Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2015) **86**, 92–104
doi:10.1111/jfb.12542, available online at wileyonlinelibrary.com

Water discharge affects Atlantic salmon *Salmo salar* smolt production: a 27 year study in the River Orkla, Norway

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(Received 2 June 2014, Accepted 9 September 2014)

A model that explains 48% of the annual variation in Atlantic salmon *Salmo salar* smolt production in the River Orkla, Norway, has been established. This variation could be explained by egg deposition, minimum daily discharge during the previous winter and minimum weekly discharge during the summer 3 years before smolt migration. All coefficients in the model were positive, which indicates that more eggs and higher minimum discharge levels during the winter before smolt migration and the summer after hatching benefit smolt production. Hence, when the spawning target of the river is reached, the minimum levels of river discharge, in both winter and summer, are the main bottlenecks for the parr survival, and hence for smolt production. The River Orkla was developed for hydropower production in the early 1980s by the construction of four reservoirs upstream of the river stretch accessible to *S. salar*. Although no water has been removed from the catchment, the dynamics of water flow has been altered, mainly by increasing discharges during winter and reducing spring floods. In spite of the higher than natural winter discharges, minimum winter discharge is still a determinant of smolt production. Hence, in regulated rivers, the maintenance of discharges to ensure that they are as high as possible during dry periods is an important means of securing high *S. salar* smolt production.

Key words: egg deposition; hydropower regulation; smolt abundance; smolt age; water flow; water temperature.

INTRODUCTION

The freshwater production of Atlantic salmon *Salmo salar* L. 1758 varies considerably throughout its distribution, depending on the physical, chemical and biological characteristics of each river (Symons, 1979). Within each river, a number of environmental factors may affect production, such as river discharge, water temperature, water chemistry, feeding opportunity and the degree of interspecific and intraspecific competition at different times of the year (Egglishaw & Shackley, 1985). The average production, when studied over years, may be denoted by the carrying capacity of the river, given a sufficient spawning escapement to meet the egg deposition target maximizing the production of smolts (Solomon, 1985; Chaput *et al.*, 1998).

Although the mortality of *S. salar* is usually density dependent in fresh water (Jonsson *et al.*, 1998), density-independent mortality may occur under special

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*Author to whom correspondence should be addressed. Tel.: +47 91661101, email: arne.jensen@nina.no environmental conditions. The earliest life stages (eggs and alevins) of salmonids are probably the most vulnerable to floods (Jensen & Johnsen, 1999). In extreme conditions, parr may also become exposed to a risk of mortality that is considerably higher than normal, for instance during summer droughts (Elliott, 1994), winter droughts (Gibson & Myers, 1988) or extremely high flood events (Allen, 1951; Elwood & Waters, 1969; Seegrist & Gard, 1972). In fact, even when the variations in winter discharge are modest, the survival of *S. salar* parr has been shown to decrease with decreasing discharge (Gibson & Myers, 1988; Hvidsten, 1993; Cunjak *et al.*, 1998).

Variations in water temperature, both annual and seasonal, influence the whole ecosystem of a river, including invertebrate production, and hence the food supply and growth of fishes. Although many factors may influence this growth, it is generally accepted that water temperature, fish size and level of energy intake (ration size) are the three most important variables (Brett *et al.*, 1969; Elliott, 1975*a*, *b*, 1994). The optimum temperature for the growth of *S. salar* parr has been estimated between 16 and 20° C, at both maximum and reduced rations (Jonsson *et al.*, 2001). The transformation from parr to smolt in *S. salar* is partly size dependent (Økland *et al.*, 1993), so in years of slow growth, some parr have to remain in the river for one additional year before they reach the size necessary to smolt. In the meantime, they occupy habitats in the place of younger individuals, who in turn fail to survive, so a slow growth rate during the parr stage increases the mean smolt age.

Environmental factors such as water discharge and water temperature are usually independent of human activities, although global climate change now implies changes in water temperatures and river discharges throughout the distribution area of *S. salar*, which in turn affects the entire life cycle of this species (Todd *et al.*, 2011). In regulated rivers, however, both factors can be manipulated, in favour as well as in disfavour of *S. salar* production. Streams regulated for hydropower, defined as lotic reaches downstream of dams, collectively exhibit a range of environmental alterations attributable to impoundments (Ward & Stanford, 1979). In such rivers, water masses are normally stored in reservoirs during periods of high discharge, and released in periods when electricity is required, usually during winter. In this way, the annual flow regime and hence water temperatures may be considerably altered, which in northern rivers usually involves increased winter discharge and reduced spring floods.

The *S. salar* in the River Orkla, central Norway, is one of the largest populations in this country. A total of 90 km of this river is available to anadromous salmonids (*S. salar* and brown trout *Salmo trutta* L. 1758) and annual reported catches of *S. salar* by recreational anglers have reached 36 t (Statistics Norway, 2014). During the period 1983–2011, with the exception of 2 years (1989 and 2003), *S. salar* smolt production was estimated upstream of Meldal (*i.e.* the upper 48 km of the river stretch accessible to anadromous salmonids). Earlier, Hvidsten & Ugedal (1991) and Hvidsten (1993) analysed some of these data (1983–1991), and by using an index for the lowest daily water discharges for the three winters prior to smolt descent, they demonstrated a positive relationship between smolt density and minimum winter discharge. Since that time, smolt data for 19 additional years (1992–2011) have been available for analysis. In this study, the relationship between minimum winter discharge and smolt production has been re-analysed to identify in more detail at which stage juveniles were most vulnerable to low winter discharges. Also, the annual variation in smolt production was analysed in relation to summer discharge, water chemistry (phosphorus concentration), smolt age and egg deposition. A multiple regression model was developed to describe

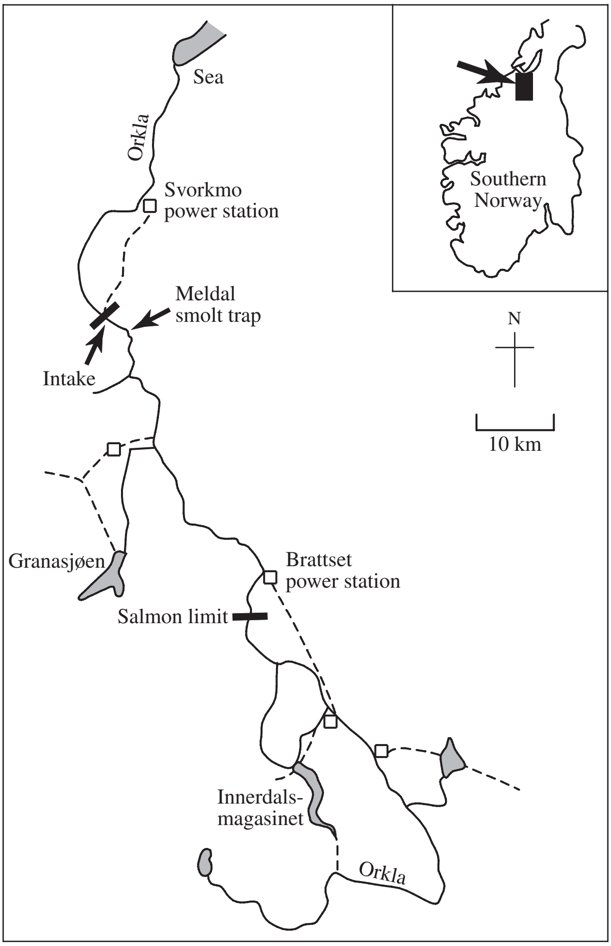

FIG. 1. The River Orkla with the smolt study area (the stretch of river from the smolt trap at Meldal to the uppermost location accessible to *Salmo salar*), the power stations (☐) and the reservoirs (▨).

quantitatively the relative importance of these environmental and biological factors for smolt production.

MATERIALS AND METHODS

STUDY AREA

The River Orkla is located at 63° N; 10° E in central Norway, has a catchment area of 3092 km^2 and drains into the sea *via* the fjord Trondheimsfjorden (Fig. 1). The reported mean annual catch of *S. salar* during the period 1980–2012 was 16 t (Statistics Norway, 2014), which consists of grilse, two sea-winter (SW) and three SW fish. Most *S. salar* are 3 or 4 years old when they smolt and migrate to sea during a 1 month period in spring, mainly in May (Hvidsten *et al.*, 1995).

The river was developed for hydroelectric purposes in the early 1980s, and since 1983, the flow of water in *c*. 39% of the catchment has been under human control. A total of four reservoirs have

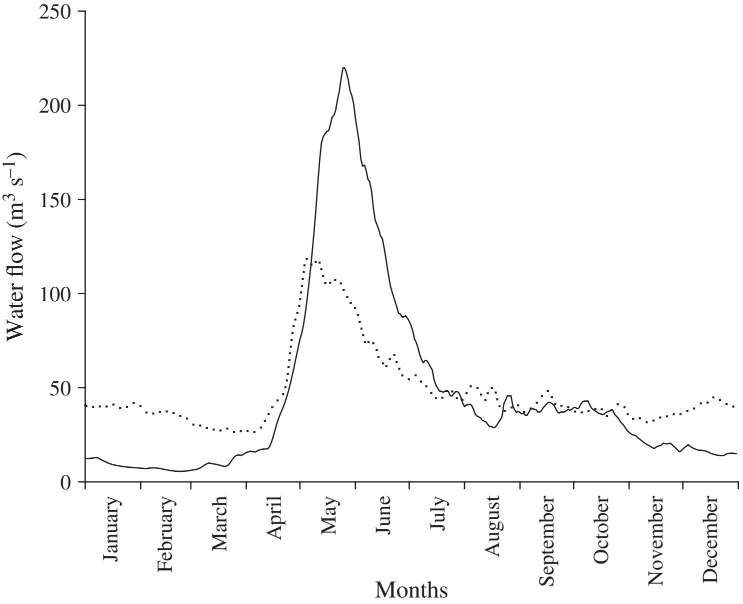

FIG. 2. Annual fluctuations of mean discharge in the River Orkla at Meldal (St. 121.22.0.1001.0 Syrstad) before (____, 1940–1982) and after (......., 1983–2011) the hydropower-related regulation of the discharge. Data from the Norwegian Water Resources and Energy Directorate (NVE).

been constructed, two of which (Innerdalsmagasinet and Granasjøen) are artificial, for which farmland was flooded as part of the impoundment (Fig. 1). All reservoirs are located upstream of the river stretch accessible to *S. salar*, and no water has been removed from the catchment. The mean annual discharge in the River Orkla at Meldal during the period 1940–2012 was 48 $m^3 s^{-1}$, increasing to 66 $m^3 s^{-1}$ at the outlet to the sea at Orkanger. Because of this regulation, the water flow has been considerably reduced during early summer (May to July) and increased during winter (November to April) (Fig. 2), which has affected water temperatures. Before implementation of the hydropower regulation, the natural winter discharge (1 January to 30 April) could be as low as 1–2 $m^3 s^{-1}$ at Meldal, and the mean daily discharge during winter was 8·8 $m^3 s^{-1}$. The guidelines associated with the Royal Resolution of 16 June 1978, by which permission was granted by the Norwegian Government to regulate the River Orkla for hydropower development, requested a minimum winter flow of 10 $m^3 s^{-1}$ at Brattset. Over the first 29 years after the implement of the hydropower regulation, the mean minimum flow was 15·3 $m^3 s^{-1}$ (Table I). The new flow regime reduced the water temperature by 1–1·5° C during the summer. In the uppermost 4 km of the river stretch accessible to *S. salar* [upstream of the outlet of the Brattset power station (Fig. 1)], the rate of discharge has been reduced to 0·5 $m^3 s^{-1}$ during winter, which contrasts with the minimum flow of 10 $m^3 s^{-1}$ as requested by the Norwegian Government further downstream.

ESTIMATION OF SMOLT PRODUCTION

Smolt production of *S. salar* was estimated by a mark and recapture method. First, presmolts (individuals > 110 mm natural tip length) were captured during March to April using electrofishing gear, marked by fin clipping, and released again within 60 min in the same area as they had been caught. Observed mortality before release was <1%. Second, descending smolts were captured at Meldal, situated 35 km upstream from the sea (Fig. 1), using net traps (1983–2011) and rotary screw traps (2002–2011). In this river, *S. salar* smolts migrate to sea mainly during the darkest part of the night (Hvidsten *et al.*, 1995), so the traps were operated each night from 22

TABLE I. Sampling year, minimum daily winter discharge (Q_{W1day}, $\mathrm{m}^3\ \mathrm{s}^{-1}$), average minimum winter discharge over 7 days (Q_{W7days}, $\mathrm{m}^3\ \mathrm{s}^{-1}$), average maximum discharge over 7 days during June (Q_{J7days}, $\mathrm{m}^3\ \mathrm{s}^{-1}$), average minimum discharge over 7 days during summer (Q_{S7days}, $\mathrm{m}^3\ \mathrm{s}^{-1}$), river-water concentrations of phosphorus (geometric mean, $\mu\mathrm{g\ l}^{-1}$), mean *Salmo salar* smolt age (years ± 95% C.I.) and egg deposition (eggs m^{-2}, 4 years displaced) for the period 1983–2011

	Discharge						
Year	Q_{W1day}	Q_{W7days}	Q_{J7days}	Q_{S7days}	Phosphorus ($\mu\mathrm{g\ l}^{-1}$)	Mean smolt age (years)	Egg deposition (eggs m^{-2})
1983	11·05	11·20	87·54	18·93	6·58	3·04 ± 0·02	2·74
1984	16·12	17·52	117·92	29·25	6·84	3·08 ± 0·02	4·26
1985	17·53	21·37	59·53	26·80	6·54	3·51 ± 0·04	4·15
1986	14·29	14·74	94·57	30·75	7·25	3·54 ± 0·04	4·88
1987	14·81	15·03	103·46	46·12	9·29	3·61 ± 0·03	3·65
1988	16·42	16·97	66·99	15·97	6·22	3·52 ± 0·04	3·96
1989	21·72	25·38	106·39	18·36	5·31	–	4·88
1990	22·36	22·82	93·89	21·86	4·92	3·75 ± 0·02	5·90
1991	18·68	20·49	168·60	16·03	4·89	3·76 ± 0·02	10·87
1992	14·29	19·37	90·16	18·54	2·39	3·54 ± 0·03	3·13
1993	12·31	12·72	68·94	36·00	2·93	3·43 ± 0·03	6·46
1994	15·87	15·87	86·07	18·70	5·50	3·62 ± 0·02	5·47
1995	19·27	19·62	278·12	16·82	5·64	3·48 ± 0·03	3·40
1996	8·63	8·81	130·03	14·93	5·05	3·30 ± 0·03	5·02
1997	19·04	19·79	304·96	18·32	5·88	3·80 ± 0·02	2·76
1998	15·39	17·11	73·10	25·18	4·27	3·81 ± 0·03	1·50
1999	12·07	22·79	45·57	17·22	3·95	3·75 ± 0·03	4·88
2000	15·87	16·32	110·27	17·02	4·09	3·78 ± 0·04	5·76
2001	13·55	14·61	40·68	23·16	4·82	3·34 ± 0·04	1·94
2002	19·12	19·76	55·87	15·04	3·04	3·28 ± 0·03	0·89
2003	8·69	10·57	41·96	14·39	5·63	–	1·61
2004	18·72	20·15	69·63	19·07	5·26	3·31 ± 0·04	3·44
2005	15·87	25·30	117·13	27·12	–	3·09 ± 0·02	3·83
2006	13·67	15·31	42·15	11·73	–	3·62 ± 0·04	6·32
2007	14·26	26·24	77·80	26·95	–	3·73 ± 0·04	6·70
2008	15·38	18·00	73·76	16·62	4·55	3·84 ± 0·04	4·50
2009	12·13	13·95	49·55	25·35	4·00	3·67 ± 0·05	2·50
2010	9·59	11·42	117·42	21·31	6·28	3·26 ± 0·05	5·00
2011	17·62	19·30	164·84	43·69	6·93	3·71 ± 0·06	3·10

April to 15 June each year, except for some nights with high discharge, when the traps were blocked with debris.

The proportion of tagged smolts in the trap catches was used to estimate smolt production [defined as the number of smolts (N) in the river at the time of tagging using the Peterson estimator with Chapman correction (Ricker, 1975): $N = (M + 1)\ (C + 1)\ (R + 1)^{-1}$, where M is the number of tagged fish, C is the total catch of smolts in the traps and R is the number of tagged fish recaptures in the traps]. Smolt production was estimated over a 48 km stretch upstream of Meldal, *i.e.* upstream of the only hydropower tunnel intake in the part of the river accessible to *S. salar* (Fig. 1). The wetted river area was estimated at 3 050 000 m^2, and the estimated smolt numbers were recalculated to give the number 100 m^{-2}, without correcting for variation in flow. All sampling was performed after the flow regulation was implemented.

EXPLANATORY VARIABLES

The environmental variables that could help explain annual variation in smolt production include discharge characteristics (several different metrics from both summer and winter flows), water chemistry (phosphorus concentration), smolt age (as a proxy for water temperature) and egg deposition.

The influence of winter discharge can be quantified in different ways; in this study, the lowest mean daily as well as weekly discharges between 1 January and 30 April were used (Table I). The maximum weekly discharge during June and the minimum weekly discharge during summer (1 July to 30 September) were also tested for its possible influence on survival during the swim-up and juvenile stages, respectively (Table I). All discharge variables were also tested with time lags from 1 to 4 years before smolt migration, to evaluate at which juvenile stage in the life cycle any bottleneck might have occurred. Discharges were recorded by the Norwegian Water Resources and Energy Directorate (NVE).

The concentrations of phosphorus in the river water (in $\mu g\ l^{-1}$) were measured at Meldal by the Norwegian Institute for Water Research according to Standards Norway (NS 4724:1984) between four and 12 times each year (except in 2005–2007). These data were not normally distributed, and to dampen the effect of some extreme values, annual geometric mean values were used in the analyses (Table I).

The egg deposition upstream of Meldal was estimated by counting ascending adult *S. salar*, gathering catch statistics including frequencies of females, and by estimating fecundity, expecting the frequency of females to be similar among spawners as in the catches. Between 1994 and 2011 (except 1995), the annual numbers of ascending adult *S. salar* were determined using a Logie fish counter (produced by Aquantic Ltd; www.aquantic.com), located close to the intake of the Svorkmo power station, 2 km downstream of the sampling site for smolts (Fig. 1). During the periods with good visibility, the Logie counter was calibrated with video cameras, and all counts were adjusted accordingly. To obtain the numbers of ascending *S. salar* during 1979–1993 and 1995, regression between the Norwegian Official Catch Statistics (Statistics Norway) in 1994 and 1996–2002 (from 2002 onwards, the collection of data was reorganized, so later years were omitted) and the number of ascending fish was established using the following equation: $Y = 3{\cdot}01\ X + 2200$ ($n = 8$, $r^2 = 0{\cdot}92$, $P < 0{\cdot}001$), where Y = number of ascending *S. salar* and X = number of caught *S. salar*. The counter did not differentiate between *S. salar* and *S. trutta*, and the total count was reduced according to the proportion of *S. trutta* reported by anglers each year (2·5–13·9%). The predominant mass range of female *S. salar* spawners in the River Orkla was 3–7 kg. The mean number of eggs was estimated at 1522 (1104–2518) kg^{-1} fish mass ($n = 32$). The deposition of eggs was weighted according to the proportion of 3 and 4 year-old smolts in each smolt cohort (Table I).

STATISTICAL METHODS

Smolt production was modelled by a multivariate linear regression model, where the best model was found by a single term deletion procedure from the full model and the distribution of the residuals checked by normal quantile plots. The smolt production residuals were analysed for possible autocorrelation by the partial autocorrelation function (Wei, 2005). To avoid overfitting, the multivariate models were validated by a full cross-validation (Hair *et al.*, 1998). A full cross-validation procedure leaves out one observation (year) at the time from the data set, fits the model to the remaining observations and then predicts the smolt production for the left-out observation. The predictive performance of the model can then be evaluated by the squared correlation between the observed response values and the cross-validation predictions. All statistical analyses were performed by the statistical computing language R (www.r-project.org).

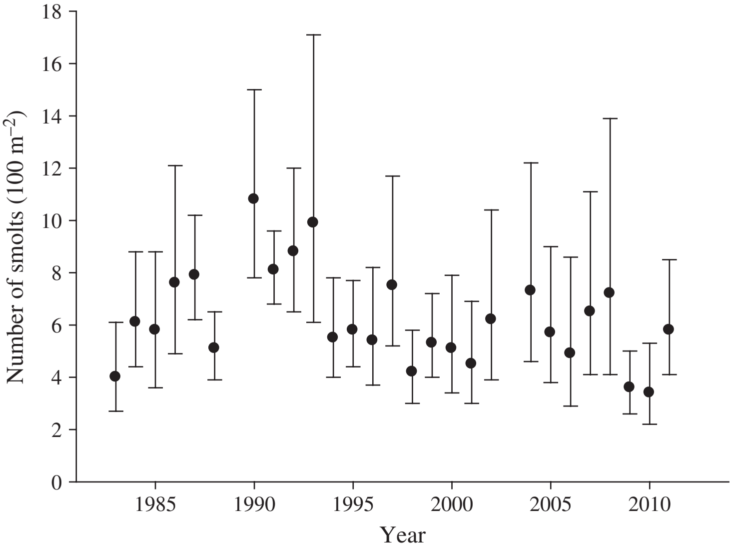

FIG. 3. Estimated population densities of *Salmo salar* smolts in the River Orkla during the period 1983–2011. Vertical bars are 95% C.I.

RESULTS

Annual *S. salar* smolt production varied between 3·4 and 10·8 smolts 100 m^{-2} (Fig. 3), and the mean ± S.D. annual smolt density was estimated at 6·2 ± 1·8 individuals 100 m^{-2} ($n = 27$).

The best model for predicting smolt population density was the following model with three variables: egg deposition weighted according to annual smolt age distribution, minimum daily discharge during the previous winter and minimum weekly discharge during the summer 3 years before smolt migration, *i.e.* the first summer for the 3 year-old smolts (Table II). No significant partial autocorrelation in the smolt production residuals was found; the partial autocorrelation with lag 1 year was as low as 0·1.

Comparing predicted and estimated smolt densities (Fig. 4), the model explained 48% of the variation in annual smolt production, although the cross-validation procedure indicated that the model's predictive ability was somewhat lower. The coefficient of determination between the observed response values and the cross-validation predictions was 0·32. The distribution of the residuals corresponded well with the

TABLE II. Estimated ± S.E. coefficients for the different variables in the *Salmo salar* smolt production model

Variable	Estimate ± S.E.	*t*-value	*P* (>|*t*|)
Intercept	1·324 ± 1·758	0·75	>0·05
E_D	0·506 ± 0·201	2·52	<0·05
Q_{W1day}	0·249 ± 0·089	2·80	<0·05
Q_{S7days}	0·074 ± 0·035	2·13	<0·05

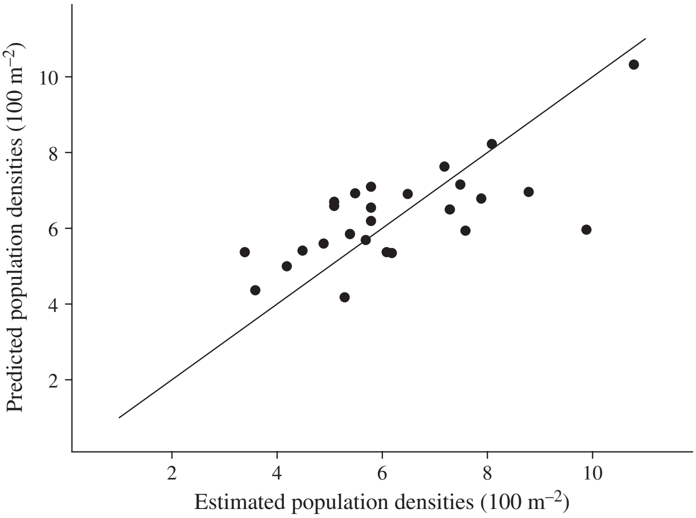

Fig. 4. Comparison between estimated population densities of *Salmo salar* smolts in the River Orkla during the period 1983–2011, and densities predicted by the smolt production model in the same period.

theoretical normal quantiles, except for the smolt production in 1993, where the model prediction was much lower than the observed value (the point at 9·90 and 5·95 in Fig. 4). If the 1993 data are omitted, the model will explain 63% of the variation in annual smolt production.

The three explanatory variables have low pair-wise correlations, all < 0·23 in absolute value, and can be assumed to be relatively independent of each other, a property that simplifies interpretation of the model.

Two examples can illustrate the variation in smolt production with changing egg deposition and discharge. If it is assumed that the two discharge variables are held constant, the model predicts that an increase in egg deposition with 1 egg m^{-2} will increase smolt production by 0·5 smolt 100 m^{-2}. Alternatively, if the minimum daily discharge decreases from its mean value (15·3 m^3 s^{-1}) to the minimum winter discharge of 10 m^3 s^{-1} as required by the Norwegian Government, and the two other explanatory variables are held constant, the predicted smolt production will decrease by 1·3 smolt 100 m^{-2}.

The probable effect of the hydropower regulation on smolt production in the River Orkla upstream Meldal is illustrated in Fig. 5, by predicting smolt production for the period 1973–2011 (*i.e.* 10 years before and 29 years after the implementation of the hydropower regulation), holding egg deposition constant at its mean value of 4·4 eggs m^{-2} for the period 1983–2011. The mean predicted values increased from 3·0 smolts 100 m^{-2} before the regulation to 6·3 smolts 100 m^{-2} after the regulation (Fig. 5). Predictions before 1983 are uncertain because of extrapolation of one of the predictor variables (winter discharge) outside the range used in modelling, but the predictions clearly suggest higher smolt production after the hydropower regulation.

DISCUSSION

In the River Orkla, 48% of the annual variation in *S. salar* smolt production could be explained by egg deposition, minimum daily discharge during the winter before smolt

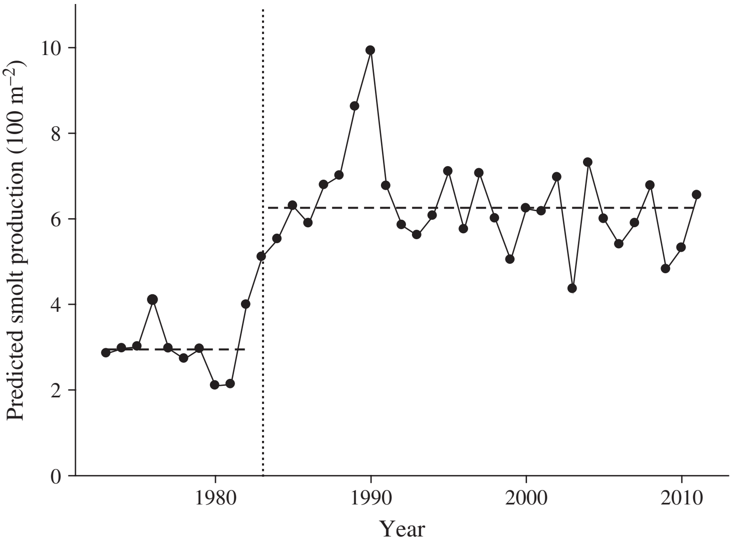

FIG. 5. Annual variation in *Salmo salar* smolt production in the River Orkla during the period 1973–2011 predicted from the smolt model, using discharge data from the Norwegian Water Resources and Energy Directorate (NVE) and setting the egg deposition to be constant at 4·4 eggs m^{-2}. ...., the date when the regulation was implemented; ----, mean predicted values for smolt production before (1973–1982) and after the hydropower regulation (1983–2011).

migration and minimum weekly discharge during the summer 3 years before smolt migration. All coefficients in the model are positive, which indicate that more eggs and higher minimum discharge during the last winter before smolt migration and the first summer after hatching benefit smolt production.

The inclusion of egg deposition in the model suggests that, in some years, this variable was below the target that maximizes the production of smolts (Solomon, 1985; Chaput *et al.*, 1998). Management of the Norwegian populations of *S. salar* is now based on performance indicators, which include spawning target (Forseth *et al.*, 2013), and the spawning target for the River Orkla has been set at 4 (3–5) eggs m^{-2} wetted area. Nests may be patchy distributed throughout the river stretch (Einum *et al.*, 2008); hence, smolt production may also increase at egg depositions higher than the spawning target. Any systematic underreporting of catches of adult *S. salar* would systematically overestimate egg deposition, and if the reported annual catch had been, for example, only 80% of the actual catch, the egg deposition would have been *c*. 7% lower than that estimated in Table I. This rather modest reduction in egg deposition would not affect the main conclusions of the paper.

The model predicts that low discharges, both in winter and summer, affect smolt production negatively. The minimum daily mean discharge during the winter before smolt migration and the minimum weekly discharge during the summer 3 years before smolt migration were the two most important environmental variables. In both cases, the model suggests increased mortality of parr in periods of low flow. This is consistent with studies undertaken in the Catamaran Brook in Canada, where a significant correlation was found between mean winter flow and survival in different juvenile stages (eggs to 0+, 0+ to 1+ and 1+ to 2+ years) of *S. salar* in five of the six winters

(Cunjak & Therrien, 1998; Cunjak *et al.*, 1998). Higher survival in winters with high discharge was attributed to the provision of a more suitable habitat (Cunjak *et al.*, 1998). In six rivers in Newfoundland and New Brunswick, Gibson & Myers (1988) studied the effects of winter and summer river discharge on the survival of eggs and age 0 year *S. salar*. For all rivers combined, survival and winter discharge were positively related. In addition, the hypothesis that summer discharge was unrelated to survival rate could not be rejected. There was, however, evidence that higher summer discharge enhances survival in the Miramichi and Northwest Miramichi Rivers of New Brunswick.

Because of an expected fertilizing effect following the construction of the four reservoirs, *S. salar* smolt production was expected to increase temporarily, similar to that observed for invertebrates and fishes after experimental fertilization of rivers (Koksvik *et al.*, 2002; Wipfli *et al.*, 2003; Slavik *et al.*, 2004; Guyette *et al.*, 2013). In the River Orkla, however, phosphorus concentration was not identified as significant in the model.

Data on water temperature were missing from a part of the study period, so the mean smolt age of each cohort of *S. salar* smolts was used as a proxy for water temperature. This variable was, however, not included in the model, which suggests that the annual variation in growth rate is of secondary importance compared with density-independent mortality from the loss of habitat at low discharge.

Some environmental variables that were not included in the analyses, including ice cover, may have been important for smolt production. Although there is a lack of systematic data on ice formation in the River Orkla, extreme ice formation (up to *c.* 3 m thick) was observed in the river during the winter of 2009–2010. Smolt estimates made for the following spring (2010) were the lowest recorded in the time series (Fig. 2). In general, the length of time for which the river is covered with ice has decreased as a result of higher winter water temperatures following the regulation of the flow of the River Orkla, by virtue of the fact that the bottom water is now used for power generation. *Salmo salar* populations are supposed to consume more energy when exposed to an open river without ice during winter than when living under ice cover (Finstad *et al.*, 2004). On the other hand, episodes of freezing and thus ice clogging of fish habitats have probably been less common since the discharge became controlled following the hydropower regulation, so the survival rates of juvenile *S. salar* should thus have been improved. Ice formation is also expected to clog sites where juveniles can hide, and pre-smolts have been observed frozen in frazil ice on river beds (N. A. Hvidsten, unpubl. data). Linnansaari & Cunjak (2010), however, found the highest mortality of juveniles before ice formation in Catamaran Brook, Canada. In addition, juveniles are suggested to be able to hide in substratum chambers where they may find elevated water temperatures (Erkinaro *et al.*, 1994).

The winter discharge in the River Orkla has increased since the hydropower development, and this variable appears to be the main obstacle in smolt productivity. Given the same egg deposition every year (4·4 eggs m^{-2}), the model predicted an increase in the average smolt production following the implementation of the new flow regime (Fig. 5). This increased smolt production is in accordance with the increased catches of adult *S. salar* in the river since the implementation of the hydropower regulation (L'Abeé-Lund *et al.*, 2006).

Increased production of *S. salar* smolts after hydropower regulation, such as in the River Orkla, is unusual. In this river, all reservoirs are located upstream of the river stretch accessible to *S. salar*, no water is removed from the catchment, and the decreased minimum winter discharge of $10\,m^3\,s^{-1}$ is rather high compared with the mean annual discharge of $66\,m^3\,s^{-1}$ at its outlet to the sea. Hence, the effects of river regulation on fish populations depend greatly on the design of the regulation and the dynamics of the new flow regime, including the regulations on minimum flow.

This study was funded by the Norwegian Concession Fund, the Power Companies in River Orkla, the Norwegian Environment Agency, the Norwegian Institute for Nature Research (NINA), Orkla Fellesforvaltning (a landowners' organization), the Norwegian Water Resources and Energy Directorate and the Norwegian Electricity Industry. The authors would like to thank all those who participated in the field work for their invaluable contribution, as well as S. Engen for statistical advice.

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