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Is juvenile salmon abundance related to subsequent and preceding catches? Perspectives from a long-term monitoring programme

E. Niemelä, J. Erkinaro, M. Julkunen, and E. Hassinen

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The abundance of wild Atlantic salmon in the River Teno system has been monitored since the 1970s by estimating salmon catches and juvenile salmon densities at permanent electrofishing sites. Analysis of the time-series has shown significant relationships between juvenile densities (0+ and 1+) and subsequent 1SW and 2SW catches. Corresponding significant relationships have been detected between 1SW and 2SW female salmon in the catches and subsequent fry and parr densities. Monitoring juvenile densities allows evaluation of spawning escapement 1 and 2 years earlier, confirming the stock status information provided by catch statistics. These relationships between juvenile abundance and catches suggest that the monitoring programme has included feasible and biologically relevant variables and proper methodologies. Increasing trends were detected in the numbers of 1SW and 2SW salmon in catches between 1977 and 2003. Similarly, fry abundance indicated long-term increasing trends at most sites. Significant relationships were detected between abundances of subsequent sea-age groups in catches (1SW vs. 2SW 1 year later, etc.), indicating that strong smolt year classes influence the abundance of several subsequent sea-age groups, and that such relationships permit forecasting future catches of multi-sea-winter salmon by 1SW salmon catches.

Keywords: long-term monitoring, prediction, relationships, trends in abundance.

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E. Niemelä, J. Erkinaro, M. Julkunen, and E. Hassinen: Oulu Game and Fisheries Research, Finnish Game and Fisheries Research Institute, Tutkijantie 2, FIN-90570 Oulu, Finland. Correspondence to E. Niemelä: tel: +358 205 751 412; fax: +358 205 751 879; e-mail: eero.niemela@rktl.fi.

Introduction

Monitoring has been defined by Yoccoz *et al.* (2001) as a process of gathering information about a system at different points in time to assess its state and to draw inferences about temporal changes in that state. Monitoring programmes are used to assess spatial and temporal biological trends, with emphasis usually on evaluating the efficiency of management policies. Long-term monitoring is important in understanding ecological phenomena driven by slowly evolving processes, rare, or episodic events, and highly variable, subtle, or complex processes (Franklin, 1989; Elliot, 1990). A key objective of long-term investigations is to provide reliable estimates of baseline variation and to detect any long-term trend in the mean baseline level. Scientific objectives focus on learning and developing an understanding of the dynamics of the target species or phenomenon, and management objectives include the production of information that is useful in making informed management decisions (Elliot, 1994; Yoccoz *et al.*, 2001). Especially in the case of a multivariate problem, long-term data are necessary to provide the required degrees of freedom in statistical analysis. Many ecological phenomena are slow processes that occur over long time scales in a cyclic manner. Long-term studies are clearly essential to determine the frequency and ecological significance of such cycles, because short-term studies may lead to erroneous conclusions about the magnitude and direction of the change if the variance of the estimates exceeds the magnitude of the phenomenon of interest (Elliot, 1994). Moreover, the spatial extent of sampling should be selected to permit inference for generalization to the entire area of interest (Yoccoz *et al.*, 2001).

Over recent decades, Atlantic salmon (*Salmo salar* L.) populations have declined, or have already been extirpated, in most parts of the species' distribution area (Parrish *et al.*, 1998; ICES, 2002). Specific reasons for the continued decline are often unclear, but multiple factors, including overfishing, altered oceanic conditions, and freshwater habitat degradation, are probably responsible (e.g. Dempson *et al.*, 1998; Parrish *et al.*, 1998; Hutchinson *et al.*, 2002). High rates of exploitation in ocean fisheries have been associated with many stock declines, but the abundance of many stocks nevertheless continues to fall despite great reductions in marine salmon fisheries during the past couple of decades (Windsor and Hutchinson, 1994; Parrish *et al.*, 1998; Dempson *et al.*, 2001; ICES, 2002). However, some stocks in the Northeast Atlantic, especially in northern Scandinavia (Norway, Finland), fluctuate in a cyclic manner with no declining trend (Niemelä *et al.*, 2004), and the pre-fishery abundance of the northern stocks has even improved in recent years (ICES, 2003).

Management of salmon stocks is often, or should be, dependent on scientific information about the characteristics and status of the stocks, revealed by various research and monitoring programmes. Ideally, monitoring programmes should be based on long-term data collection providing understanding of the dynamics of the spawning stock and recruitment, as well as of critical population levels (e.g. Kennedy and Crozier, 1993; Parrish *et al.*, 1998; Prévost and Chaput, 2001). However, no such data are available for most salmon rivers in the world, and other methods must be employed, such as transposing a known stock-recruitment relationship from index rivers or a fixed spawning target corrected for local habitat features (O'Connell and Dempson, 1995; Chaput *et al.*, 1998; Milner *et al.*, 2000). For instance, scientific advice from the International Council for the Exploration of the Sea (ICES) for national and international management of salmon stocks is largely based on stock-recruitment data from a handful of index rivers around the North Atlantic, and on pre-fishery abundance estimates that are calculated retrospectively from the salmon catches in home waters (Potter *et al.*, 2004).

The ideal stock-recruitment data series are especially difficult to obtain in large rivers where full control of ascending and descending fish is difficult or impossible. In the absence of information on the size of the spawning population and the number of smolts migrating to the sea, surrogate variables or indices must be used. Typically, the river catch is used as an index of the run size or spawning escapement (e.g. Chadwick, 1985; Winstone, 1993; Saltveit, 1998; Romakkaniemi *et al.*, 2003), and juvenile salmon densities during the freshwater phases are used as an index of the subsequent smolt production (Kennedy and Crozier, 1993).

The objective of the present study was to examine the utility of the long-term monitoring programme for the Atlantic salmon stocks in the River Teno, northern Finland/Norway, by studying the interrelationships between the two major long-term time-series: annually estimated salmon catches of different sea-age groups, and juvenile salmon densities in age groups 0+ (underyearlings, fry) and 1+ (yearling, parr). The comparisons include both validation of the spawning escapement indices, as indicated by catch statistics, in relation to the subsequent juvenile abundance, and also the testing of whether juvenile salmon densities can be related to subsequent catches. In addition, long-term temporal patterns in the time-series were analysed, especially the relationships between, and predictive abilities of, abundance estimates for four subsequent sea-age groups (1−4SW).

Material and methods

Study area

The large Subarctic River Teno (Tana in Norwegian) in northern Europe (70°N, 28°E) drains a catchment area of 16 386 km^2 into the Barents Sea (Figure 1), and represents one of the few remaining large salmon rivers with healthy and abundant wild salmon stocks that still supports large-scale salmon fisheries in both freshwater and coastal waters (Niemelä *et al.*, 2004). In addition to the main stem, there are more than 20 spawning tributaries with distinct salmon sub-populations (Figure 1). The total length of river accessible to adult salmon is c. 1270 km.

The importance of the River Teno to the wild salmon production of the entire North Atlantic is considerable, because the salmon catch of the Teno 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). Management and conservation of the River Teno salmon stocks are based on fishing regulations, because all stocking is prohibited, and salmon production is entirely dependent on natural production.

More information on the biological characteristics and life histories of the River Teno salmon stock is presented, *inter alia*, by Erkinaro *et al.* (1997), Niemelä *et al.* (1999a), and Niemelä (2004).

Salmon stock monitoring

Long-term monitoring of salmon in the River Teno system comprised two main components: juvenile production estimates based on electrofishing programmes (Niemelä *et al.*, 1999a, b) and adult salmon abundance (catch) estimates based on catch statistics and catch samples (e.g. Niemelä *et al.*, 2000b; Niemelä, 2004). Since 1979, juvenile salmon densities have been monitored at 35 permanent electrofishing sites in the River Teno and at 10 sites in the River Inarijoki (Figure 1; Niemelä *et al.*, 1999a, b). These sites were selected to represent a variety of fluvial shoreline habitats, both favourable and less suitable for juvenile salmon, and embrace a broad spectrum of juvenile salmon densities and habitat characteristics. A standardized removal fishing method was used throughout the monitoring programme (Bohlin *et al.*, 1989). Monitoring takes place between 15 July and 15 August, and each site is fished once a year in strict rotation, as close to the same date as possible (see Niemelä *et al.*, 1999a, b, for the long-term monitoring methods), to minimize the effect of possible

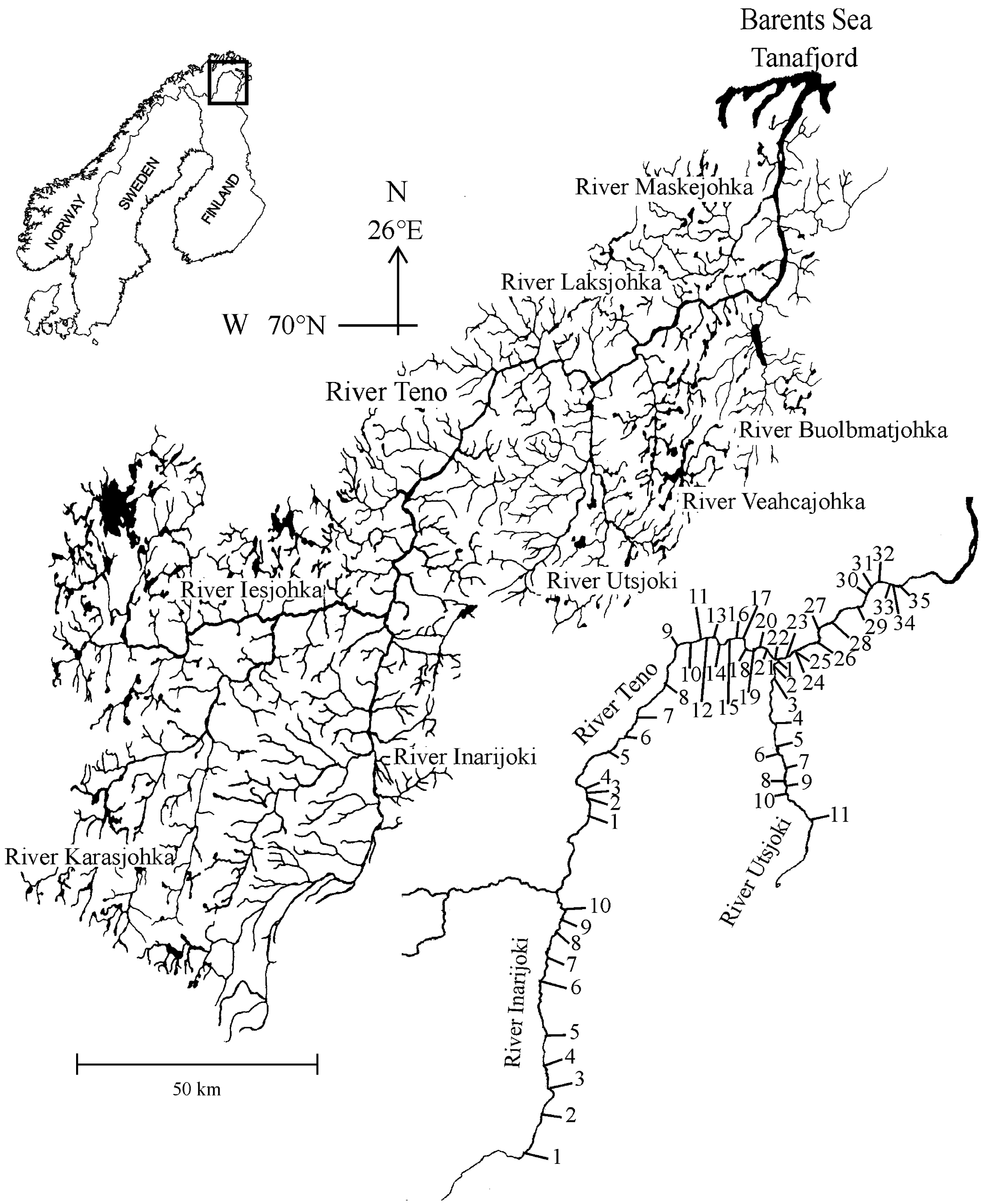

Figure 1. Permanent electrofishing sites in the River Teno system.

seasonal changes in environmental conditions and juvenile salmon abundance (see Niemelä *et al.*, 2001).

A three-pass removal method and Moran–Zippin maximum likelihood calculations were used to estimate the density of fry (0+) and 1+ parr. These groups consist typically 45–55% and 25–30% of the total juvenile salmon abundance, respectively (Niemelä *et al.*, 1999a). The densities of juvenile salmon are presented as fish per 100 m^2 and expressed as mean annual density for all sites of both Rivers Teno and Inarijoki. Sampling sites were also assigned to three different clusters for both rivers, combining similar sites based on density levels and their fluctuations (see Niemelä *et al.*, 1999b). The site clusters roughly represent sites with high density (cluster 1), medium density (cluster 2), and low density of fish (cluster 3), with fry and parr considered separately. Detailed descriptions of the electrofishing and estimation methods used are given by Niemelä *et al.* (1999a, b, 2000a).

In the absence of true measures of the sizes of salmon runs, the salmon catch is considered to represent a surrogate of abundance. There are no quotas to catch salmon in the River Teno system, so the numbers of salmon caught are taken to indicate actual variations in the population. Salmon stocks in the River Teno system are conserved and managed by fishery regulation only, because all fish releases are prohibited. The total annual weights of salmon catches were estimated from postal questionnaires completed by local fishers and tourist anglers, and weight was then converted into numbers of fish using the sea-age distribution of catch samples typically comprising 1000–5000 annual samples. The rate of compliance with postal questionnaires was c. 75% among local fishers (commercial and recreational) and tourist anglers.

Statistical analyses

The estimated numbers of female salmon in 1SW, 2SW, and 3SW groups in annual catches (year n) were related to the annual mean densities of fry (year $n + 1$) and 1+ parr (year $n + 2$) by regression analysis. During preliminary analyses, it was noticed that nearly all regressions included autocorrelation in their error terms, so in the final regression analyses the AR(1) error structure was used (autoregressive error at lag 1). The analysis was performed using SAS version 8.2 PROC MIXED. For the tributary River Inarijoki, the total catch of female salmon (1SW and 2SW) in the entire Teno system was used as an index of spawning abundance, because complete catch data in numbers for this river and for all years were unavailable. However, positive and significant correlation in the numbers of 1SW salmon of a limited number of years between Rivers Teno and Inarijoki ($r = 0.478$, $p < 0.05$) indicated simultaneous fluctuations in 1SW salmon stocks within the entire Teno system.

In the River Teno main stem, catches during the peak run comprise fish from various sub-populations, whereas in August, the active upmigration phase is mostly complete (Erkinaro *et al.*, 1999; Økland *et al.*, 2001) and the August catch would be the best indicator of the number of fish actually spawning in the main stem. However, the annual numbers of fish would have remained low, because >90% of the female salmon catch of the Teno main stem is taken in June and July, and new regulatory measures introduced in the mid-1990s shortened the fishing season in August compared with previous years, so reducing the representativeness of female age groups in samples. The numbers of female salmon were nevertheless significantly correlated between June/July and August (Spearman correlation; 1SW, $r = 0.960$, $p < 0.001$; 2SW, $r = 0.886$, $p < 0.001$; 3SW, $r = 0.964$, $p < 0.001$) before the shortening of the fishing season, so the total annual catches were therefore also used for the Teno. Fecundities of female salmon in different sea-age groups varied between c. 2000–8000, 5000–15 000, and 10 000–23 000 in 1SW, 2SW, and 3SW female salmon, respectively (Erkinaro *et al.*, 1997).

We also related the annual densities of fry and 1+ parr of the River Teno main stem to the subsequent estimated catches (by number) of 1SW, 2SW, and 3SW salmon belonging to the same year classes. The regression model with autoregression error structure was similar to that in the experiment relating adult salmon abundance to subsequent juvenile densities (see above). Owing to the annual variation in the smolt ages between years in the River Teno system (Englund *et al.*, 1999) and between sea-ages (Niemelä *et al.*, 2000b), the numbers of salmon from each year class that recruited to the catch over several years were combined. For example, when related to fry density, the recruited number of 1SW salmon in the catch included fish that were caught 3 (smolt age 2 years, mean <0.1% of the smolt ages of 1SW salmon; Niemelä *et al.*, 2000b), 4 (3 years, 20%), 5 (4 years, 57%), 6 (5 years, 21%), and 7 (6 years, 2%) years later.

Examination of potential temporal trends in the abundance of virgin 1–4SW salmon was restricted to the period 1977–2003, because the 1+ parr detected in 1979 when monitoring was started were offspring of the 1977 spawning population. The trends for adult salmon and fry and 1+ parr ($\log_{10}(x + 1)$ transformed) were analysed by regression. Cross-correlation analysis was used to identify the concurrence of salmon stock variation between consecutive sea-ages in the period 1975–2003. Cross-correlation for a positive lag indicates a relationship between the number of salmon of different sea-ages that number of years later, or for a negative lag that number of years earlier. The hypothesis was that if the number of 1SW salmon influences the numbers of 2SW, 3SW, and 4SW salmon in subsequent years, a cross-correlation of this type should be detectable. Similar relationships were also examined between other sea-age groups (2SW vs. 3SW; 2 SW vs. 4SW; 3SW vs. 4SW). Variation in the number of salmon in the catch for consecutive years from 1975 to 2003 was studied with autocorrelation analysis performed separately on age groups 1–4SW. The hypothesis was that if the numbers of salmon in the catch show a temporal pattern, an autocorrelation should be detected. The autocorrelations were analysed before and after trend removal. The significance of the cross-correlation and autocorrelation was accepted if the 95% confidence limit for the correlation was exceeded.

Results

Significant positive regressions were found for the River Teno between the number of 2SW female salmon in the catch and subsequent fry density at all electrofishing sites combined, as well as in site clusters 2 and 3 (Table 1). There was also a significant relationship between the number of 3SW females in the catch and fry density in site

Table 1. Dependence of salmon fry (0+) density (dependent variable) in various clusters and at all sites on the estimated numbers of 1SW, 2SW, and 3SW salmon in the previous years' catch (independent variable) in the Rivers Teno and Inarijoki by regression model with autoregression AR(1) covariance structure.

River/juvenile fish age	Dependent variable	Independent variable	Number of years	AR(1) coefficient*	p-Value of likelihood ratio†	p-Value of regression‡	r^2_{tot}§
Teno/0+	Cluster 1	1SW	26	0.41	0.046	0.821	0.013
	Cluster 2	1SW	26	0.56	0.003	0.765	−0.002
	Cluster 3	1SW	26	0.88	0.0001	0.080	−0.127
	All sites	1SW	26	0.84	0.0001	0.811	−0.005
Inarijoki/0+	Cluster 1	1SW	26	0.76	0.008	0.975	−0.001
	Cluster 2	1SW	26	−0.05	0.849	0.614	0.009
	Cluster 3	1SW	26	0.36	0.274	0.331	−0.033
	All sites	1SW	26	0.66	0.026	0.999	−0.001
Teno/0+	Cluster 1	2SW	26	0.44	0.025	0.394	−0.005
	Cluster 2	2SW	26	0.47	0.011	**0.0004**	0.441
	Cluster 3	2SW	26	0.34	0.319	**0.001**	0.492
	All sites	2SW	26	0.70	0.001	**0.0001**	0.518
Inarijoki/0+	Cluster 1	2SW	26	0.20	0.565	**0.007**	0.331
	Cluster 2	2SW	26	−0.51	0.229	**0.001**	0.328
	Cluster 3	2SW	26	−0.06	0.817	0.07	0.107
	All sites	2SW	26	−0.20	0.534	**0.0001**	0.386
Teno/0+	Cluster 1	3SW	26	0.51	0.043	0.365	−0.098
	Cluster 2	3SW	26	0.45	0.062	0.126	0.195
	Cluster 3	3SW	26	0.85	0.001	**0.039**	0.199
	All sites	3SW	26	0.83	0.001	0.518	0.072

*AR (1) coefficient for autoregression corrected model.
†p-Value of a likelihood ratio χ^2 test of the difference between AR(1) corrected and ordinary linear regression models.
‡p-Value of the regression coefficient of the independent variable. Significant relationships are emboldened.
§$r^2_{tot} = 1 - [SSE/SST]$, where SST is the sum of squares for the original response variable corrected for the mean, and SSE is the final error sum of squares.

cluster 3 (Table 1). The number of 1SW female salmon was significantly related to 1+ parr density in the subsequent year at all sites combined and in cluster 1, and the number of 2SW female salmon was also related to 1+ parr density at all sites and in clusters 1, 2, and 3 (Table 2). No significant relationship between the number of 3SW female salmon and 1+ parr densities was detected.

In the River Inarijoki, the number of 2SW female salmon was significantly related to subsequent fry density for all sites combined and in clusters 1 and 2 (Table 1). Significant relationships were detected between the number of 1SW and 2SW female salmon and the subsequent 1+ parr density of all clusters and all sites combined (Table 2).

When juvenile density was related to the subsequent catch of salmon of the same year class, significant positive relationships were detected between fry density at all sites combined and the number of 1SW salmon in the River Teno (Table 3). The same was true between fry density (sites combined, clusters 2 and 3) and the number of 2SW salmon in the subsequent catch (Table 3). Similarly, parr densities (sites combined, cluster 1) were significantly related to the number of 2SW salmon in subsequent catches (Table 3).

Both salmon catch and juvenile density showed considerable annual variation over the monitoring period (Figures 2–4). A significant increasing trend in the estimated numbers of salmon in the catch in the period 1977–2003 was detected for both sexes of 1SW and 2SW salmon ($p < 0.01$). The only declining trend detected was in the number of 4SW females ($p < 0.01$), and there was no trend in the number of 3SW fish.

In parallel with increasing salmon catches, fry and 1+ parr densities (all sites combined) increased significantly ($p < 0.01$) in both rivers (Figures 3 and 4). Fry density also increased significantly ($p < 0.05$) in all clusters in the River Inarijoki and in cluster 3 in the River Teno (Figure 3). Parr densities in individual clusters showed one increasing trend ($p < 0.001$) in the River Inarijoki, in cluster 1 (Figure 4).

Positive cross-correlations were found between the number of 1SW and 2SW salmon in the same year (Pearson correlation; $r = 0.556$, $p < 0.01$), especially with a 1-year lag ($r = 0.787$, $p < 0.001$). There were positive correlations with a 1-year lag between the number of 2SW and 3SW salmon ($r = 0.544$, $p < 0.01$), between 3SW and 4SW salmon ($r = 0.593$, $p < 0.001$), and also between 3SW and 4SW salmon in the same year ($r = 0.405$, $p < 0.05$).

Table 2. Dependence of 1+ salmon parr density (dependent variable) in various clusters and at all sites on the estimated numbers of 1SW, 2SW, and 3SW salmon in the previous years' catch (independent variable) in the Rivers Teno and Inarijoki by regression model with autoregression AR(1) covariance structure.

River/juvenile fish age	Dependent variable	Independent variable	Number of years	AR(1) coefficient*	p-Value of likelihood ratio†	p-Value of regression‡	r^2_{tot}§
Teno/1+	Cluster 1	1SW	26	−0.09	0.679	**0.027**	0.195
	Cluster 2	1SW	26	0.24	0.232	0.156	0.095
	Cluster 3	1SW	26	−0.22	0.315	0.081	0.101
	All sites	1SW	26	0.22	0.280	**0.036**	0.197
Inarijoki/1+	Cluster 1	1SW	26	0.04	0.854	**0.004**	0.306
	Cluster 2	1SW	26	−0.21	0.330	**0.050**	0.098
	Cluster 3	1SW	26	−0.03	0.903	**0.002**	0.355
	All sites	1SW	26	0.02	0.938	**0.003**	0.313
Teno/1+	Cluster 1	2SW	26	−0.12	0.588	**0.012**	0.242
	Cluster 2	2SW	26	0.19	0.346	**0.006**	0.288
	Cluster 3	2SW	26	−0.55	0.011	**0.001**	0.236
	All sites	2SW	26	0.07	0.741	**0.001**	0.441
Inarijoki/1+	Cluster 1	2SW	26	−0.00	0.999	**0.001**	0.487
	Cluster 2	2SW	26	−0.15	0.441	**0.005**	0.249
	Cluster 3	2SW	26	0.29	0.190	**0.04**	0.231
	All sites	2SW	26	−0.04	0.823	**0.001**	0.563
Teno/1+	Cluster 1	3SW	26	−0.14	0.594	0.563	0.004
	Cluster 2	3SW	26	0.26	0.251	0.859	0.009
	Cluster 3	3SW	26	−0.15	0.474	0.804	0.004
	All sites	3SW	26	0.29	0.156	0.335	0.050

*AR (1) coefficient for autoregression corrected model.
†p-Value of a likelihood ratio χ^2 test of the difference between AR(1) corrected and ordinary linear regression models.
‡p-Value of the regression coefficient of the independent variable. Significant relationships are emboldened.
§$r^2_{tot} = 1 - [SSE/SST]$, where SST is the sum of squares for the original response variable corrected for the mean, and SSE is the final error sum of squares.

Negative cross-correlations were recorded between the number of 4SW salmon and the number of 1SW salmon in the same year ($r = -0.467$, $p < 0.05$). Autocorrelation analysis indicated a temporal dependence of the number of 1SW, 2SW, and 3SW salmon with a 1-year lag, owing to temporal trends in the catch. After removing the trend from the time-series, no correlations were detected.

Discussion

In this 26-year monitoring programme in the River Teno system, long-term variations in 1SW and 2SW female salmon catches explained a significant proportion of the subsequent variation in juvenile salmon abundance. In addition, variation in juvenile abundance, especially at high-density sites and when all sites were combined, explained a significant proportion of the variation in subsequent catches of 1SW and 2SW salmon. These relationships suggest that the monitoring programme included feasible and biologically relevant variables and proper methodologies.

Similar relationships have also been detected in some other salmon rivers. In the River Suldalslågen (Norway), the total catch and the number of female salmon >5 kg correlate significantly with mean fry density at all sites in the river (Saltveit, 1996). In addition, parr density in the Rivers Miramichi and Restigouche (Canada) is linearly correlated with the angling catch of large salmon (>63 cm; Chadwick, 1985). In contrast, recently increasing densities of juvenile salmon have not resulted in an increased abundance of adult salmon in the River Miramichi (DFO, 2003), a result taken to indicate a temporal change in mortality in the western Atlantic Ocean.

The most valuable indicators of salmon stock status include the run size and spawning escapement. In large rivers, long-term monitoring of salmon stock size is difficult. In most cases there is no possibility of estimating accurately the number of ascending salmon or spawning escapement, so the reported catch is used as an index of both abundance and spawning escapement (Chadwick, 1985; but see Bielak and Power, 1986a). It is also generally accepted that the catch data describe the fluctuations and

Table 3. Dependence of the estimated numbers of 1SW, 2SW, and 3SW salmon in the subsequent catch (dependent variable) in the River Teno on salmon fry (0+) and 1+ parr density (independent variable) in various clusters and at all sites by regression model with autoregression AR(1) covariance structure.

River/juvenile fish age	Dependent variable	Independent variable	Number of years	AR(1) coefficient*	p-Value of likelihood ratio†	p-Value of regression‡	r^2_{tot}§
Teno/0+	1SW	Cluster 1	20	0.69	0.003	0.079	0.222
	1SW	Cluster 2	20	0.71	0.001	0.139	0.172
	1SW	Cluster 3	20	0.70	0.007	0.141	0.187
	1SW	All sites	20	0.65	0.005	**0.024**	0.338
Teno/0+	2SW	Cluster 1	19	0.66	0.001	0.143	0.105
	2SW	Cluster 2	19	0.68	0.001	**0.008**	0.254
	2SW	Cluster 3	19	0.59	0.011	**0.046**	0.268
	2SW	All sites	19	0.66	0.001	**0.009**	0.277
Teno/0+	3SW	Cluster 1	18	0.61	0.004	0.326	0.093
	3SW	Cluster 2	18	0.61	0.004	0.545	0.054
	3SW	Cluster 3	18	0.63	0.002	0.786	−0.006
	3SW	All sites	18	0.61	0.005	0.449	0.077
Teno/1+	1SW	Cluster 1	21	0.77	0.002	0.333	0.111
	1SW	Cluster 2	21	0.77	0.002	0.128	0.196
	1SW	Cluster 3	21	0.80	0.001	0.459	−0.028
	1SW	All sites	21	0.79	0.001	0.474	0.078
Teno/1+	2SW	Cluster 1	20	0.599	0.007	**0.014**	0.366
	2SW	Cluster 2	20	0.619	0.002	0.155	0.153
	2SW	Cluster 3	20	0.651	0.001	0.981	−0.001
	2SW	All sites	20	0.593	0.006	**0.032**	0.295
Teno/1+	3SW	Cluster 1	19	0.574	0.008	0.147	0.264
	3SW	Cluster 2	19	0.648	0.001	0.291	0.015
	3SW	Cluster 3	19	0.571	0.007	0.219	0.254
	3SW	All sites	19	0.651	0.001	0.091	0.101

*AR (1) coefficient for autoregression corrected model.
†p-Value of a likelihood ratio χ^2 test of the difference between AR(1) corrected and ordinary linear regression models.
‡p-Value of the regression coefficient of the independent variable. Significant relationships are emboldened.
§$r^2_{tot} = 1 - [SSE/SST]$, where SST is the sum of squares for the original response variable corrected for the mean, and SSE is the final error sum of squares.

development of fisheries (see references in Hansen, 1988; Shelton, 2001). In the large River Teno, a counting fence operation would be difficult, if not impossible. The total salmon catch by weight is therefore converted into number of salmon in different sea-age groups, which is thought to provide a realistic index of both stock size and spawning escapement. There are no quotas to catch salmon in the River Teno system for either net fisheries or the rod fishery. The estimated number of salmon caught may therefore indicate realistic variations between years and between different parts of the system, as also revealed by the synchrony in 1SW salmon catches between the Rivers Teno and Inarijoki. The annual surveys of juvenile density allow evaluation of the spawner abundance 1 and 2 years earlier, and they too confirm the stock status information provided by earlier catch statistics. On the other hand, significant deviations in juvenile abundance from that predicted by catch estimates would indicate changes in the exploitation rate in river fisheries (cf. Erkinaro *et al.*, 1999). River catches are also successfully used as indices of abundance and have been closely linked to the subsequent density of juvenile salmon in some Baltic salmon rivers, where wild populations have improved substantially since the mid-1990s (Romakkaniemi *et al.*, 2003).

It may be assumed that large 3SW females constitute the most important sea-age group influencing the abundance of juvenile salmon, because such females comprise on average >40% of the spawning females (Niemelä, 2004), and their contribution to egg deposition is even greater owing to their high fecundity (Erkinaro *et al.*, 1997). However, the number of 3SW females was only minimally related to the abundance of juveniles. This might be a consequence of the relatively limited annual variation in their abundance in the period 1977–2003. By contrast, the abundance of 2SW females showed pronounced variation, with a significantly increasing trend in the years 1977–2003, possibly

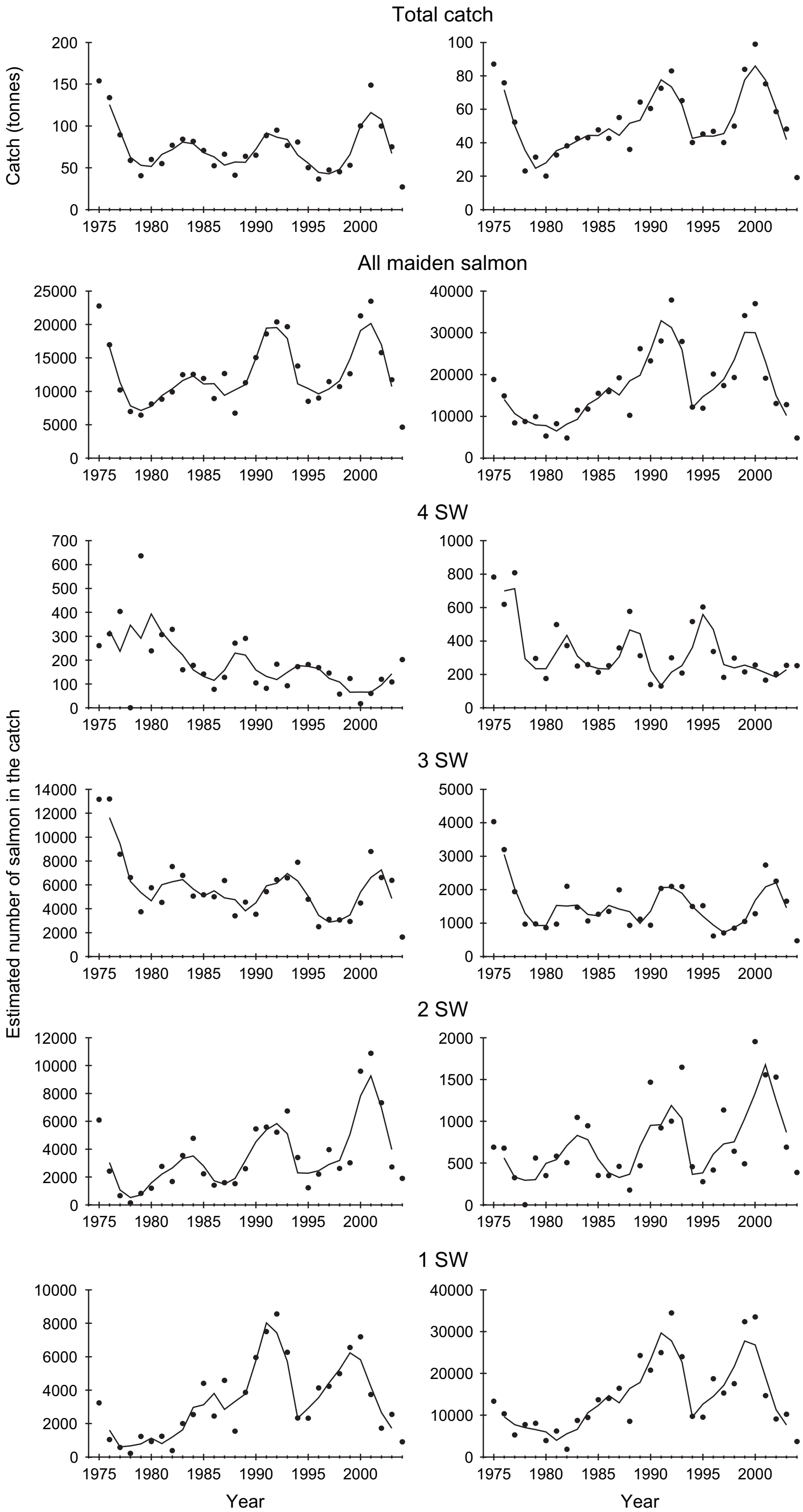

Figure 2. Total catch and estimated numbers of 1–4SW salmon in the catch in the River Teno system in the years 1975–2004. Left, females; right, males. The solid line represents the 3-year running mean in each sea-age group.

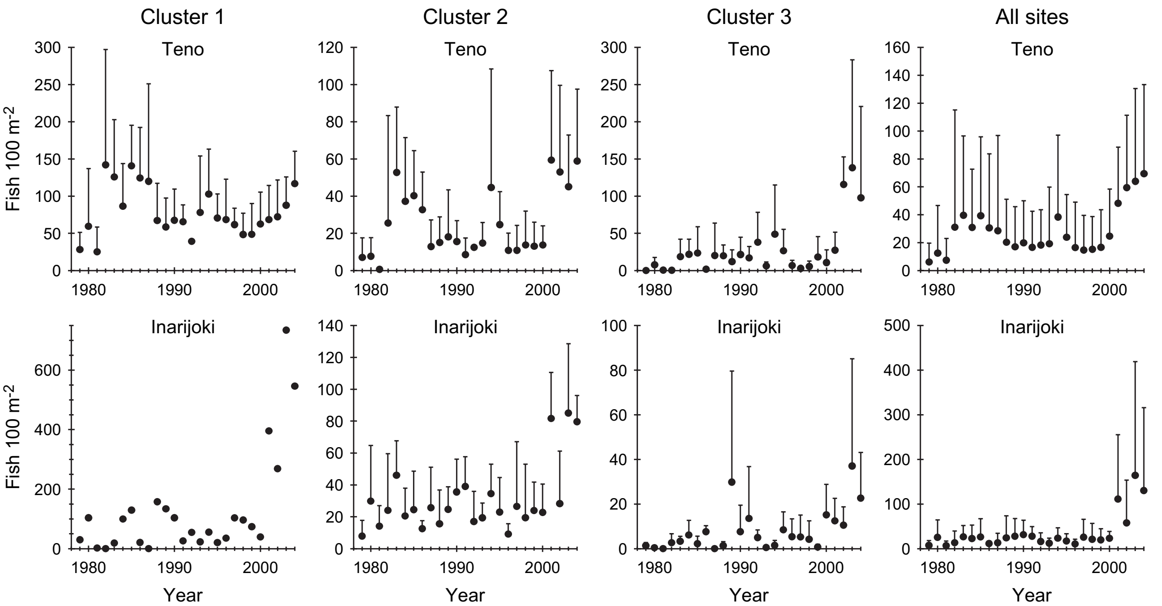

Figure 3. Densities (mean + s.d.) of salmon fry (0+) in the Rivers Teno and Inarijoki in clusters 1–3, and at all sites combined in the years 1979–2004.

reflecting cessation of the Norwegian driftnet fishery at sea in 1989, a closure that resulted in similar consequences in some Barents Sea rivers in Norway and the Russian Kola Peninsula (Jensen *et al.*, 1999). This increase in 2SW females was followed by an increase in fry abundance (Figures 2 and 3). Because of their relative abundance and high fecundity, 2SW and 3SW females produce most of the eggs in the River Teno system, but the variation in juvenile density appears to be driven by 2SW females.

There were only few relationships in the River Teno between 1SW females and density of juveniles, although the number of 1SW salmon in the catches has increased

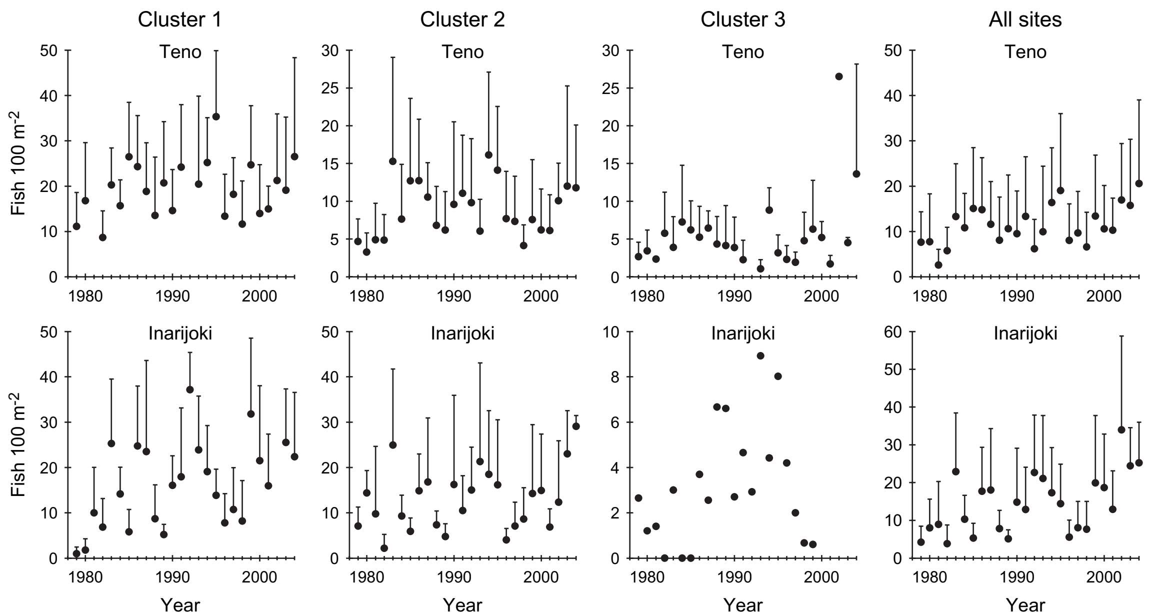

Figure 4. Densities (mean + s.d.) of 1+ parr in the Rivers Teno and Inarijoki in clusters 1–3, and at all sites combined in the years 1979–2004.

significantly. A large proportion of the 1SW salmon entering the River Teno main stem migrate to tributaries, so do not contribute to the production of juveniles in the main stem. Moreover, the new management measures introduced in 1990 in the River Teno (Niemelä *et al.*, 1999a), and the prohibition of driftnet fishing at sea since 1989 (Jensen *et al.*, 1999) have together fostered increased spawning escapement of 1SW fish into tributaries. This variation is not reflected in the juvenile densities of the River Teno main stem. By contrast, 1SW salmon constitute a large proportion of the River Inarijoki spawning population (Niemelä, 2004), and for this case, positive relationships were detected between the number of 1SW salmon in the catch and juvenile abundance.

The selection of electrofishing sites to monitor juvenile abundance in the River Teno system in 1979 has seemingly been successful, because the densities of juvenile salmon have responded to variations in the catches, both when all sites have been combined, and in clustered sites. These site clusters differ from each other in terms of density and habitat characteristics. For instance, cluster 1 in the River Teno contains the best fry sites, supposedly close to the important spawning areas. As these spawning areas may have annually received a high and quite stable number of spawners, regardless of general stock status, the annual variation in fry density may reflect some of that stability and, consequently, no relationship between 2SW female salmon number and fry density was detected for cluster 1 sites in the River Teno. In years with higher 2SW salmon abundance in the River Teno, females may have also moved into less favourable spawning areas to reproduce, possibly represented by the sites in clusters 2 and 3. Hence, clusters 2 and 3 respond to fluctuations in the catch. Milner *et al.* (1981) and Shirvell and Dungey (1983) concluded that the high spawning escapement resulted in spawning also in areas with less favourable spawning habitat. Another possible explanation is that the high-density sites in cluster 1 have reached the "carrying capacity" in most years, and increasing numbers of spawners are reflected in better recruitment only in lower-density sites in clusters 2 and 3.

Similar interpretation of the relationships with parr density is more complicated, because the observed densities at a site do not necessarily reflect a direct causal relationship with the preceding female salmon abundance nearby, as might be the case with fry. In the River Teno main stem, parr densities responded to the catches in all clusters, and especially in cluster 1. This suggests that many of the high-density sites have not yet reached "carrying capacity", and that the parr densities follow closely the abundance of the spawning population. Moreover, the relationship between the abundances of spawners and their offspring appears to be linear, at least within most of the ranges experienced during the 26-year monitoring period.

Successful management of wild salmon stocks would ideally be based on knowledge of juvenile production capacity and the number of female spawners (eggs) needed to achieve it, or on the reference points described by stock-recruitment functions (Prévost and Chaput, 2001). However, no such data are available for most salmon rivers in the world, so other methods must be employed, such as transposing a known stock-recruitment relationship or a fixed spawning target corrected for local habitat features (O'Connell and Dempson, 1995; Chaput *et al.*, 1998; Milner *et al.*, 2000). Freshwater habitat characteristics have been used to assess juvenile salmon production capacity, for example using the stream gradient as a predictor (Amiro, 1993), or by percentage habitat saturation (PHS), i.e. the sum of the predicted territory areas of individual fish in a river (Grant and Kramer, 1990). A PHS of 100% indicates that fish fully occupy the territories. In the River Teno, habitat models have been used to define reference levels for juvenile salmon density, and these methods have indicated certain areas with a high-quality habitat that failed to attain their predicted levels of juvenile salmon density (J. Erkinaro *et al.*, unpublished data). In many other salmon rivers elsewhere, changes in juvenile abundance have been monitored at different spawning levels, with the conclusion that parr populations were at a low density and below the inflexion point on their stock-recruitment curves (Chadwick and Randall, 1986).

The size and variation of the run size are highly dependent on the preceding smolt output (Chadwick, 1987; Jonsson *et al.*, 1998), fluctuations in environmental conditions at sea, and marine fishing mortality (Jonsson and Jonsson, 2004, and references therein). Oscillations in abundance can follow a long period of 20–30 years of high catches (Bielak and Power, 1986b), or a shorter period of 8 or 9 years, as in the River Teno system (Niemelä *et al.*, 2004), and can also be common over wide geographical areas (Dempson *et al.*, 1998).

The warmer sea temperatures in the Barents Sea in the late 1990s (Niemelä *et al.*, 2004) coincided with smolt cohort migrations, which recruited historically high numbers of 1SW, 2SW, and 3SW salmon in the River Teno catches in the years 1999–2002. This coincided with a higher pre-fishery abundance of multi-sea-winter salmon in the North Atlantic than in previous years (ICES, 2003). However, while the mean sea temperature since 1999 has been consistently above the long-term average, the number of 1SW fish has declined in 4 consecutive years since 2000. The recent decline in numbers of especially 1SW salmon and also to some extent of 2SW and 3SW salmon should perhaps be related to low juvenile abundance in the second half of the 1990s, rather than to unfavourable temperatures at sea.

Ultimately, the freshwater exploitation of salmon determines spawning escapement. In the River Teno, the exploitation rates in the river fisheries can approach 70% (Erkinaro *et al.*, 1999; Karppinen *et al.*, 2004), resulting at times in annual harvests of 20 000–60 000 salmon (Niemelä *et al.*, 2004). Fisheries in the main stem essentially exploit all sub-stocks of the River Teno system, and supposedly strongly influence juvenile salmon production.

The densities of fry and parr were characterized by great variation over the 26-year period from 1979 to 2004. Densities of juveniles, especially fry, gradually increased in the long term, a trend driven mainly by the strong increase in the 3–4 latest years and the low densities at the start of the monitoring period. Parr densities did not increase in most cases, probably because the high fry density in recent years has not yet induced an increasing trend in parr density.

In the River Teno, the effects of changes in juvenile abundance are slowly reflected in subsequent salmon catches, and are scattered over several years because of slow juvenile growth (Erkinaro and Niemelä, 1995), resulting in a wide range of smolt ages (2–8 years; Niemelä, 2004), and highly variable sea-ages (1–5) and repeated spawning runs (Niemelä *et al.*, 2004). Bearing this in mind, the regression models explained relatively well the variation in salmon catches in relation to the preceding juvenile abundances.

Crozier and Kennedy (1995a, b) successfully used an abundance index of salmon fry when predicting subsequent smolt production. For the River Teno, there are no annual estimates of smolt production for the entire system. Juvenile salmon density nevertheless appeared capable of predicting subsequent 1SW and 2SW salmon catches, ages that account for, on average, 70% of the total catch by number. Another possibility for prediction is the relationship between consecutive sea-ages of salmon, because significant correlations with a lag of 1 year were detected between all consecutive sea-age groups. This relationship has also been used elsewhere as a basis for forecasting yield and escapement of 2SW salmon from the yield and escapement of grilse in the preceding year (Power, 1981; Scarnecchia, 1984; Bielak and Power, 1986b; Jonsson *et al.*, 1998). On the other hand, the significant positive correlation between 1SW and 2SW salmon in the same years indicates that strong year classes may make strong contributions to several smolt cohorts, and so influence the abundance of several sea-age groups, even in the same year.

This study involved monitoring juvenile salmon abundance and subsequent catches over 26 years, and covered approximately four generations of 1SW and 2SW salmon. The slow regeneration of salmon stocks in the River Teno system highlights the importance of long-term monitoring in distinguishing and interpreting the considerable annual variation in catch estimates and juvenile abundance, and in their relationships. These relationships have statistical power only if sufficient time-series data are available. Further, Hilborn and Walters (1992) emphasized that in order to understand how recruitment responds over a range of spawning stock sizes, the stock must be observed over a sufficient range with enough observations near the extreme values to overcome time-series bias. Short-term data usually lack the statistical power to detect responses in long-term processes, because the variance can be large compared with the magnitude of the trend (Elliot, 1994).

Long-term monitoring of the River Teno salmon stocks has aimed at developing an understanding of the dynamics of these exceptionally diverse salmon stocks, which now constitute the most variable sea- and river-age combinations within the distribution area of the species, and one of the few remaining abundant large wild salmon stock complexes. Such long-term information can facilitate appropriate management decision-making in terms of utilizing and safeguarding these valuable salmon stocks.

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