (5)	24.0±6.9 (7)	11.9±3.0 (5)
10	54.8±27.5 (3)	33.8±10.7 (5)	20.8±10.4 (3)	10.1±2.9 (5)
11	41.6±0.0 (1)	52.3±9.7 (5)	48.3±0.0 (1)	11.1±3.5 (5)
12	48.2±0.0 (1)	56.7±4.6 (4)	22.2±0.0 (1)	15.7±4.6 (4)

Note: Number of rivers sampled is given in parentheses. Statistical tests were performed only if ≥3 rivers were present in each group (e.g., up to 10 years after liming; cf. Fig. 3).

Fig. 4. Annual mean densities of Atlantic salmon fry (*a*) and parr (*b*) in limed rivers with formerly reduced and lost salmon stocks, 1 year prior to liming and 9 years after liming, grouped into rivers with hydro development (solid circles) and rivers without hydro development (open circles). Equations: fry without hydro development = 5.54 years + 1.25; fry with hydro development = 3.77 years +1.98; parr without hydro development = 2.30 years + 0.39; parr with hydro development = 0.82 years + 0.51.



these rivers had been wiped out before liming commenced. Fry were found in all rivers with formerly lost stocks 1 year after liming started, except for the first 2 years in Lygna. Fry densities in both formerly lost and reduced salmon stocks remained low and unchanged during the first years after liming started (Fig. 2*a*). For these two status categories, 5 and 3 years of liming, respectively, was needed to obtain a significant increase in fry density ($p < 0.05$ and $p < 0.01$, respectively). There was a significant effect of both time after liming and population status on density throughout the study period (ANCOVA, $F_{[2,23]} = 51.220$, $R^2 = 0.801$, $p < 0.0001$). After 12 years of liming, mean fry densities in rivers with formerly lost or reduced stocks were 55 specimens per 100 m^2 for both categories (Table 2). However, the rates of increase in fish density in these two categories were not significantly different ($F_{[1,22]} = 0.445$, $p = 0.511$).

Parr densities also remained low during the first 3–5 years after the start of liming (Fig. 2*b*). For formerly lost and reduced salmon stocks, 3 and 5 years of liming, respectively, was needed to obtain a significant increase in parr densities (both $p < 0.05$). Both time after liming and population status had a significant effect on their densities (ANCOVA, $F_{[2,23]} = 28.551$, $R^2 = 0.690$, $p < 0.0001$). After 12 years of liming, mean parr densities in rivers with formerly lost or reduced stocks reached 13 and 22 specimens per 100 m^2, respectively (Table 2). However, the rates of increase in parr density in these two categories were not significantly different ($F_{[1,22]} = 0.549$, $p = 0.467$). The linear relationship between parr density and time (years) suggests that production rates are still below the carrying capacity of the rivers. We therefore expect their densities to continue to increase in the near future. Parr density of about 30 individuals per 100 m^2 have been found in some rivers that have been limed for about 20 years (B.M. Larsen, unpublished data). Such levels of parr abundance may indicate a stage close to full recovery. A somewhat more rapid restoration of young Atlantic salmon populations was found after rotenone treatment in some Norwegian rivers in which stocks had been wiped out by outbreak of *G. salaris* (Johnsen and Jensen 2003).

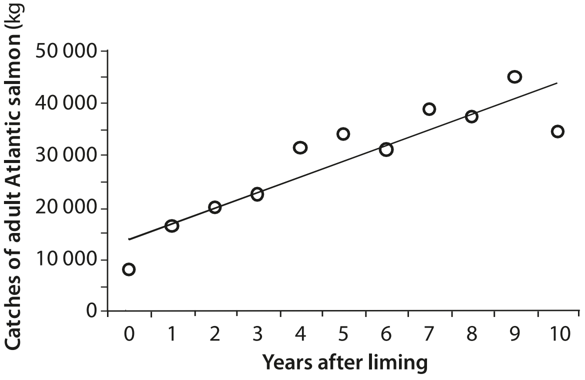
Separate analyses of the potential effects of hatchery stocking show that the rates of increase in fry density were not significantly different in rivers with and without stocking (ANCOVA, $F_{[1,18]} = 4.041$, $p = 0.060$, time × stocking

Table 4. Annual mean densities ± standard error (SE) of Atlantic salmon fry and parr in limed rivers with formerly lost and reduced stocks of Atlantic salmon, with and without hydro development, related to years after liming.

	Fry (age 0+)		Parr (age ≥ 1+)	
Year after liming	With hydro development	Without hydro development	With hydro development	Without hydro development
0	9.2±6.6 (5)	9.2±4.1 (8)	1.8±1.1 (5)	5.3±2.3 (8)
1	11.3±6.1 (5)	10.2±3.7 (8)	1.7±0.8 (5)	6.0±2.7 (8)
2	9.9±3.8 (5)	14.4±2.8 (8)	2.3±0.7 (5)	5.8±1.7 (8)
3	13.1±6.2 (5)	28.9±10.0 (8)	4.0±1.2 (5)	7.2±1.7 (8)
4	15.1±6.4 (5)	27.1±8.3 (8)	3.4±1.0 (5)	10.5±2.1 (8)
5	25.3±8.7 (5)	26.7±6.8 (8)	6.1±1.6 (5)	9.9±2.8 (8)
6	36.9±10.2 (5)	44.6±8.6 (8)	7.4±2.2 (5)	24.1±9.0 (8)
7	35.0±8.7 (5)	45.4±12.2 (8)	9.0±1.7 (5)	16.1±4.2 (8)
8	32.8±7.0 (5)	64.5±7.3 (8)	7.3±1.6 (5)	20.6±3.7 (8)
9	38.6±10.3 (4)	46.1±7.8 (8)	7.4±1.5 (4)	24.8±5.7 (8)
10	16.5±9.3 (2)	50.1±13.9 (6)	5.2±2.1 (2)	17.1±5.2 (6)
11	43.9±0.0 (1)	51.9±9.8 (5)	4.4±0.0 (1)	19.9±7.7 (5)
12	(0)	55.0±4.0 (5)	(0)	17.0±3.8 (5)

Note: Number of rivers sampled is given in parentheses. Statistical tests were performed only if ≥3 rivers were present in each group (e.g., 9 years after liming; cf. Fig. 4).

Fig. 5. Total mass (kg) of adult Atlantic salmon caught in currently limed rivers (n = 22), 1 year prior to liming and 1–10 years after liming. Equation: y = 2911.65 years + 11 356.



interaction) (Fig. 3a; Table 3). However, in a model without the interaction term, there was a significant effect of time and stocking ($F_{[1,21]}$ = 41.729, R^2 = 0.771, p < 0.001), suggesting that fry densities were higher in stocked rivers. However, the rates of increase in parr density were significantly different in stocked rivers than those with no stocking ($F_{[1,18]}$ = 8.818, p = 0.008, time × stocking interaction) (Fig. 3b; Table 3), suggesting that parr densities increased faster with time in stocked rivers than in those without such management strategy. It has earlier been found that of the rivers with lost stocks, those that benefited from such enhancement measures during the first 5 years after liming had significantly higher fry densities than unstocked rivers (Hesthagen and Larsen 2003). On the other hand, rivers with formerly reduced stocks subjected to stockings had significantly lower salmon fry densities than rivers without such mitigation measures. This is probably because the fry-to-smolt survival rate in natural salmon stocks is low, usually only between 1% and 3% (Egglishaw and Shackley 1977). The redistribution process in such fish stocks may thus confound the effects of stocking density (Solomon 1985).

Separate analyses of the potential effects of hydro development and the rates of increase in fry density were not significantly different in unaltered and altered rivers (ANCOVA, $F_{[1,16]}$ = 3.64, p = 0.081, time × regulation interaction) (Fig. 4a; Table 4). In a model without the interaction term, there was a significant effect of time and hydro development ($F_{[1,19]}$ = 46.691, R^2 = 0.846, p < 0.001), suggesting that fry density was higher in unaltered rivers. However, the rates of increase in parr density were significantly different in unaltered and altered rivers ($F_{[1,16]}$ = 12.653, p < 0.005, time × regulation interaction) (Fig. 4b; Table 4), suggesting that parr densities increased faster with time in unaltered rivers than in those with hydro development. Lower fish densities in rivers subjected to hydro development may be related to such factors as barriers to upstream migration of adults and increased mortality due to such factors relating to passage through hydropower turbines and stranding (Hvidsten and Johnsen 1997; Saltveit et al. 2001; Thorstad et al. 2005).

Official rod catch statistics of Atlantic salmon showed that the study rivers had annual yield of between 5 and 8 t before liming. There has been a significant increase in the catch of adult salmon taken in all limed rivers (n = 22), reaching nearly 45 t after 10 years of treatment ($F_{[1,9]}$ = 31.541, R^2 = 0.750, p < 0.0001) (Fig. 5). This is equivalent to 11%–12% of the total catch of wild salmon in all Norwegian rivers in recent years. The total number of angling hours have changed substantially after liming; however, the records prior to liming are defective (Mauland 2003). We suggest that rivers with no naturally produced salmon were mainly either colonized by strays from nearby rivers or by cultured fish from relatively extensive stockings in some of the rivers (cf. Table 1). The contribution of escaped farmed fish is low because the region has few aquaculture facilities. This was expected because there is a significant positive correlation between the incidence of escaped farmed salmon in rivers at the county level and the intensity of salmon farming (Fiske et al. 2006). Between 1998 and 2004, the fraction of farmed fish in the sport fishing catches of Atlantic salmon on a national level ranged between about 5% and 9%, except for a higher number in one year. The occurrence of escaped fish has been studied in more detail in the rivers Mandalselva and Tovdalselva, and between 2000 and 2005, they contributed between 1% and 4% of all adult salmon in sport fishing catches (Johnsen 2008).

All of the highly acidified and larger salmon rivers in southernmost Norway with either lost or reduced stocks of Atlantic salmon are now being limed. An exception is Otra, where catches of Atlantic salmon increased considerably from the mid-1990s to 2005 (Kroglund et al. 2008*a*). First, an industrial pollution effluent was removed from the river in 1995, which highly improved the water quality. Secondly, low parr density and genetic studies suggest that most of the adult salmon caught in Otra were produced in neighouring rivers. Although there have been an increasing number of self-reproducing salmon in Otra from 1995 to 2005, the river cannot be used as a reference. In addition to our limed rivers, Atlantic salmon have suffered to some extent from acidification in some 20 smaller rivers, which are not yet limed. These rivers are mainly located in the southwestern and western parts of Norway. Official rod catch statistics of Atlantic salmon exist for 14 of these rivers. An analysis based on data during the last 11 years of the study period for these rivers, i.e., from 1996 to 2005, showed a significant increase in three salmon stocks only; Dirdalselva ($p < 0.005$), Daleelva in Vaksdal ($p < 0.05$), and Daleelva in Høyanger ($p < 0.05$). The catch in Dirdalselva made up a large proportion of the total catch in these 14 rivers, being 1624 kg out of a total of 4412 kg in 2005. In upper part of the catchment area of this river, there is a lake-liming project, with a possible effect on the water quality on the salmon rearing stretch. Furthermore, the Dirdalselva is located close to two limed rivers, from which it may receive strays. In Daleelva in Vaksdal, large-scale stockings have been carried out. Thus, we conclude the natural recovery in Atlantic salmon stocks in unlimed acidified rivers in southern Norway has been limited.

In recent years, major reductions in fossil fuel emissions have improved water quality in previously acidified waters (Skjelkvåle et al. 2003, 2005). However, water quality in unlimed reaches of the study rivers is still inadequate for the survival of smolts of Atlantic salmon, which is the most sensitive stage (Kroglund et al. 2001, 2007, 2008*b*). These rivers therefore still need to be limed to sustain healthy populations of Atlantic salmon and probably will continue to be needed for many years to come. We therefore regard liming as the only reason why salmon in the study rivers have exhibited a significant increase in catch in recent years. In southern Norway, these rivers are located in the only region in which salmon stocks have developed positively from 1989 to 2004 (Fiske et al. 2006; Vøllestad et al. 2009). Salmon stocks in western Norway neighboring the limed rivers furthest north have suffered a pronounced reduction in abundance in recent years. However, catches in some salmon rivers in northern Norway have demonstrated positive trends, on the basis of data until 2000–2002 (L'Abée-Lund et al. 2006; Vøllestad et al. 2009).

The yield of Atlantic salmon in limed rivers with 40–45 t is now making an important contribution to total Norwegian catches. We expect that catches in these rivers will continue to increase to more than 70 t after about 20–25 years of liming. This is equivalent to the mean annual catches of salmon for the 5 years with the highest historical catches in the study rivers (cf. Hesthagen and Hansen 1991). River catches by anglers are indirect but robust indices of salmon abundance (L'Abée-Lund et al. 2006). However, historical records tended to underestimate catches in comparison with present-day statistics. Historical catches were therefore somewhat higher than the predicted maxima in the limed rivers. This may be due to the fact that several of the limed rivers have been subjected to substantial physical encroachments through hydropower development, which has reduced their salmon production capacity in spite of their satisfactory water quality.

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