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Disentangling local from macroenvironmental effects: quantifying the effect of human encroachments based on historical river catches of anadromous salmonids

Jan Henning L'Abée-Lund, Thron O. Haugen, and Leif Asbjørn Vøllestad

Abstract: In this paper, we use dynamic factor and intervention analysis to identify and quantify the effect of human encroachments on anadromous salmonid catches in 22 Norwegian rivers over a 128-year period. In particular, we address effects of hydropower development, gravel removal, and stock enhancement (fish ladder construction and stocking). The methods allow for quantification of perturbation effects in the river environment on the annual catch, after removing long-term temporal trends at the appropriate spatial scale. The estimated effects of the encroachments differed among rivers, indicating that the mechanisms differ among rivers even for the same type of encroachment. In three rivers where hydropower development and stock enhancement had occurred, a significant increase of 0.8–9.8 tonnes (t) (34%–44%) was estimated, whereas a significant reduction of 11.2 t (38%) was estimated for the river where gravel removal had taken place. For rivers with additional biological information available, we find support for our estimated effects. In general, removal of gravel significantly reduced catch and there were positive effects of fish ladder constructions and variable effects of hydropower development and stocking (both positive and negative coefficients).

Résumé : Nous utilisons l'analyse factorielle dynamique et l'analyse d'intervention pour identifier et quantifier les effets des empiétements humains sur les captures de salmonidés anadromes dans 22 rivières de Norvège sur une période de 128 ans. En particulier, nous nous intéressons aux effets des développements hydroélectriques, des enlèvements de gravier et des améliorations de stock (constructions d'échelles à poissons et empoissonnements). Les méthodes permettent de quantifier les effets de perturbations dans l'environnement de la rivière sur la récolte annuelle, après avoir retiré les tendances temporelles à long terme à l'échelle spatiale appropriée. Les effets estimés des empiétements diffèrent d'une rivière à une autre, ce qui indique que les mécanismes varient en fonction des rivières pour un même type d'empiétement. Dans trois rivières (développement hydroélectrique, amélioration de stock), nous évaluons l'accroissement à 0,8–9,8 tonnes (t) (33–44 %), alors que dans la rivière d'où on a retiré du gravier, nous calculons une réduction significative de 11,2 t (38 %). Dans les rivières pour lesquelles il existe des informations biologiques additionnelles, nous obtenons des données qui appuient nos conclusions. En général, le retrait du gravier réduit la récolte de manière significative, la construction d'échelles à poissons a des effets positifs, alors que le développement hydroélectrique et l'empoissonnement ont des effets variables (coefficients positifs et négatifs).

[Traduit par la Rédaction]

Introduction

Most aquatic organisms spend their entire lives in either the marine or freshwater habitat, but individuals of species such as the anadromous salmonids may utilize both marine and freshwater habitats (Groot and Margolis 1991; Shearer 1992). Freshwater and marine habitats differ in many important features. For instance, in the northern hemisphere, productivity is higher in marine habitats compared with freshwater habitats (Gross et al. 1988). Seasonal changes (e.g., tempera-

ture) are more pronounced in freshwater temperate habitats, which also are spatially constrained compared with marine habitats. Anadromous salmonids reproduce in freshwater, and the juveniles stay in this habitat for up to several years before transforming into smolts and migrating to the marine environment (Groot and Margolis 1991; Shearer 1992; Elliott 1994). Because of the different characteristics of freshwater and marine habitats, the juveniles and adults are subjected to different selection pressures, and at least for Atlantic salmon (*Salmo salar*), it has been shown that growth and

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J.H. L'Abée-Lund,^{1,2} T.O. Haugen,³ and L.A. Vøllestad. University of Oslo, Department of Biology, P.O. Box 1050, Blindern, N-0316 Oslo, Norway.

¹Corresponding author (e-mail: lbl@nve.no).

²Present address: Norwegian Water Resources and Energy Directorate, P.O. Box 5091 Majorstuen, N-0301 Oslo, Norway.

³Present address: Norwegian Institute for Water Research, P.O.Box 173 Kjelsås, N-0411 Oslo, Norway.

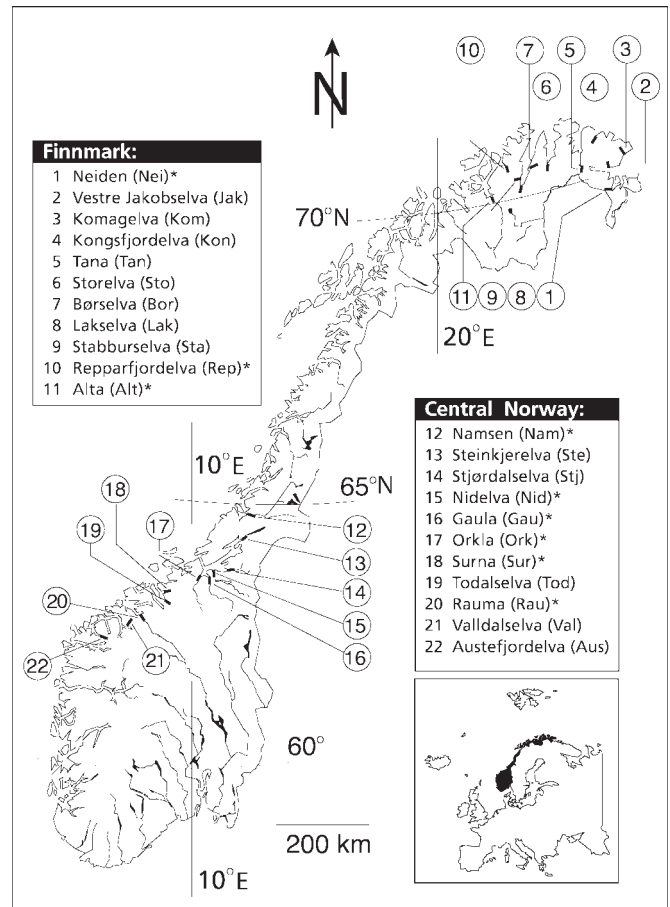
mortality are density-dependent in freshwater and density-independent at sea (Jonsson et al. 1998). Another important aspect of anadromous salmonids is their ability to home to their river of origin to spawn, increasing the potential for evolution of local adaptations (e.g., Ricker 1972; Hendry et al. 2004).

The effect on anadromous populations of human encroachments on the freshwater habitat may be difficult to detect and quantify, as it may be difficult to disentangle the local effects from the effects of macroclimatic and other large-scale effects (variation in growth and survival at sea). However, individuals from neighbouring populations intermingle at sea (Groot and Margolis 1991; Hansen and Jacobsen 2003), exposing them to more or less identical conditions during the postsmolt phase. Thus, the macroclimatic changes that may impact marine growth and survival act in the same way on populations utilising the same marine area (Beamish and Bouillon 1993; Friedland 1998; McKinnell and Karlström 1999). In contrast, changes in the freshwater habitat will affect individual populations differently. In a recent study, L'Abée-Lund et al. (2004) found coherence and similarity in the temporal variation in grilse proportion in Atlantic salmon from rivers draining into large fjord systems in Norway, indicating similarities in, for example, migration routes and environmental forcing at the regional scale. However, if population dynamics is mainly controlled by within-river factors, among-population abundance should be less correlated. Clearly, the relative role of marine and freshwater processes as agents affecting the population dynamics may change over time, and within-river perturbations will potentially result in such a change.

Throughout their range, anadromous salmonids are important commercial species, and recording of life history variables, number of spawners, or catch has been undertaken for more than 100 years in a number of populations (Groot and Margolis 1991; Shearer 1992). The existence of long-term data series makes anadromous salmonids valuable model organisms for understanding the underlying processes causing temporal and spatial variation in population size (Grenfell et al. 1998; Haydon et al. 2001). Such data series are valuable, as parameter estimates from models obtained from data-rich populations can be used for analysing variation in data-sparse populations (Prévost et al. 2003). Annual river catches from anglers may be considered an index of population size (Gee and Milner 1980; Crozier and Kennedy 2001; Thorley et al. 2005). It is also possible to remove any temporal trends in angling (changes in fishing regulations and fishing effort) using appropriate statistical techniques. However, this may not apply to very small populations (Peterman and Steer 1981; Beaumont et al. 1991).

In this paper, we present an analysis of Norwegian inter-river catch correlations and use dynamic factor and intervention analyses to test for possible effects of major human encroachments in a selected set of rivers. As the temporal trends were not the main focus of this study, we adjust the catch data for regional trends. In particular, we test the hypothesis that there is a relative decrease in annual catches in rivers where assumed negative human perturbations (hydro-power development, depletion of gravel) have taken place and a relative increase in rivers where stock enhancement (stocking, fish ladder constructions) have occurred.

Fig. 1. Study rivers and their locations in Norway. The rivers of special interest for studying effects of human encroachments are marked with asterisks. River abbreviations are given in parentheses.



Materials and methods

Catch data

The present study is based on the Norwegian Official Statistics of nominal catch data (total weight) of Atlantic salmon, anadromous brown trout (*Salmo trutta*), and anadromous Arctic char (*Salvelinus alpinus*) from 22 rivers situated in two discrete regions in Norway (Fig. 1; Table 1). Data from nine of these rivers (Table 2) were used to test effects of human interventions using intervention analysis (IA). Data from the remaining 13 rivers were used in a dynamic factor analysis (DFA) to investigate the correlation structure among rivers to find the best covariation structure for the intervention analyses (see below).

The salmonid catch records have been collected by the Norwegian Official Statistics since 1876 (Hansen 1986). Since 1876, it has been an obligation for the local salmon management authorities to collect and report total catches in each river. Before 1968, the records comprised the total catches of Atlantic salmon, anadromous brown trout, and anadromous Arctic char; after 1968, the catches were divided between species. Originally, the catch was recorded in weight, but afterwards also including numbers. The legal fishing season is restricted to summer and early autumn, differing somewhat among rivers. For almost all rivers, the catches comprise

Table 1. Characteristics of 22 Norwegian rivers (from two regions: central Norway and Finnmark) where mean (\pm standard deviation (SD)) annual nominal catch (kg) of anadromous salmonids (1876–2003) and mean proportion (%; \pm SD) of Atlantic salmon, *Salmo salar* (1983–2003), in the nominal catch of anadromous salmonids have been monitored.

River	Latitude (N)	Longitude (E)	River length (km)	Mean discharge ($\text{m}^3\cdot\text{s}^{-1}$)	Mean annual catch (kg)	Proportion	N
Central Norway							
Austefjordelva	62°04'	6°19'	5.5	4.96	314 \pm 425	77.7 \pm 15.3	108
Valldalselva	62°18'	6°15'	17	15.08	686 \pm 652	61.8 \pm 19.0	122
Rauma	62°33'	7°41'	43	41.03	2517 \pm 1523	No data	125
Todalselva	62°49'	8°42'	8.5	14.63	230 \pm 199	45.1 \pm 25.0	101
Surna	62°58'	8°40'	58	55.15	3285 \pm 2632	73.4 \pm 9.5	125
Orkla	63°18'	9°50'	88	65.57	7678 \pm 5585	92.5 \pm 3.9	128
Gaula	63°21'	10°14'	112	95.43	14039 \pm 7466	89.1 \pm 5.8	128
Nidelva	63°16'	10°22'	6	85.12	1652 \pm 1207	75.9 \pm 11.8	128
Stjørdalselva	63°26'	10°54'	55	74.52	4231 \pm 3236	87.2 \pm 7.5	128
Steinkjerelva	64°02'	11°30'	6	64.25	802 \pm 858	73.8 \pm 26.4	116
Namsen	64°28'	11°35'	84	303.28	13889 \pm 7206	91.6 \pm 3.6	124
Finnmark							
Alta	69°58'	23°23'	46	90.77	7613 \pm 6439	86.5 \pm 5.0	110
Repparfjordelva	70°27'	24°20'	27	30.45	1908 \pm 1653	98.1 \pm 1.5	95
Stabburselva	70°11'	24°54'	15	21.33	1121 \pm 1142	88.3 \pm 4.6	120
Lakselva	70°04'	24°55'	70	25.56	2675 \pm 2039	88.7 \pm 3.7	126
Børselva	70°18'	25°32'	63	18.32	901 \pm 877	88.7 \pm 5.7	121
Storelva	70°22'	26°28'	31	14.41	481 \pm 456	92.6 \pm 4.3	79
Tana*	70°28'	28°20'	288	124.42	40151 \pm 29836	96.3 \pm 1.1	128
Kongsfjordelva	70°39'	29°15'	13	7.32	571 \pm 529	96.3 \pm 3.2	92
Komagelva	70°14'	30°32'	39	8.28	2479 \pm 2399	78.4 \pm 10.0	89
Vestre Jakobselva	70°06'	29°20'	3.5	12.54	458 \pm 487	96.5 \pm 2.9	110
Neiden*	69°42'	29°24'	79	5.95	2961 \pm 2727	95.1 \pm 3.5	118

Note: Latitude and longitude give geographical position of river mouth. River length (maximum distance that anadromous salmonids ascend in each river) and mean discharge (annual mean discharge) are river characteristics. N, number of years of observations.

*Catch in Finland is not included.

recreational rod catches only. In two rivers (Tana, Neiden), some commercial fishing with fixed and drifting nets is performed. Anadromous Arctic char occur in our study only in the Finnmark rivers. The annual incidence of anadromous brown trout and Arctic char in the nominal catches varied among rivers and among years within rivers, so it was not possible to estimate the catch for only Atlantic salmon for the whole study period. Thus, we analysed data for all salmonids combined.

The incidence of escaped farmed Atlantic salmon in the recreational river angling catch has been monitored annually since 1989 in several Norwegian rivers. Although considerable variation exists among rivers (0.3%–23.1%) in this period (1989–2000), the grand mean incidence of escaped salmon is low (<10%) and no significant time trend was observed (Fiske and Aas 2001). The effects of escaped farmed salmon in the analyses may be assumed to be random and negligible. None of the investigated rivers has been influenced by acidification.

In this study, all analyses have been performed on the nominal river catch of anadromous salmonids in the period 1876–2003. The analyses assume that the nominal catch reflects the fluctuations in catches and the development in the fisheries (Hansen 1986). Recent studies from Iceland and Great Britain demonstrate that catch statistics reflect the size

of the spawning run (Gudjonsson et al. 1995; Crozier and Kennedy 2001; Thorley et al. 2005). Nominal catch statistics are used by the International Council for the Exploration of the Sea (ICES) to describe status and development of Atlantic salmon in Norway and other countries (ICES 2002).

The quality of the catch data has probably improved over time, introducing a possible bias. Despite this constraint, long-term data series are important for scientific hypothesis-making and management decisions. The Norwegian Official Statistics of nominal catch records of adult Atlantic salmon has undergone several improvements since their start in 1876. There was a change in reporting procedure in 1968 and 1992, but this only introduced more detail into the statistic and does not influence our set of data. Fishing method, effort, and recording of anglers' catch of anadromous salmonids in rivers changes over time. Our main assumption is that fishermen who report their catches are equally prone to report fish independently of fish size, i.e., the reported fish is a random sample of the fish that was captured in a specific river for a given year. There is no available data on the reporting behaviour of Norwegian salmon anglers that can be used to test this assumption. Further, we assume that any changes in reporting procedure or willingness will covary among rivers, at least within regions. Thus, a procedure

Table 2. Characteristics of the rivers studied.

River	Year of start of hydropower production	Watershed (km ²) (percent used for hydropower)	Runoff (million m ³) (percent stored)	Anadromous river length (km)	Natural production	Annual stocking	Stocking period
Neiden	1953	2960 (2)	946	67	450 juv	7–31 nn+n fry and juv	1965–1985
Repparfjordelva		1090	662	27+21	?	6–125 nn fry and juv	1931–1982
Gaula	1924	3659 (7)	3090 (5)	112	300–500 smolt	? nn+n fry and juv	1950s–1960s
						5 n smolt	1975–2000
						0	
Rauma	1948	1202 (11)	1356 (14)	43	?	0	
Alta	1987	7373 (80)	2333 (7)	46	?	0	
Surna	1968	1200 (50)	1883 (20)	40	80–140 smolt	35 n smolt	1968–2000
Namsen	1948	3283 (52)	9113 (13)	111+65	20–50 000 egg	0–400 nn+n fry	1881–1993
Orkla	1982	3053 (85)	2119 (7)	88	130–300 smolt	3–135 nn juv	1950–1979
						7–9 n smolt	1980–1988
Nidelva	1910	3110 (98)	2993 (41)	6	~25 smolt	6* nn juv	1950s–2000
						2–5 nn smolt	

Note: Estimated number ($\times 1000$) of natural production and stocked Atlantic salmon (*Salmo salar*) of native (n) or non-native (nn) origin; juv, juvenile; ?, unknown; *, annual mean number. Increase in river length in Repparfjordelva and Namsen is due to construction of fish ladders.

adjusting for regional-scale temporal trends will remove such reported artefact effects.

Study sites

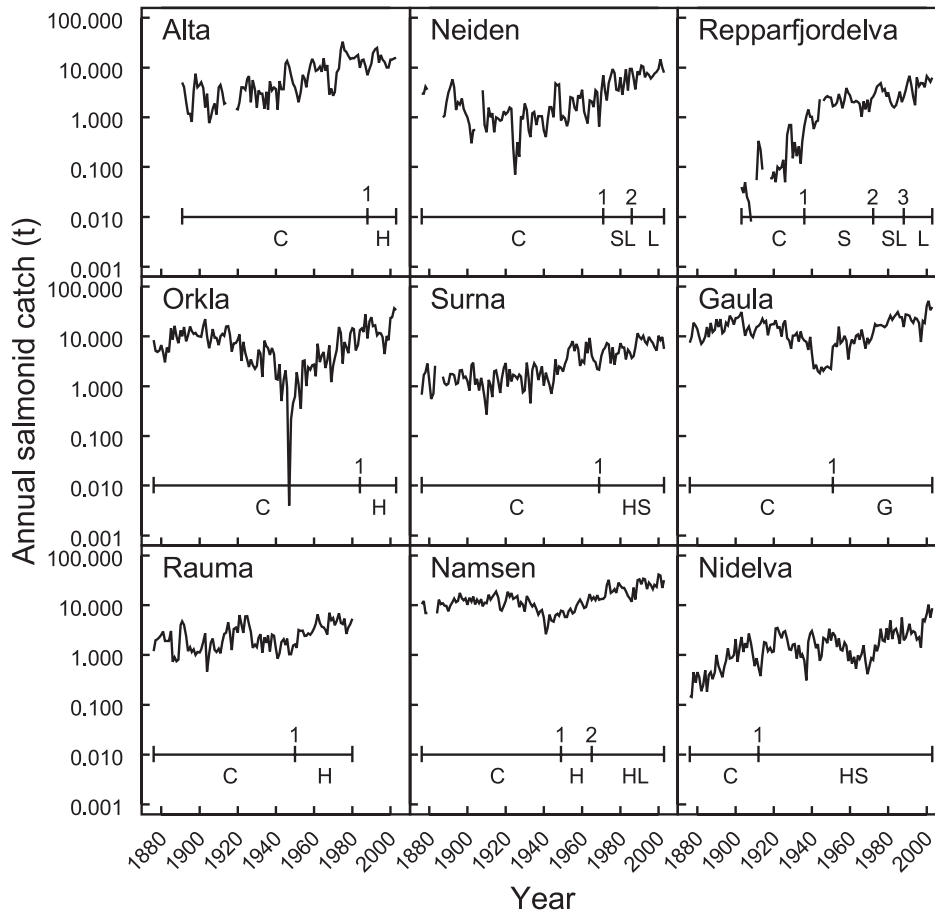
We focus mainly on nine Norwegian rivers from two different regions (central Norway and Finnmark) where different kinds of human encroachments (hydropower development, depletion of gravel, stock enhancement) have occurred during the 20th century (Fig. 1; Table 2). These rivers have in common that nominal catch records of anadromous salmonids exist for the period 1876–2003. Data from a set of rivers within the same regions were selected to represent the temporal variation at the regional scale. Three criteria were used in selecting these rivers. First, the catch records should contain data from almost the entire period. Rivers with missing values for more than 20 years at the start of the series are excluded. Single years without any data were treated as missing and not zero, as catch records before and after the year lacking data indicated that a zero catch was highly unrealistic. Second, the rivers should be clustered geographically with these nine rivers of specific interest. Third, because all nine rivers of interest contain a surplus of multi-sea-winter salmon, we excluded rivers dominated by grilse (one-sea-winter salmon). We expect that grilse behave differently from multi-sea-winter fish (Mills 1989), leading to differences in growth and survival (Hansen and Jacobsen 2003; Jonsson et al. 2003). In total, this resulted in a data set containing 11 rivers from central Norway and 11 rivers from Finnmark (Fig. 1; Table 1).

The effect of stock enhancement (fish release and fish ladder construction) has been tested in two rivers, Repparfjordelva and Neiden. Repparfjordelva is the least physically affected river in the present study. Initially, Atlantic salmon fry and juveniles were released in the natural Atlantic salmon reaches, but afterwards stocking took place in areas not normally accessible for anadromous salmonids. A fish ladder situated 27 km upstream from the estuary was constructed in 1956, increasing the passable river by another 21 km. In Neiden, Atlantic salmon fry and juveniles were released in the area with naturally reproducing Atlantic salmon. A fish ladder (situated 12 km from the estuary) was built in 1968 to improve the ascent of anadromous salmonids to 67 km of naturally occurring salmonid habitat. In both rivers, the number of juveniles released was small compared with the size of the natural production (Table 2; Fig. 2).

The effect of gravel removal has been tested in Gaula, which had been significantly altered during 1953–1985 by extraction of ~4 million m³ of gravel. In some areas, this activity has lowered the river bottom by 2 m and, in other areas, left a clay bottom. Different age classes of young Atlantic salmon have been released since 1950s, mainly in the upper part of the river. However, the numbers released were small compared with the natural production (Table 2; Fig. 2).

Hydropower development may differ strongly among schemes. The effect on anadromous salmonids varies considerably between schemes, and we have investigated the effect of hydropower development in seven rivers (Table 2; Fig. 2). Rauma is least affected, whereas Nidelva is heavily affected both in water storage and by the fact that water from almost the entire watershed is lead through turbines. To reduce the

Fig. 2. Annual catches (tonnes (t)) of salmonids in the nine rivers of special interest. Periods with different kinds of encroachments are indicated: C, control period; H, hydropower; S, Atlantic salmon (*Salmo salar*) stocking; L, ladder; G, gravel removal. Numbers above horizontal line indicate intervention incidents.



negative effect of hydropower, Atlantic salmon juveniles and smolts have been released in several rivers. The amount of this stocking varies considerably among rivers and between years in relation to the natural production (Table 2; Fig. 2). The numbers of released fish were low in Namsen and high in Nidelva and Orkla compared with the estimated natural production of similar age groups. In Namsen, nine fish ladders currently in operation have increased the passable river length for anadromous fish from 111 km to 176 km. Fish ladder construction started in the late 1950s, but they did not function satisfactorily until the late 1970s (A. Rikstad, County Environmental Administration, Statens Hus, N-7734 Steinkjer, Norway, personal communication). All stocking has been performed upstream of the natural anadromous reaches.

Two rivers used in this analysis (Rauma and Steinkjerelva) were infected by the parasitic monogenean *Gyrodactylus salaris* in the late 1970s. This led to a rapid and dramatic decline in the Atlantic salmon population (Johnsen and Jensen 1986). All catches from 1980 onwards were excluded from the data analyses for these rivers.

Statistical modelling

A number of studies have demonstrated that annual salmonid catch in a specific river is correlated with the catch in other

rivers in the region (e.g., Friedland 1998; Peterman et al. 1998; McKinnell and Karlström 1999). Such a correlation is assumed to result from usage of similar oceanic habitat use must be accounted for. However, as the spatial covariation scale is not predefined or fixed (Mueter et al. 2002), the spatial covariation structure in the time series data should be explored in order to find the most appropriate scale. Here we do so by employing dynamic factor analysis (DFA; Zuur et al. 2003) on standardized ln-transformed annual catches ($Y_{j,t}$):

$$(1) \quad Y_{j,t} = (y_{j,t} - \bar{Y}_j) / s_{Y_j}$$

where $y_{j,t}$ is the ln-transformed total catch in river j for year t , \bar{Y}_j is the population-specific overall mean for ln-transformed annual catches, and s_{Y_j} is the corresponding standard deviation. DFA is a multivariate time-series analysis technique used to estimate underlying common patterns in a set of time series. (i) We use this technique to assess the number of common temporal trends (M) in nontarget populations. (ii) By exploring the factor loading (z) pattern to the fitted trends, we can infer the most adequate spatial scale over which to estimate the regional covariate. The mathematical formulation used in DFA can be written as

$$(2) \quad Y_{j,t} = z_{j,1}\alpha_{1,t} + z_{j,2}\alpha_{2,t} + \dots + z_{j,M}\alpha_{M,t} + e_{j,t}$$

where $\alpha_{k,t}$ is the k th common trend, $z_{j,t}$ is the factor loading, and $e_{j,t}$ is noise. In matrix notation, this can be written as

$$(3) \quad \mathbf{y}_t = \mathbf{Z}\boldsymbol{\alpha}_t + \mathbf{e}_t$$

where \mathbf{y}_t is a $N \times 1$ vector containing the values of the N time series at time t , $\boldsymbol{\alpha}_t$ represents the values of the M common trends at time t , and \mathbf{e}_t is a $N \times 1$ noise component, which is assumed to be normally distributed with mean 0 and covariance matrix \mathbf{R} . The $N \times M$ matrix \mathbf{Z} contains the factor loadings and determines the exact form of the linear combinations of the common trends. The aim of DFA is to model all the time series using as low M as possible and still explain the data reasonably well. The optimal M is selected using a model selection metric called the consistent Akaike's information criterion (CAIC; Zuur et al. 2003). After finding the most supported M , we assign the individual rivers to the respective trend curves according to their factor loadings. Based on these trend curve assignments, we then estimate standardized annual mean catch values for each trend curve group ($X_{k,t}$) to be used as the regional covariates in intervention analyses (see below). All DFAs were performed using the R-based Brodgar software (<http://www.brodgar.com/>).

To estimate the effect of local human encroachments on within-river catch, we used IA (sensu Box and Tiao 1975). The general form of the intervention time series model can be written as

$$(4) \quad Y_t = f(\boldsymbol{\beta}, \mathbf{x}, \boldsymbol{\xi}, t) + e_t$$

where t is time, Y_t is the variable of interest at time t , e_t is a stochastic noise component, and $f(\boldsymbol{\beta}, \mathbf{x}, \boldsymbol{\xi}, t)$ is the dynamic component of Y_t . The dynamic component includes an estimated set of parameters $\boldsymbol{\beta}$, a group of covariate series \mathbf{x} , and a set of intervention series $\boldsymbol{\xi}$. Embedded in $\boldsymbol{\beta}$ are detrending parameters and parameters describing the magnitude of intervention effects. The covariate series \mathbf{x} are additional time series that may be related to the time series of interest, in our case the mean regional catch (X_i). The intervention series, $\boldsymbol{\xi}$, are used to signal the occurrence of an intervention in the dynamics of the time series of interest. In our case, all intervention events are a priori known (Fig. 2). Hence, the core model structure fitted the data in our study looks like this:

$$(5) \quad Y_t = \omega_0 \xi_t + x_t + \gamma_t + e_t$$

where γ_t is a detrending function (fitted as a polynomial function), x_t is the detrended X_t , ω_0 is the magnitude of a step intervention, and in the case of just one intervention incidence (I),

$$(6) \quad \xi_t = \begin{cases} 0, & t < I \\ 1, & t \geq I \end{cases}$$

The noise term e_t was individually modelled for each river of interest based on the Ljung–Box chi-square white-noise test and augmented Dickey–Fuller stationarity test. For all models fitted, the temporal autocorrelation could be accounted for by fitting no higher than second-order ARMA models:

$$(7) \quad \mu_t = \phi_1 \mu_{t-1} + \phi_2 \mu_{t-2} + \varepsilon_t - \theta_1 \varepsilon_{t-1} - \theta_2 \varepsilon_{t-2}$$

where ϕ_m and θ_m are the m -order autoregressive and moving average coefficients, respectively, ε_t is i.i.d. (i.e., independent and identically distributed), and μ_t is the expected value of Y_t . All the IA modelling was performed using PROC ARMA (with input variables) in SAS Version 9.1 (<http://support.sas.com/documentation/onlinedoc/sas9doc.html>). All models were fitted using the maximum likelihood method, and model selection was based on AIC.

Human perturbations in freshwater may affect catches of adult salmonids mainly via two processes — juvenile survival and the probability of capture of adults. Processes that affect juvenile survival will not be detected immediately after a perturbation (i.e., a delayed effect can be expected), whereas effects on the probability of capture will appear immediately and might decrease with time as the result of compensatory efforts. We fitted models including a delayed effect corresponding to the population-specific age of maturation (5–7 years; Alta, Namsen, Repparfjordelva (Dahl 1910; Jensen et al. 1999), Gaula (J.H. L'Abée-Lund, unpublished data), Orkla (Hvidsten et al. 2004), Surna (S.J. Saltveit, Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, N-0318 Oslo, Norway, personal communication)). We found no evidence (comparing AIC values for pairs of similar models with and without delayed response) for delayed responses except for the case of Gaula. All the rest of the tests presented are therefore based on nondelayed intervention effects.

The data quality has probably improved over time and, hence, may potentially have caused a sampling bias in the data. We have dealt with this problem by including the regional mean catch of salmonids as a covariate in all models, assuming that the report rate is similar within regions. In addition to this action, we have performed resampling procedures (nonparametric bootstrapping; Manly 1997) where the direction and degree (variance) of sampling bias have been set to vary over time. We tested the effect of increasing and decreasing report rates over time, where the change ranged from 10% to 40% difference in report rate between first year and last year in the catch time series. Similarly, we also tested the effect of varying the sampling error over time (but with no net trend) between 10% and 40% of reported values. The resampled catch series were subjected to new intervention analyses under the originally favored model structure. Under each resampling regime (140 in total), 1000 resamples and intervention analyses were performed. Inferences on the robustness of the originally estimated intervention effects were made by comparing the original parameter estimates with the resulting variation in the bootstrapped intervention effect parameters (the median and 2.5 and 97.5 percentiles). The bootstrapping was conducted using the %BOOT macro developed for SAS (available from <http://support.sas.com/ctx/samples/index.jsp?sid=479>).

Results

The DFA revealed that the temporal data of salmonid catches from all nontarget rivers could most effectively (i.e., lowest CAIC) be modelled by two general trends (embedded figure in Fig. 3). Although there was no distinct clustering into the two predefined central Norway and Finnmark regions

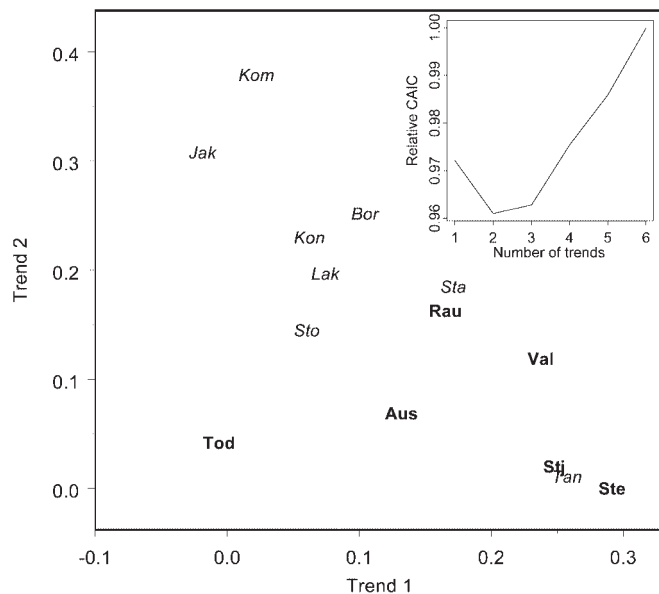
Table 3. Parameter estimates for the selected ARMA intervention models (based on Akaike’s information criterion).

River	Intercept	Temporal autocorrelation structure				Detrending parameters	
		ar(1)	ar(2)	ma(1)	ma(2)	Linear	Quadratic
Gaula	-2.02±0.58 (0.0006)	0.85±0.07 (<0.0001)		0.32±0.12 (0.0087)		0.016±0.013 (0.2263)	0.0016±0.0004 (0.0003)
Repparfjordelva		-0.59±0.10 (<0.0001)		-0.44±0.11 (<0.0001)		0.024±0.005 (<0.0001)	-0.0004±0.0001 (0.0002)
Neiden	-0.62±0.16 (0.0002)	0.40±0.09 (<0.0001)				-0.003±0.004 (0.4394)	0.0004±0.0001 (0.0076)
Surna	0.95±0.23 (<0.0001)	0.27±0.09 (0.0041)				0.029±0.009 (0.0011)	-0.0002±0.0002 (0.4272)
Nidelva		0.52±0.08 (<0.0001)				0.022±0.008 (0.0078)	0.0011±0.0002 (<0.0001)
Namsen	-1.39±0.51 (0.076)	0.54±0.08 (<0.0001)				0.016±0.011 (0.1611)	0.0012±0.0003 (<0.0001)
Alta	-0.64±0.23 (0.0070)	1.53±0.13 (<0.0001)	-0.80±0.11 (<0.0001)	1.16±0.16 (<0.0001)	-0.58±0.13 (<0.0001)	0.011±0.004 (0.0044)	
Rauma		0.52±0.09 (<0.0001)					
Orkla		0.94±0.03 (<0.0001)		0.59±0.09 (<0.0001)			

Note: Standard errors are provided and *p* values (*t*-based) appear in parentheses below each parameter estimate. ar and ma correspond to autocorrelation and they are indicated in Fig. 2.

*Note that this effect has been delayed by 6 years.

Fig. 3. Factor loadings for the salmonid catch data series obtained by the model containing two common trends. Based on the relative (to maximum) consistent Akaike’s information criterion (relative CAIC), the model containing two common trends was the most supported one (inset figure). Rivers from central Norway are noted in bold, and Finnmark rivers are noted in italics. Factor loadings are unitless. River abbreviations: Tod, Todalselva; Aus, Austefjordelva; Rau, Rauma; Val, Valldalselva; Stj, Stjørdalselva; Ste, Steinkjerelva; Kom, Komagelva; Jak, Vestre Jakobselva; Bor, Børselva; Kon, Kongsfjordelva; Lak, Lakselva; Sta, Stabburselva; Sto, Storelva; Tan, Tana.



(Fig. 3), there was a general tendency for the Finnmark region rivers to cluster as a group with generally high loading to trend 2, whereas the central Norway rivers generally clus-

tered with high loading to trend 1. Two rivers deviated from this pattern (Tana (Tan) and Todalselva (Tod)) and therefore were excluded when estimating regionwise standardized mean catches (X_t). These regionwise standardized mean catches were used as covariates in all the following intervention analyses.

The intervention analyses described 50%–91% of the variation in the individual time series (Table 3), and for all rivers except Repparfjordelva, regional mean catches had a significant positive effect on the individual river catches. The effects of the detrending using regional mean catch as covariate and of the interventions are illustrated (Fig. 4). The analyses further revealed that three of the four rivers (Alta, Orkla, Rauma, and Namsen) where effects from hydropower alone on annual salmonid catches could be estimated had positive effect coefficients. Although none of the hydropower effect coefficients was significant ($p = 0.06$ – 0.65), they were close to being so for the two rivers Namsen and Rauma (p values of 0.09 and 0.06, respectively). Only Alta showed signs of negative effect from hydropower development, but the estimated effect was far from significant ($p = 0.66$).

In the two rivers where hydropower development was combined with compensatory stocking (Surna and Nidelva), no significant effect was found. In Surna, there was a tendency that the combined effect was negative ($p = 0.13$). In Namsen, there was a significant positive effect of the combined hydropower development and construction of fish ladder actions (intervention 2), resulting in an increase of 9.8 t·year⁻¹. The increase corresponded to about 44% of the annual mean catch.

In both rivers where enhancement measures were undertaken (Neiden and Repparfjordelva), annual catches increased significantly after starting the stocking program (Table 3). The increase represented an estimated annual increase in catch of 0.8 t (39%) in Repparfjordelva and 1.6 t (34%) in

Cubic	Region	Intervention effects			R^2_{adj}
		1	2	3	
$1.25 \times 10^{-5} \pm 3.88 \times 10^{-6}$ (0.0017)	0.58±0.12 (<0.0001)	-1.49±0.36 (0.0001)*			0.80
	0.14±0.09 (0.1721)	0.39±0.10 (0.0001)	-0.04±0.23 (0.8580)	0.36±0.25 (0.1520)	0.91
	0.20±0.09 (0.0262)	0.55±0.18 (<0.0001)	-0.18±0.39 (0.8865)		0.69
$-3.36 \times 10^{-6} \pm 1.64 \times 10^{-6}$ (0.0428)	0.44±0.15 (0.0054)	-0.50±0.33 (0.1305)			0.71
$1.13 \times 10^{-5} \pm 2.22 \times 10^{-6}$ (<0.0001)	0.41±0.14 (0.0070)	-0.02±0.15 (0.8817)			0.71
$9.91 \times 10^{-6} \pm 2.68 \times 10^{-6}$ (0.0003)	0.56±0.13 (0.0001)	0.66±0.39 (0.0927)	0.84±0.38 (0.0296)		0.75
	0.56±0.12 (<0.0001)	-0.11±0.26 (0.6552)			0.75
	0.61±0.19 (0.0016)	0.51±0.26 (0.0552)			0.50
	0.43±0.16 (0.0086)	0.59±0.44 (0.1916)			0.65

and moving average, respectively. The intervention effect coding corresponds to their chronological appearance, and their nature is described in Table 2

Neiden. However, in both rivers, stocking was combined with construction of fish ladders. After terminating the stocking programs, annual catches remained unchanged.

Gravel removal in Gaula resulted in a significant decrease in annual salmonid catches (Table 3). The difference in catches before and after gravel removal corresponds to an annual reduction of 11.2 t or 38%.

The bootstrap tests demonstrated that the estimated intervention effects were generally robust to assumptions about temporal variation in sampling bias. We found a change in the degree of significance (α level = 0.05) in just 7.8% of the 140 bootstrap regimes performed. For instance, the weak positive effect of hydropower development on salmonid catches found for Rauma and Namsen became very significant when assuming that the report rate should increase to a 20% higher level than reported during the entire time series period. The same was the case for Nidelva, but here the intervention was both hydropower development and stocking of juvenile salmon. The negative tendency from hydropower development found in Alta became slightly significant ($p = 0.046$) when assuming that temporal variation in report error should be 20% higher than reported, but not for higher or lower levels of variation. In general, the intervention effects were most sensitive to high levels (i.e., >30%) in variation of the sampling error. For instance, although Gaula, Repparfjordelva, and Neiden had very robust intervention effect estimates towards temporal trends in sampling error and at lower levels of variation in sampling errors, the intervention effects changed markedly at variation levels above 30%. At such high levels of sampling variance, annual salmonid catches were estimated to drop markedly in Gaula (because of gravel removal), to not increase significantly in Repparfjordelva (after construction of fish ladder and enhancement stocking actions), and to decrease significantly in Neiden (after terminating the stocking actions).

Discussion

Here, we have used DFA and IA to identify and quantify the effects of various human encroachments on recreational catches of salmonid fishes in Norwegian rivers. In this way, we adjust for temporal trends that might occur at a regional scale, regional variation in reporting practice and fishing regulations, and temporal autocorrelation. We document strong negative effects of gravel removal, positive effects of fish ladder constructions, and variable effects of hydropower development and stocking (both positive and negative coefficients). The reported estimates of intervention effects were generally shown to be robust towards assumptions about temporal variation in sampling bias.

Marine environmental conditions are known to change over decades (Mann and Lazier 1991), and postsmolt survival has been documented to vary with these fluctuations (Friedland 1998; Mueter et al. 2002). Thus, it is reasonable to believe that variations in river catch records also reflect the effects of marine conditions. Other catch records of Atlantic salmon from the same area also show consistency for between-river comparisons (Friedland 1998; McKinnell and Karlström 1999), suggesting that the catches are influenced by the same marine conditions. The method presented here adjusts for temporal variation at the regional scale.

The DFA indicated that rivers in northern and central Norway exhibited different temporal trends in catch, indicating strong regional effects. Further, the analysis revealed synchrony in among-river catches within regions (with few exceptions). There is large variation in climatic condition along the Norwegian coast. The most striking variation occurs off the Lofoten area (69°N). The warm North Atlantic drift secures relatively high (although reduced in a northerly direction) and stable water temperature along the Norwegian coast. However, north of Lofoten the effect of the drift is

considerably weakened and sea temperatures are more variable (see L'Abée-Lund et al. 1989; Orvik et al. 1995). Although the sea temperature is low in the Barents Sea, the density of zooplankton is still relatively high (Dalpadado et al. 2003) and gives rise to important marine fisheries. The feeding areas are situated near the mainland, and Rikardsen et al. (2004) show that Atlantic salmon after leaving their natal northern Norway rivers as smolt start feeding earlier than smolt from rivers in central Norway. The exact marine distribution of salmon from rivers in northern Norway is unknown, although available data indicate a northerly distribution compared with populations from southern Norway during the first year at sea (Hansen and Jacobsen 2003). Atlantic salmon in their second year at sea, however, may undertake a migration further south and intermingle with southern populations (Hansen and Jacobsen 2003). The Atlantic salmon during their first year at sea seem to follow the main surface currents northwards into the Norwegian Sea and then spread out over wide areas (Holm et al. 2000). However, the sampling effort has been very low in the Barents Sea and the Greenland Sea.

Our analyses are based on total river catches; thus, we are not able to detect possible within-river effects that do not affect the total river catches. This problem may arise in situations where the encroachment (e.g., power plant) has a negative local effect in one part of the river and positive effects in other parts. For instance, dramatic declines in the density of juveniles and catch of adult Atlantic salmon were registered in areas close to the hydropower plant in Alta, whereas increased catches have been reported for the lower parts of the river in the first decade of operation (Tor Fredrik Næsje, Norwegian Institute of Nature Research, Tungasletta 2, N-7485 Trondheim, Norway, personal communication).

Furthermore, other within-river changes occurring at the same time will be difficult to detect without detailed information and (or) study. For example, in Gaula and Orkla, substantial mining activities occurred from the late 1600s to the late 1980s and the termination of this activity improved water quality in the affected river sections (approximately 30 and 15 km, respectively). In Gaula, this water quality improvement may have masked an even larger negative effect of the encroachment than that observed. Unfortunately, data on water quality are only available for the later part of the time series (since the mid-1980s) and it was impossible to use water quality as a covariate in the analysis. In Orkla, we observed a nonsignificant positive trend after the hydropower development. This increase in catch was concurrent with reduced mining activity in the late 1970s, resulting in low contamination of heavy metals in the lower reaches of Orkla in the early 1980s and onwards (Jensen et al. 1998). As only the lower 15 km of the anadromous reach was affected, the improved water quality may have induced a small part of this positive effect on the salmonid catch.

The reliability of catch data is a subject for discussion. A critical assumption in our analyses is consistency in both fishing regulations and exploitation rate within and among rivers. Regulations of the river fisheries have remained consistent in Norway during most of the study period. The most pronounced change is a relatively recent reduction in the length of the fishing season, especially in rivers with small salmon populations (Fiske and Aas 2001). Our study rivers,

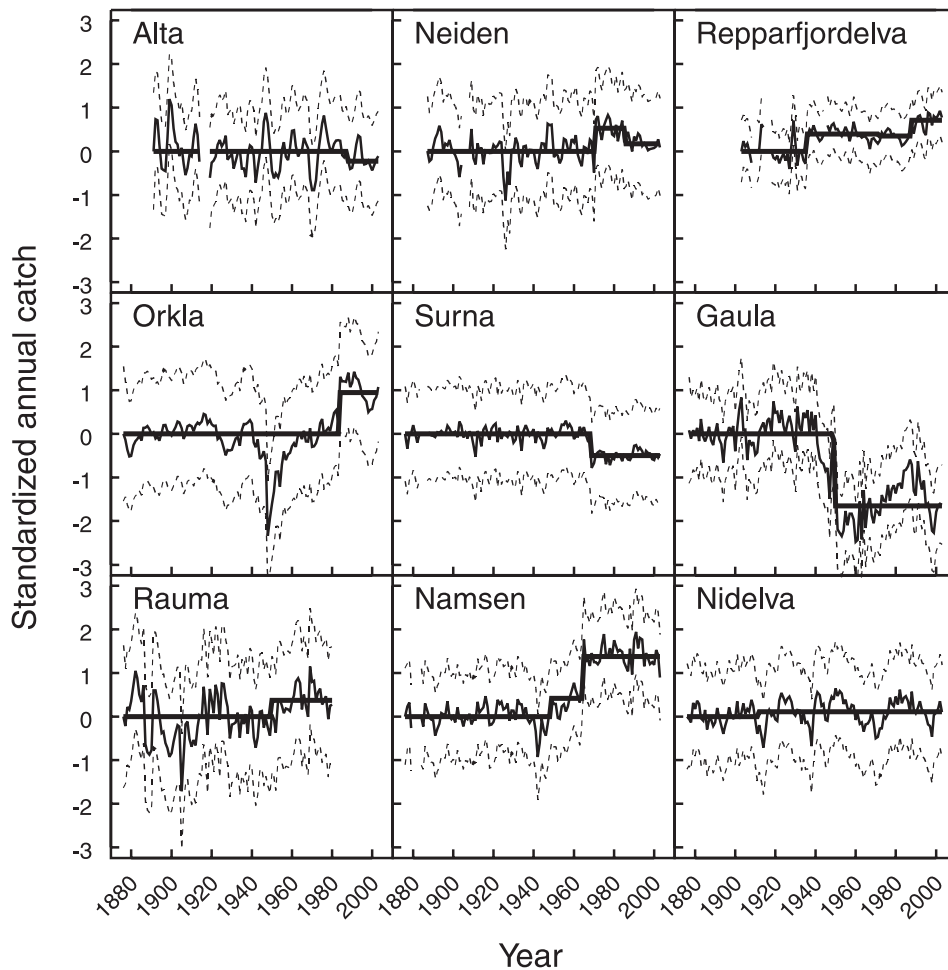
however, have been little affected by this. In rivers where variation in exploitation rate has been estimated over time, no systematic trends are found. For instance, in two different Norwegian rivers, Aurland and Lærdal, it has been shown that anglers caught the same proportion of the spawning population 10 years after the hydropower plant came online as they did before this perturbation (Sættem 1995). For the rivers used in the present analyses, we do not have this kind of information.

Marine exploitation patterns have changed over time, with the most dramatic change being the start of offshore drift netting for Atlantic salmon in 1960. The Norwegian drift-net fishery was banned in 1989, significantly affecting the structure of the Norwegian spawning run (Jensen et al. 1999). After the cessation of the drift-net fishery, the mean size of grilse increased and the total catch of grilse increased in the four rivers where this has been studied in detail. No changes were observed for the catch of multi-sea-winter fish. It is thus evident that this fishery has affected grilse more strongly than larger fish. However, we have excluded time series from rivers dominated by grilse from our analyses, therefore the effect of this change in the marine fishery may be of minor importance. Other changes in marine exploitation have of course taken place during the 128 years covered by these time series. However, the effects have not been documented, and we have assumed that the changes are the same, at least on the regional scale used here. If so, the use of appropriate covariates in the statistical models has adjusted for these effects.

The observed effects of the encroachments differed both between encroachment types and among rivers with the same type of encroachment, indicating that the mechanisms differ among rivers. The largest observed effect was for Gaula, where ~4 million m³ of gravel were removed from the river bed during 1953–1985. This extraction of gravel destroyed some of the best spawning areas for Atlantic salmon (Heggberget 1986), leaving the rearing habitat for juvenile fish consisting of substrate of small size and occasionally marine deposits such as clay. Densities of both invertebrates and juvenile salmon and brown trout in these areas are significantly lower than expected (JoVegard Arnekleiv, Freshwater and Inland Fisheries Laboratory, Norwegian University of Science and Technology, N-7491 Trondheim, Norway, personal communication). Also, more turbid water results from continuous flushing of the clay layer, which has been shown to negatively affect riverine ecosystems (Waters 1995). Thus, there is a clear relationship between production of invertebrates and juveniles and the catch of adult salmonids.

Enhancement measures such as stocking and building of fish ladders significantly increased annual catches. In Neiden and Repparfjordelva, stocking was combined with building fish ladders, thus the effect of each encroachment type could not be estimated. However, after terminating the stocking program, catches remained unchanged, indicating that the positive effect of the encroachment was mainly due to the building of fish ladders and the increase in the river area producing anadromous salmonids. The effect of building fish ladders was also positive Namsen. In Surna, hydropower development and stocking have taken place simultaneously, leading to a nonsignificant negative effect. However, it is impossible to

Fig. 4. Annual detrended catches (solid lines; standard deviation units with confidence bounds (dashed lines)) of salmonids in the nine rivers of special interest. The estimated effect sizes for the various interventions are displayed as thick solid lines.



estimate the unique effects for the two encroachment types. Stocking was found to have a positive (nonsignificant) effect on annual catches when the fish was stocked as smolt and constituted a large proportion of the total smolt production, as in Surna. In total, there was no obvious positive or negative effect of fish stocking in these rivers. Also, this is the general conclusion from reviews on fish stocking, i.e., effect sizes vary strongly depending on the species, population, and environmental conditions (Einum and Fleming 2001). A number of authors suggest that the long-term effect in most cases will be negative because of the negative genetic and ecological interactions between hatchery-reared and native fish (Hindar et al. 1991; Einum and Fleming 2001; McGinnity et al. 2003).

In Orkla, estimated smolt production of Atlantic salmon has increased by a factor of up to 1.8 following hydropower development (Hvidsten 1993). This has been attributed to an increase in winter water discharge. In Alta, annual surveys since 1981 have revealed a decline in density of juvenile Atlantic salmon in the upper reaches concurrently with a decrease in the catch of adults (Forseth et al. 1996). In some rivers, stranding of juvenile salmonids has led to increased mortality (as shown for Nidelva; Hvidsten 1985). Hvidsten (1985) demonstrated that for anadromous brown trout, the stranding led to a significant reduction in productions, whereas the Atlantic salmon mortality was not affected. Furthermore,

enhancement measures (stocking and fish ladders) significantly increased annual catches (Neiden and Repparfjordelva). For Repparfjordelva, it was especially interesting that the catch tended to increase after stocking was terminated.

For the regulated rivers, no significant effect of hydropower development on the annual catch of anadromous salmonids was observed. However, for Rauma and Namsen, we observed a positive and marginally significant effect. For Orkla, the effect was also positive, but nonsignificant. Only for Alta did we find a negative effect, but the estimate was nonsignificant. These results were contrary to our expectations of negative effects based on the scientific literature (e.g., Ward and Stanford 1979). Changes resulting from hydropower development may explain the deviation. For example, hydropower schemes have caused changes in the hydrological regime of the rivers by water being stored during periods of high discharge (mostly spring snowmelt) and released in periods with reduced runoff, as in winter when the power needs are greatest. However, water has not been diverted from the river systems. In Orkla, an increase in smolt production of Atlantic salmon following hydropower development has been attributed to an increase in winter water discharge (Hvidsten 1993). The increase in smolt production lends support to our analysis that the relative catch in Orkla has increased after hydropower development. A significant negative correlation between the size of the spring flood and the biomass and

year-class strength of both Atlantic salmon and anadromous brown trout has been demonstrated for one undeveloped river (Jensen and Johnsen 1999). The water flow during spring, especially the intensity of spring flood, seems to determine to a large extent the recruitment of brown trout in Spanish and French rivers (Cattanéo et al. 2002; Lóbon-Cerviá and Rincón 2004). Thus, the reduced spring flood as a result of hydro-power development may lead to increased recruitment in some rivers. To what extent increased recruitment is translated into increased smolt production will depend on how juvenile rearing habitat is influenced by the encroachment. Given a surplus of spawners, it is often assumed that populations of salmonids in rivers are regulated by density-dependent processes. For Atlantic salmon, few stock–recruitment curves summarizing such density-dependent regulation have been published (but see Buck and Hay 1984; Chadwick 1985; Jonsson et al. 1998), and for the rivers studied here, no such information exists. Changes in hydrological regimes may also change the shape of the stock–recruitment relationships.

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