Temporal synchrony and variation in abundance of Atlantic salmon (Salmo salar) in two subarctic Barents Sea rivers: influence of oceanic conditions¹

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Abstract: Long-term variation in Atlantic salmon (*Salmo salar*) stocks was analyzed in two Barents Sea rivers, the Teno and Näätämöjoki, that represent the northernmost distribution area of the species. In contrast to most of the North Atlantic area, these rivers are among a group of northern salmon rivers that, despite wide annual variation in catches, demonstrate no consistent trend for declining abundance. Variations in abundance were generally synchronous for the total catch and numbers of 1-sea-winter (1SW) and 2SW salmon during period of 1972–2003. Part of the variation observed in catches could be related to ocean climate conditions as the mean seawater temperature in July during the year of smoltification for the Kola section of the Barents Sea was significantly related to numbers of 1SW, 2SW, and 3SW salmon in the large River Teno. In contrast, NAO (North Atlantic Oscillation) indices were not related to salmon catches. The latest increase (1999–2001) in salmon catches in these rivers reflects both temporarily improved oceanic conditions and past management measures affecting offshore, coastal, and river fisheries.

Résumé : Nous avons analysé les variations à long terme des stocks du saumon atlantique (*Salmo salar*) dans deux rivières tributaires de la mer de Barents, la Teno et la Näätämöjoki, qui représentent l'aire de répartition la plus boréale de l'espèce. Contrairement à ce qui se passe dans la majeure partie de la région de l'Atlantique nord, ces rivières appartiennent à un groupe de cours d'eau qui, malgré d'importantes variations annuelles des prises, n'affichent pas de tendance soutenue de déclin d'abondance. Les variations d'abondance se manifestent généralement de façon simultanée dans les prises totales, les nombres de saumons ayant passé un hiver (1SW) et deux hivers (2SW) en mer durant la période de 1972–2003. Une partie de la variation observée dans les prises pourrait être reliée aux conditions climatiques de l'océan, puisque, les années de transformation en saumoneau, la température moyenne de l'eau de mer en juillet dans la section de Kola de la mer de Barents est significativement reliée aux nombres de saumons 1SW, 2SW et 3SW dans la grande rivière Teno. En revanche, il n'y a pas de relation entre les indices NAO (oscillation nord-atlantique) et les prises de saumons. La dernière augmentation des prises (1999–2001) de saumons dans ces rivières reflète à la fois une amélioration temporaire des conditions océaniques et les mesures d'aménagement du passé qui ont affecté les pêches au large, sur les côtes et dans les rivières.

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Introduction

In many areas of the North Atlantic, populations of salmon (Salmo salar) either are in a state of decline or have already been extirpated (Parrish et al. 1998) such that concern over the continued survival of the species has been given more attention in recent years (Potter and Crozier 2000). Other stocks, while somewhat stable, have shown little or no improvement. In the past, high rates of exploitation in ocean fisheries were often associated with many stock declines and were seen as a serious threat to the future conservation of salmon (Mills 1993). Marine exploitation rates had been estimated in the range of 70%-90% on multi-seawinter (MSW) components, whereas 1-sea-winter (1SW) stocks were commonly harvested at 40%-60% (e.g., Hansen 1988, 1990; Dempson et al. 2001). Yet, abundance of many stocks continues to fall despite the absence of, or great reduction in, directed marine salmon fisheries (Parrish et al. 1998; Friedland et al. 2003*a*; Dempson et al. 2004).

Specific reasons for the continued decline in abundance of salmon stocks are often not clear, but as stated by Parrish et al. (1998), multiple factors are likely responsible. To summarize, these factors typically result in reduced smolt output, increased marine mortality, and decreased sea age at maturity (Parrish et al. 1998; Jonsson et al. 2003). Thus, finding and studying salmon populations still considered generally "healthy", or those consistently achieving conservation spawning requirements, can often be problematic. Exceptions, however, include some salmon populations in northernmost Norway, Finland, and Russia that are not necessarily following the general decline observed in other Atlantic salmon stocks, but seem to fluctuate in the absence of a consistent decreasing trend (Jensen et al. 1999; ICES 2002).

With the potential for increased exploitation of the northern salmon stocks, impacts resulting from the proposed expansion of salmonid aquaculture into these northern areas, and the uncertain consequences resulting from global climate change (e.g., Turrell and Shelton 1993; Bigg 2000; Drinkwater 2000), it is important to examine the dynamics of salmon in rivers that still support abundant salmon stocks. Consequently, in this paper we examine the synchrony and long-term trends in abundance of salmon in two stocks from a small geographic area in the northernmost range of the Atlantic salmon distribution area that flows into the Barents Sea, namely, the Rivers Teno and Näätämöjoki, in the context of whether these northern stocks co-vary and follow the general declining trend of many other North Atlantic salmon stocks. Hansen and Quinn (1998), and more recently Friedland et al. (2003a, 2003b), suggested that the environmental conditions during the first months following migration to sea are critical periods influencing the subsequent growth, survival, and by extension, the abundance of salmon. Because the inflow of warmer water masses in the southwest is of crucial importance for the climate of the Barents Sea, with climate alternating between warm and cold periods (Loeng et al. 1992; Ingvaldsen et al. 2003), we also analyze whether the crucial influence of spring environmental conditions on salmon abundance, as suggested by Friedland et al. (2003a), can be detected in the northern Barents Sea rivers, the Teno and Näätämöjoki.

Materials and methods

Study area

The subarctic Rivers Teno (Tana in Norwegian) (70°N, 28°E; catchment area 16 386 km²) and Näätämöjoki (Neidenelva in Norwegian) (69°N, 29°E; catchment area

2962 km²), border rivers between Norway and Finland, empty into the Barents Sea in a small geographical area on the coast of northernmost Norway (Fig. 1). More than 1100 km of the River Teno system are accessible to salmon, including the main stem and more than 20 tributaries supporting distinct substocks (Elo et al. 1994). Extensive salmon fisheries occur in the River Teno with a variety of gear, including weirs, gill nets, drift nets, seines, and rods (Henriksen and Moen 1997; Erkinaro et al. 1999). Distribution of salmon in the River Näätämöjoki covers 220 km along the main stem and two major tributaries (Niemelä et al. 2001). Salmon stocks in the Rivers Teno and Näätämöjoki are conserved, maintained, and enhanced only by fishery regulations as stocking of reared fish is prohibited in these systems.

Catch data and abundance estimation

In the absence of absolute measures of the salmon run sizes, the salmon catch is considered to represent a surrogate of abundance as used in other investigations (e.g., Friedland et al. 2003a). There are no salmon catch quotas in these rivers, and therefore, numbers of salmon caught are assumed to reflect actual variations in population abundance. The total weight of yearly salmon catches was estimated from postal questionnaires sent to fishermen and by catches converted into numbers of fish using the sea-age distribution of yearly catch samples.

Scale samples of adult Atlantic salmon of the River Teno were collected by fishers using various gears throughout the fishing seasons of 1972–2003. Sampling took place in the middle section of the river covering 120 km within the area located between 70 and 190 km from the mouth (Fig. 1). In the River Näätämöjoki, rod and line, gill net, and seine were used to collect the scale material within the lowermost 60 km of the river throughout the fishing seasons of 1975– 2003. Samples from the River Teno comprised 28 161, 7010, 10 179, 661, 22, and 2308 1SW, 2SW, 3SW, 4SW, and 5SW salmon and previous spawners, respectively. Samples from the River Näätämöjoki comprised 5508, 1734, 1360, 28, and 274 virgin 1SW, 2SW, 3SW, and 4SW salmon and previous spawners, respectively.

Statistical analyses

Co-variation in salmon stock abundance between the Rivers Teno and Näätämöjoki and linkages associated with Barents Sea temperature data was determined from Pearson correlation analyses based on the total declared catch of 1SW, 2SW, and 3SW salmon and all sea ages combined, as similarly carried out by McKinnell and Karlström (1999) examining co-variation in abundance of Baltic salmon stocks and in exploratory analyses of Friedland et al. (2003*a*) for North American stocks of salmon. However, correlation analyses are often confounded by problems associated with autocorrelation (Pyper and Peterman 1998). To account for autocorrelation in our analyses, we followed the approach outlined by Peterman et al. (1998) where corrected degrees of freedom ($N^* - 2$) are determined according to the following formula:

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_{j}^{N/5} r_{xx}(j) r_{yy}(j)$$

Fig. 2. Mean sea temperature (°C) calculated from average values integrated vertically from 0 to 50 m across all stations of the Kola section for the month of July, 1969–2002.



where N is the number of sample pairs, $r_{xx}(j)$ and $r_{yy}(j)$ are the sample autocorrelations of x and y at lag j.

Temporal trends in salmon catches were examined and analyzed in two ways. First, scatter plots of abundance (catch) were constructed, and the estimated numbers of salmon by sea-age class, or the total catch in weight, was examined graphically by LOWESS regression (Trexler and Travis 1993), where each point in a series is predicted by a weighted combination of points around it in a regression equation (Wilkinson et al. 1986). Examination of LOWESS plots assisted in qualifying whether there were potential trends in the data. The optimal smoothing parameter selection was based on corrected Akaike's information criterion (AICc), and parameters were calculated by SAS PROC LOESS (SAS Institute Inc. 2001). Catches were then analyzed by autoregression-corrected regression analyses. Dependent variables included estimated total catch in the Rivers Teno and Näätämöjoki, estimated numbers of 1SW-4SW and previously spawned (PS) salmon in the River Teno catch, and 1SW-3SW and PS salmon in the River Näätämöjoki catch. Year was used as the independent variable. As virtually all linear regression models included autocorrelation in their error terms, the AR(1) error (autoregressive error at lag 1) structure was used. The validity of the AR(1) error structure model was compared with the ordinary least-squares regression model by likelihood ratio χ^2 tests. If the difference between models was not significant (p > 0.05), then the ordinary regression model was selected for the trend analysis. The analysis was performed by SAS PROC MIXED (SAS Institute Inc. 2001).

To examine co-variation between salmon abundance and ocean climate information, as explained above, we used the average sea temperatures in July at depths of 0-50 m, obtained from the Kola section in the Barents Sea (Tereshchenko 1996; S. Prusov, Polar Research Institute of Marine Fisheries and Oceanography, PINRO, unpublished data; Fig. 2). The Kola section is located along longitude $33^{\circ}30'E$ in the central Barents Sea and intersects the Murman current from $70^{\circ}30'N$ to $72^{\circ}30'N$ (Fig. 1). The July temperature was selected to represent the conditions that young salmon from the northern rivers encounter when first entering the sea (cf. Friedland et al. 2003*b*). Temperature data were calculated from average values of every 5th metre

integrated vertically from 0 to 50 m across all stations of the transect as described by Ottersen and Stenseth (2001) and Ozhigin et al. (2003). The Kola section is in close proximity to the rivers, and temperatures in the Kola section are significantly correlated with the temperatures in the central Barents Sea (Ingvaldsen et al. 2003), indicating that this section is representative for the variability of the Atlantic domain in the Barents Sea.

In addition to sea temperature, the NAO (North Atlantic Oscillation; Hurrell 1995) index was related to salmon catches. In this regression analysis, the independent variables were from the principal component adjusted Winter (December–March) NAO index during the first sea winter for each sea-age group and from the station-based NAO index in July during the first summer at sea (NAO Index Data were provided by the Climate Analysis Section, National Centre for Atmospheric Research, Boulder, CO 80307, USA, available from http://www.cgd.ucar.edu/~jhurrell/nao.html).

Results

The mean annual salmon catches from the Rivers Teno (1972-2003) and Näätämöjoki (1975-2003) were 139 tonnes (t; standard deviation (SD) = 48) and 9 t (SD = 3), respectively. In some years, more than 200 t of salmon have been caught in the River Teno, equivalent to a harvest of more than 60 000 fish (Fig. 3). Although the salmon run in the rivers was dominated by 1SW salmon (Table 1), MSW fish do make important contributions, for example, MSW fish comprise an average of 79% of the River Teno catch by weight.

Salmon abundance was positively correlated among the Rivers Teno and Näätämöjoki for 1SW (r = 0.590, p = 0.010) and 2SW (r = 0.748, p = 0.010) salmon and for the total catch (weight) where all sea ages are combined (r = 0.663, p = 0.007), suggesting simultaneous fluctuations in abundance of these northern stocks. However, 3SW salmon were not significantly correlated (p = 0.095).

Estimated salmon catches in the Rivers Teno and Näätämöjoki vary widely among years (Fig. 3). The lowest and highest figures show a threefold difference but no apparent trend for decreased abundance. However, numbers of 4SW salmon (River Teno) show a declining trend, but at the same time, there has been an increasing tendency for increased numbers of previous spawners in the River Teno catch (Table 2). In the River Näätämöjoki, the total salmon catch indicated an increasing trend over years (Table 2).

There were significant positive relationships between the mean sea temperatures in July in the year of smoltification and numbers of 1SW, 2SW, and 3SW salmon in the subsequent catches in the River Teno (Table 3). However, no such relationships were observed in the River Näätämöjoki. The adjusted winter and station-based NAO indices in the first July at sea after smolt run did not show relationships with the subsequent numbers of salmon in the catches.

Discussion

In contrast to observations of declining populations of salmon in many areas of the North Atlantic, stocks examined in this study from northern Norway and Finland have not shown any consistent decline in overall abundance. This is

Table 1. Sea age composition and corresponding proportion of males in Atlantic salmon (*Salmo salar*) samples from the Rivers Teno and Näätämöjoki (both emptying into the Barents Sea in northern Europe).

	River Teno		River Näätämöjoki			
Sea age	Sea age (%)	Males (%)	Sea age (%)	Males (%)		
1	58	81	62	86		
2	15	17	19	20		
3	21	22	16	32		
4	1	65	<1	75		
5	<1	100				
PS	5	44	3	56		
Ν	48 341	27 669	8904	5700		

Note: PS, previous spawners; *N*, total number of samples.

despite continued high rates of fishing that can approach 70% in rivers such as the Teno (Erkinaro et al. 1999), resulting in annual harvests of $20\ 000 - 60\ 000$ salmon. The River Teno salmon catch has accounted for up to 15% of all riverine Atlantic salmon harvests in Europe (1995–2001) and as much as 22% in 2001 (ICES 2002).

Jensen et al. (1999) reported a significant increase in catch of 1SW fish in two Norwegian rivers, Repparfjordelva and Altaelva, in the close proximity to the River Teno, following the closure of the Norwegian drift-net fishery in 1989. Similar responses were noted in two Russian rivers in the Kola Peninsula since 1989 (Jensen et al. 1999). When a longer time period is examined, i.e., 1980-2002, the numbers of 1SW salmon in the catch of five northern Norwegian rivers have also increased significantly, in particular since 1989-1990. This is also attributed to the closure of the marine drift-net fishery (Ugedal et al. 2002). In the present study, high abundance of 1SW salmon has been observed since 1990, although the long-term trend is not significant when the entire period of 1973-2003 is considered. Notwithstanding the last 3 years of lower catches of 1SW salmon, the increase in the 1SW component during the 1990s could be due, in part, to a combined result of the closure of the Norwegian drift-net fishery (1989) and the increase in mesh sizes in the gill-net fisheries in the River Teno introduced in 1990.

Variability among salmon runs, as evidenced from catch (Rivers Teno and Näätämöjoki), is generally consistent between the rivers for 1SW and 2SW salmon and for the overall abundance when sea-age classes are combined in terms of weight, but not for 3SW salmon. The latter could be related to the overall lower contribution of 3SW salmon to the Näätämöjoki catch (~10%) compared with the Teno catch (~27% 3SW). Similar synchrony in catch fluctuations has been recorded between three other northern Norwegian rivers (Ugedal et al. 2002).

Previous investigations have established linkages between ocean climate signals and co-variation in survival or abundance of multiple salmon stocks (e.g., Friedland 1998; Friedland et al. 2003*b*). The synchrony or co-variation in abundance implies sharing or encountering similar environmental conditions at various life-history stages, although we note that different sea-age classes can be present in different areas owing to the length of time that fish remain at sea (Hansen and Quinn 1998). Consequently, knowledge of **Fig. 3.** Estimated yearly catches by weight (tonnes; all sea ages combined) or by numbers for 1-sea-winter (1SW), 2SW, 3SW, and 4SW salmon (*Salmo salar*) and previous spawners for Rivers Teno and Näätämöjoki. The solid line represents the LOWESS regression trend with individual smoothing values (F) shown separately for each component.



Year

Table 2. Results of trend analys	es between the estimated	d numbers of salmon at	t different sea-age class	ses or total catch by weight (kg
all sea ages combined) versus ye	ear for Rivers Teno and	Näätämöjoki.		

River	Dependent variable	No. of years	Autoregression coefficient AR(1) of autoregression- corrected model	<i>p</i> value of likelihood ratio χ^2 test of the difference between AR(1)-corrected and ordinary linear regression model ^{<i>a</i>}	<i>p</i> value of the regression coefficient of year (significance of the trend of the selected model)	Direction of the trend
Teno	1SW	31	0.53	0.002 ^{AR}	0.163	
	2SW	31	0.52	0.002 ^{AR}	0.602	
	3SW	31	0.56	0.001 ^{AR}	0.322	
	4SW	29	0.65	0.005 ^{AR}	0.002	Declining
	Previous spawner	30	0.88	<0.0001 ^{AR}	0.046	Increasing
	Total catch (kg)	32	0.68	< 0.0001 ^{AR}	0.703	
Näätämöjoki	1SW	19	0.02	0.944 ^{LR}	0.423	
	2SW	19	0.44	0.043 ^{AR}	0.387	
	3SW	19	0.52	0.026 ^{AR}	0.904	
	Previous spawner	19	-0.03	0.899 ^{LR}	0.759	
	Total catch (kg)	29	0.319	0.076 ^{LR}	0.026	Increasing

Note: Autoregression-corrected regression model or ordinary linear regression model was selected for trend analysis depending on the results of the likelihood ratio tests. Where statistically significant results for a year effect occurred, the direction of the trend was noted. SW, sea-winter.

^{*a*}If the *p* value is <0.05, then the AR(1)-corrected regression was selected for valid model of the trend analysis (superscripted by AR), otherwise the ordinary regression model was selected (superscripted by LR).

Table 3	6. Co-variation	between t	he mean	July sea	a temperature	from th	e Kola	section	of the	Barents	Sea and	estimated	numbers	s of
salmon	caught by sea-	-age class	of River	s Teno a	ınd Näätämöj	oki.								

	Dependent	No. of	AR(1) coefficient for autoregression-	<i>p</i> value of likelihood ratio χ^2 test of the difference between AR(1)-corrected and	<i>p</i> value of regression coefficient of
River	variable	years	corrected model	ordinary linear regression model ^a	temperature ⁰
Teno	1SW	31	0.61	0.001 ^{AR}	0.023*
	2SW	31	0.5	0.004^{AR}	0.050*
	3SW	31	0.62	< 0.0001 ^{AR}	0.002**
	4SW	29	0.89	< 0.0001 ^{AR}	0.584
Näätämöjoki	1SW	19	0.03	0.901 ^{LR}	0.376
	2SW	19	0.42	0.104 ^{LR}	0.058
	3SW	19	0.5	0.030 ^{AR}	0.493

Note: Data were lagged according to the respective year salmon migrated out of the rivers as smolts and thus potentially influenced by spring marine environment conditions. Dependence of the salmon catch on temperature was analyzed by autoregression-corrected regression model or ordinary linear regression model depending on the results of the likelihood ratio tests. SW, sea-winter.

^{*a*}If the p value is <0.05 then the AR(1)-corrected regression model was selected for regression model (superscripted by AR), otherwise ordinary regression model was selected for valid model (superscripted by LR) for numbers of salmon on temperature.

^bStatistical significance of the dependence of salmon catch on temperature was indicated by asterisks: *, p < 0.05; **, p < 0.01.

salmon migration and distribution is fundamentally important. In the present study, no relationship with the NAO index and salmon stock fluctuation was detected, although the NAO index has been shown to influence the catches (Friedland et al. 2003a) and trends in sea age at maturity (Jonsson and Jonsson 2004) of Atlantic salmon in other investigations.

Precise knowledge of the location of specific feeding grounds of northern salmon populations, such as the Rivers Teno and Näätämöjoki, is still for the most part unknown, but it is believed to cover a large area of the Northeast Atlantic Ocean. Some data exist to substantiate this general belief. For example, salmon from the Kola Peninsula migrate to and feed at least as far away as the Faroe Islands as about 20% of salmon tagged north of Faroes were later recovered in the northern Russian area (Hansen and Jacobsen 2003).

Although accurate information on ocean migration patterns may be lacking, what is known is that northern European stocks of salmon leave rivers as smolt and enter the Barents Sea environment. In addition to noted fluctuations in salmon abundance, available information on sea temperatures from the Kola section also indicate considerable variation over years. For example, there was a rapid decrease in temperature towards the end of the 1970s, followed by a general increase overlaid by shorter-term variation. Earlier studies have demonstrated that the Kola temperatures show periodic fluctuations with periods of 3.3 and 7.3 years (Loeng et al. 1992; Ingvaldsen et al. 2003) and that the fluctuations are clearly linked to atmospheric forcing (Ådlandsvik and Loeng 1991). The climatic conditions affect the advection, growth rate, and distribution of zooplankton and fish larvae (e.g., Skjoldal et al. 1992; Giske et al. 1998), as well as fish population parameters such as growth, recruitment, migration, and distribution (e.g., Ottersen and Loeng 2000; Stenseth et al. 2002).

Other investigations of long-term climate variability in the Barents Sea have shown that the sea temperatures in 1990s were the warmest since the 1950s (Ingvaldsen et al. 2003).

In parallel, smolt cohorts from the years 1998 and 1999 in the River Teno recruited historically high numbers of 1SW, 2SW, and 3SW salmon in the catches in 1999 and 2000, 2000 and 2001, and 2001 and 2002, respectively. These increases followed warmer sea temperature conditions during the years of smolt migration. However, although sea temperatures since 1999 have been above the long-term average, the number of 1SW fish has declined in three consecutive years since 2000. The reason for the decline in numbers of 1SW salmon could be related to lower smolt output followed by the low spawning escapements in the mid-1990s rather than to unfavorable temperatures at sea.

Following the increase in sea temperatures during the late 1990s, the numbers of PS salmon in the River Teno catches have also increased significantly. This is related to the higher numbers of 1SW fish in 1999–2000, as most of the PS salmon have spawned first as 1SW salmon and then spent a full year at sea before spawning a second time.

Fluctuations in the salmon abundance in relation to environmental conditions at sea should be taken into account when the effectiveness of the fisheries management regulations is assessed, as these fluctuations in the abundance can mask the effects of the regulatory measures. On the other hand, the relationships between stock variations and marine conditions may be obscured by the fact that the status of the stocks is poor and the environmental conditions may be impossible to discriminate from other factors, e.g., fishing. In the present study, these relationships could be analyzed for abundant salmon stocks with no overall declining trend. Fluctuations in catches can be quite severe and occur commonly over wide geographical areas (Dempson et al. 1998). Fluctuations can occur over a long periods of between 20 and 30 years (Bielak and Power 1986) or with shorter oscillating periods of between 8 and 9 years, such as in the rivers Teno and Näätämöjoki. Antonsson et al. (1996) found that the abundance of salmon stocks in northern Iceland demonstrated fluctuations similar to those found in the Kola Peninsula (Russia) 2-3 years earlier and hypothesized that stocks in other areas of the North Atlantic Ocean may show similar fluctuations in abundance with time differences based on the rate of movement of the ocean currents.

The northern salmon rivers are characterized by large natural fluctuations in both 1SW and MSW salmon stocks. This offers the possibility of examining further the potential influence of sea environmental conditions on salmon stocks with variable life histories. To date, the Rivers Teno and Näätämöjoki have been isolated from most human-induced impacts observed to affect negatively the production of salmon in many other populations (see Parrish et al. 1998) and hence confound attempts at establishing similar associations in those stocks. Thus, although many stocks of North Atlantic salmon continue to show declines in abundance (ICES 2002), particularly of the MSW component, the importance of maintaining and studying these largely pristine salmon stocks in northern Europe cannot be underestimated.

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