

# Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river

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**Abstract:** We used over 154 000 scale samples collected from salmon fisheries in the large River Teno system over a 40-year period to quantify life history diversity and long-term trends. We identified 120 different life history strategies, including combinations of smolt (2–8) and sea ages (1–5) and previous spawning events. Most strategies were rare; 60% of individuals matured after 1 year at sea following 3–5 years in fresh water. Age at maturity changed with an increase in two-sea-winter salmon and previous spawners and a decline in three-sea-winter fish. Smolt age distribution showed a decreasing proportion of age-3 smolts, while that of age-5 smolts increased. Fishing gear and fishing season times selected for fish differing in life history strategies. Temporal variation in life histories reflected changes in both fisheries and the changing environment. There was an inverse relationship between years spent in fresh water and sea age. Biocomplexity was manifested by the multiple year classes (6–11) present in annual runs, which increased with years, reflecting an increase both in previous spawners and sampling effort. The high number of cohorts spawning simultaneously each year indicates strong generational overlap, which has been suggested to maintain genetic diversity and thereby resilience via the portfolio effect.

**Résumé :** Nous avons utilisé plus de 154 000 échantillons d'écaille prélevés de pêches au saumon dans le grand réseau du fleuve Teno sur une période de 40 ans pour quantifier la diversité des cycles biologiques et les tendances à long terme. Nous avons décelé 120 stratégies de cycle biologique différentes incluant des combinaisons d'âges de saumoneaux (2–8) et au stade marin (1–5) et d'épisodes de frai antérieurs. La plupart des stratégies étaient rares; 60 % des individus atteignaient la maturité après 1 année en mer suivant 3–5 années en eau douce. L'âge à la maturité a changé avec l'augmentation des saumons ayant passé deux hivers en mer et des frayeurs répétitifs, et une baisse des saumons ayant passé trois hivers en mer. La distribution des âges de saumoneaux est caractérisée par une diminution de la proportion de saumoneaux de 3 ans, alors que celle des saumoneaux de 5 ans a augmenté. Les engins de pêche et le moment des saisons de pêche ont entraîné la sélection de poissons présentant des stratégies de cycle biologique différentes. La variation dans le temps des cycles biologiques reflète des changements tant dans les pêches que du milieu ambiant. Il existe une relation inverse entre les années passées en eau douce et l'âge en mer. Une biocomplexité se manifeste dans les multiples classes d'âge (6–11) présentes dans les migrations annuelles qui augmentent au fil des années, reflétant une augmentation tant du nombre de frayeurs répétitifs que de l'effort d'échantillonnage. Le grand nombre de cohortes frayant simultanément chaque année indique un fort chevauchement des générations, et il a été suggéré que ce phénomène maintiendrait la diversité génétique et, du coup, la résilience par l'entremise de l'effet de portefeuille. [Traduit par la Rédaction]

## Introduction

Biocomplexity in fish populations, that is, their diversity and variation in life history and genetic characteristics, provides resilience to disturbances by spreading risk temporally and spatially and thus contributes to long-term sustainability (Stearns 1992; Hilborn et al. 2003; Schindler et al. 2010). Sufficient diversity in populations is also a prerequisite for sustainable fisheries (Hilborn et al. 2003; Hutchinson 2008). Typically, diversity comprises variation in the age at maturity — individuals from the same cohort reproducing in different years — or iteroparity with the possibility of repeated spawning events for individual fish; both types of diversity allocate reproductive effort across multiple years and stabilize populations under environmental variability (Schindler

et al. 2010; Moore et al. 2014). It is therefore important to characterize the levels of, and changes in, diversity in exploited populations so that the potential importance of biocomplexity for sustaining productivity can be assessed. Such data also provide a baseline for assessing the potential effects of climate change.

Anadromous salmonid fish exhibit especially wide variation in life histories among fish species. These salmonids vary greatly both in time spent in fresh water before the oceanic migration and in duration of the marine feeding migration and connected timing of return migration to fresh water for spawning (e.g., Klemetsen et al. 2003). The simplest set of different salmonid life histories is that of pink salmon (*Oncorhynchus gorbuscha*) and the most complex those of steelhead trout (*Oncorhynchus mykiss*; Thorpe

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1998; Moore et al. 2014) and Atlantic salmon (*Salmo salar*; Klemetsen et al. 2003; Niemelä et al. 2006a).

Life history variation in Atlantic salmon is matched by few, if any, other fish species. Juvenile years spent in freshwater residence and the subsequent years spent at sea are the main drivers causing variation in age and size at maturity (Hutchings and Jones 1998; Klemetsen et al. 2003; Niemelä et al. 2006a). Some individuals also reach maturity in fresh water at ages between 1 and 5 in a size range of ~7–15 cm (Myers et al. 1986; Fleming 1996; Heinimaa and Erkinaro 2004). Anadromous life history types range from the most common group of one-sea-winter salmon (1SW; return to fresh water for reproduction after staying one winter at sea) to four- or even five-sea-winter salmon (4–5SW; e.g., Niemelä et al. 2006a). In addition, further variation in life history strategies is added by previous spawners, which return to fresh water after a few months or 1 or more years of reconditioning at sea after the previous spawning migration (e.g., Niemelä et al. 2006a; Chaput and Benoit 2012).

The abundance of Atlantic salmon has declined markedly throughout the North Atlantic since the 1970s (ICES 2017). The reasons for this continuing decline are often not clear, but multiple factors are likely responsible (Friedland et al. 2009; Chaput 2012). A loss of phenotypic diversity has also been reported, namely a general decline in age at maturity, although marked variation exists between rivers and regions (Klemetsen et al. 2003). In particular, a declining number of large multi-sea-winter (MSW) salmon has been evident (e.g., Youngson et al. 2002; Chaput 2012), which has recently also been documented in Chinook salmon (*Oncorhynchus tshawytscha*) across the Northeast Pacific Ocean (Ohlberger et al. 2018). However, in recent years an opposite trend has been observed, namely a decline in 1SW fish in certain areas, e.g., in Norway (Otero et al. 2012; Jonsson et al. 2016). Historically, many populations across the species' range have exhibited a wide spectrum of life histories, including various smolt ages and multiple groups of sea ages of first-time spawners and previous spawners, e.g., in the Baltic Sea (Järvi 1948), Norway (Abrahamsen 1968; Jonsson et al. 1991; L'Abée-Lund et al. 2004), northwestern Russia (Studenov et al. 2008), Scotland (Shearer 1992), and eastern North America (Schaffer and Elson 1975; Saunders and Schom 1985). In addition to selective fisheries targeting large salmon (e.g., Consuegra et al. 2005; Gauthier-Ouellet et al. 2009), hatchery propagation and introgression with farmed escaped fish can reduce life history diversity within populations and homogenize the dynamics of wild salmon populations (Moore et al. 2010; Karlsson et al. 2016; Bolstad et al. 2017).

Given the widespread losses of salmon population diversity and the extent to which river systems are affected by anthropogenic threats, it is important to assess diversity in river systems that are still relatively intact. The large River Teno system in northernmost Europe is characterized by remarkable genetic (Vähä et al. 2007, 2008, 2017) and life history (Niemelä et al. 2006a) diversity, and has not been subjected to stocking. In the present study, we used the 40-year time series of scale samples collected from adult salmon of the River Teno system to (1) quantify the life history diversity of the Teno salmon population complex as a whole and in selected subpopulations, (2) assess the long-term trends in this diversity, and (3) provide guidelines for monitoring life history diversity in large, diverse population complexes and their components that are subjected to different fisheries.

## Materials and methods

### Study area

The River Teno system (Norwegian: *Tana*, Sami: *Deatnu*) is located in northern Europe (68°–70°N, 25°–27°E) and forms the bor-

der between northern Finland and Norway, draining into the Tanafjord at the Barents Sea (Fig. 1). More than 1100 km of different stretches of the system is accessible to anadromous salmon, including the main stem, the large headwater branches, and numerous smaller tributaries (Fig. 1). Genetic studies have revealed a highly structured population complex consisting of nearly 30 demographically independent, genetically distinct, and temporally stable population segments in tributaries and different parts of the main stem (Vähä et al. 2007, 2008, 2017; Aykanat et al. 2015). The River Teno is one of the few remaining large river systems that still supports multiple and abundant wild Atlantic salmon populations; various forms of recreational and net fisheries in the river yield annual freshwater catches between 80 and 250 t, or 20 000 – 60 000 individual salmon (Niemelä et al. 2006a; Anonymous 2018). Typically, the majority (50%–60%) of the salmon catch is taken in the recreational rod fishery, the next most important gears being weir (~20%) and stationary gill nets (10%–20%), and the smallest proportion (~10%) being taken with drift nets (Anonymous 2016). The net fisheries are practiced by locals, mostly native Sámi, and are based on special fishing rights connected to land use, ownership, or inherited rights.

In addition to the extensive fishery in the main stem, salmon fishing is also operational in most of the tributaries, but there is less variation in fishing methods in the latter. In most tributaries, little or no net fishing is operated or allowed, although in some larger tributaries net fishing forms a significant share of the catch. A special management regime is practiced in the River Pulmankijoki (Fig. 1), where all salmon fishing takes place in a central lake by gill nets and the fluvial stretches are closed for salmon fishing.

Salmon stocks of the River Teno system are managed and fisheries regulated by bilateral agreements between Finland and Norway, in addition to national regulations in both countries, with the aim of conserving the wild stocks but also supporting sustainable fisheries. Stocking of reared fish or eggs is strictly forbidden in the River Teno system.

### Scale samples and their analyses

More than 154 000 scales were collected from Atlantic salmon harvested over a 40-year period (1975–2014) in the River Teno system (refer to online Supplementary material, Table S1<sup>1</sup>) by recreational tourist anglers and local fishers using various net and rod fishing methods (see previous description; Fig. 2). The scales were collected by a network of trained fisherman — equipped with standard measuring boards and scales — that was established by the Finnish Game and Fisheries Research Institute (currently: Natural Resources Institute Finland (LUKE)) in the 1970s and later complemented on the Norwegian side by the County Government of Finnmark and the Tana River Fish Management. The network has been maintained and developed with the aim of covering all fishing methods, the entire fishing season, and different parts of the River Teno system (cf. Niemelä et al. 2005, 2006a). The fishermen measured the length and mass of the fish in their catches, and recorded the sex of the fish, date of capture, and location and fishing gear used. Scales were dried and archived in paper envelopes at room temperature at the Teno River Fisheries Research station of LUKE in Utsjoki, Finland.

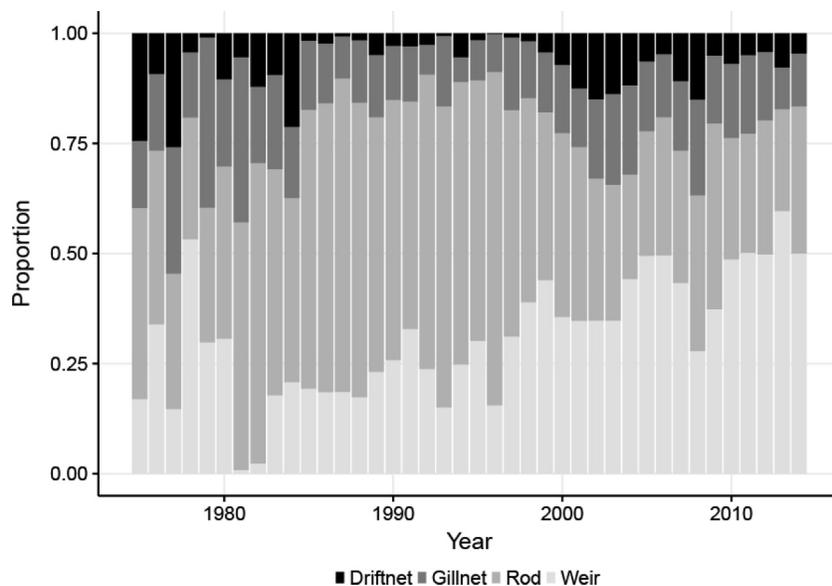
The river and sea age (1SW: one-sea-winter salmon; 2SW: two-sea-winter salmon; etc.) and possible previous spawning history of each individual were determined via assessment of scale growth rings by trained experts according to international guidelines for Atlantic salmon scale reading (ICES 2011). Annually, a small number of escaped farmed salmon are captured and sampled in the River Teno fishery in addition to the wild salmon (Erkinaro et al. 2010). The farmed salmon were distinguished based on external

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0343>.

**Fig. 1.** The River Teno system in northernmost Europe. The Teno main stem, referred to in this study, is the stretch of river from the confluence of the headwater tributaries Inarijoki and Kárašjohka to the Barents Sea.



**Fig. 2.** Proportions of samples collected between different fishing gear types in the Teno mainstem fisheries across the study period.



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characteristics by fishermen, and later confirmed by scale growth patterns consistent with their history of captive rearing (Fiske et al. 2005). Farmed salmon were excluded from the present study. The total mass of yearly salmon catches was estimated from postal questionnaires sent to fishermen, interviews, and logbooks. The total yearly catch was then converted into estimated numbers of fish in catch using the sea age distribution of yearly catch samples (cf. Niemelä et al. 2005), weighted by user groups in different parts of the system, which reflects the main gear types and parts of the fishing season used by each group of fishers.

Samples were collected both in the fishery of the main stem and from tributaries. We selected a representative set of tributaries for this study from different parts of the river system that had the longest time series data and sufficient numbers of samples available per year. These tributaries include (from the lower to the upper part of the system) Máskejohka, Pulmankijoki, Vetsijoki, Utsjoki, Kuoppilasjoki, Inarijoki, Kárásjohka, and Iešjohka (Fig. 1). In addition, the samples collected along the ~210 km long main stem were separated to form two separate groups, termed here the lower part of the main stem (from the estuary up to the Norwegian–Finnish border; 60 km) and the upper part of the main stem (from the border to the junction of Inarijoki and Kárásjohka; 150 km) (Fig. 1).

In the absence of catch quotas and monitoring of the total number of salmon entering the River Teno, the total salmon catch is considered to represent a reasonable index of abundance (cf. Niemelä et al. 2005; Thorley et al. 2005). There are significant correlations in the catch between fishing methods, indicating that — in general — environmental conditions are stable enough to allow effective fishing for all fishing methods in different parts of the system throughout the season. In addition, we have detected correlations between run size and catch in monitoring programs at tributaries of the Teno (Anonymous 2018; P. Orell, M. Länsman, M. Falkegård, and J. Erkinaro, unpublished data). Therefore, here we use catches as indices reflecting run sizes (Niemelä 2004; Niemelä et al. 2009).

### Statistical methods

Diversity in life history strategy was quantified by evaluating unique combinations of years that salmon spent in fresh water and in the ocean and the number of reproductive events. An individual-based rarefaction curve with 95% unconditional confidence intervals was used to determine the relationship between the number of strategies described and the number of individuals sampled throughout the 40-year period. After rank-ordering the life history strategies by their frequencies, the proportion of each strategy was plotted against its rank. Temporal variation in the number of strategies between 1975 and 2014 was visualized by building individual-based rarefaction and extrapolation curves for each 5-year period (cf. Chao et al. 2014). Variation in strategy diversity among rivers was determined by comparing raw richness along with sampling effort and estimated Hill number of order 1 (Hill 1973). Hill number of order 1 represents the exponential of Shannon's entropy and weights strategies according to their frequency. This index is sensitive to sampling size and was extrapolated with 95% unconditional confidence intervals obtained by bootstrapping following Chao et al. (2014).

The main components of the life history strategy — sea age and river age — were assessed separately for trends across time and space. Sea age includes the reproductive status of salmon (first time or repeat spawner) and the time spent at sea before maturation. The proportion of the main sea age groups, 1–3 sea-winters (1–3SW) and previous spawners (representing more than 99% of individuals), were analyzed with separated generalized linear models using the quasibinomial family to account for overdispersion. The year, month, and location of capture, the fishing gear used, and the sex of each individual were included as independent variables, along with the 1-year lagged dependent variable to

move autocorrelation in residuals. A two-way interaction between sex and month and a three-way interaction between the year, location, and sex were also introduced as explanatory variables. Model selection was performed with a hypothesis-testing approach using backward selection with *F* tests. Post hoc analyses were performed using Wald tests with Bonferroni adjustment of *p* values for pairwise comparisons. Mean values displayed in the different figures are least squares means (cf. Lenth 2016).

Proportions of the three most frequent smolt age groups (3–5 years; representing more than 96% of individuals) were analyzed separately with generalized additive models using the quasibinomial family. The location of capture and age at sea were included as independent variables together with year of smoltification inside a smoothing function using cubic regression splines. This allowed the determination of eventual nonlinear variations in proportions of smolt age groups over years. Cross-validation was used to determine the optimal amount of smoothing. The significance of explanatory variables and smoothing term were assessed using *F* tests.

Analyses were performed using R software (R Core Team 2015), the INEXT package for the rarefaction curves, and the estimations of Hill numbers (Hsieh et al. 2016) and the mgcv package for the generalized additive models (Wood 2011). An alpha risk of 0.05 was used for all analyses.

## Results

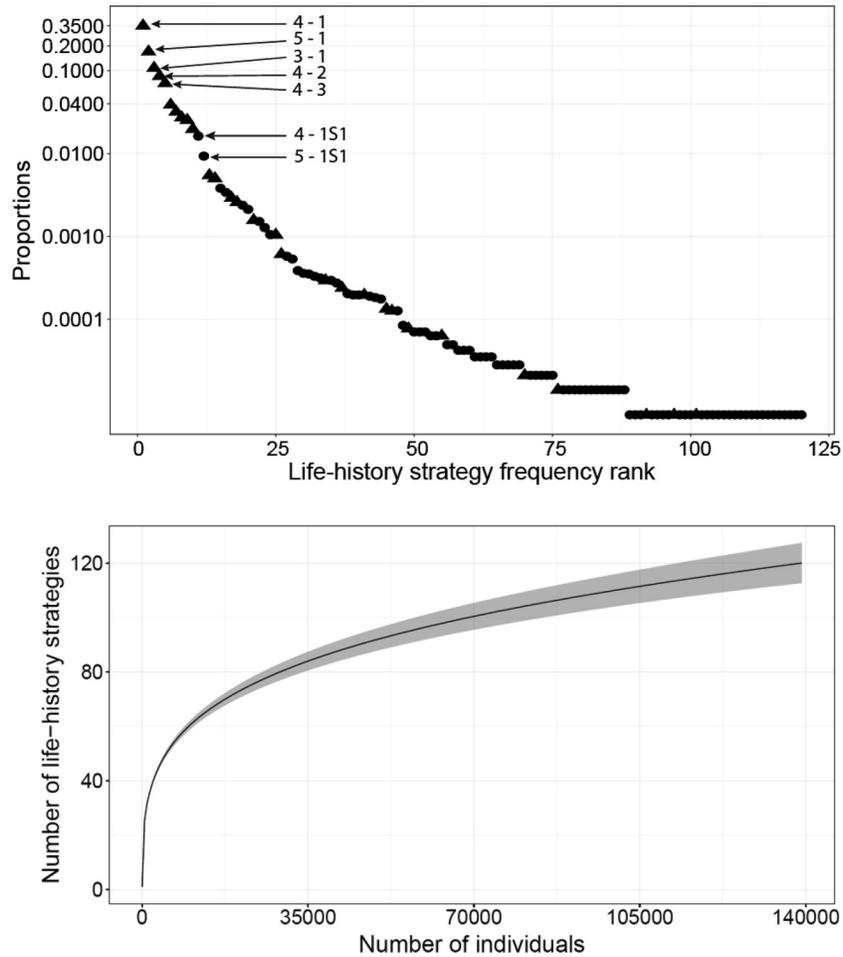
### Large diversity in life histories in the Teno system

A total of 120 life history strategies were quantified over the 40-year study period, including smolt ages ranging from 2 to 8, maiden sea ages from 1 to 5, and a variety of previous spawners. Twenty-nine different strategies were identified for maiden salmon, 54 strategies for alternate spawners (2 or more years between spawning migrations), and 37 strategies for consecutive spawners (spawning migrations in consecutive years), i.e., 76% of strategies belonged to repeat spawners. Hence, most life history strategies were rare (Fig. 3). One-quarter of the total number of strategies were identified only once, whereas the five most common strategies comprised 79% of the individuals sampled. The most common combinations were 4–1 (river age – sea age; 49 992 individuals; 35% of samples), 5–1 (24 276; 17%), 3–1 (15 407; 11%), 4–2 (12 280; 9%), and 4–3 (10 090; 7%). Although the sampling effort was relatively high, the rarefaction curve did not reach an asymptote (Fig. 3), and new rare strategies could potentially still be discovered by increasing the number of samples.

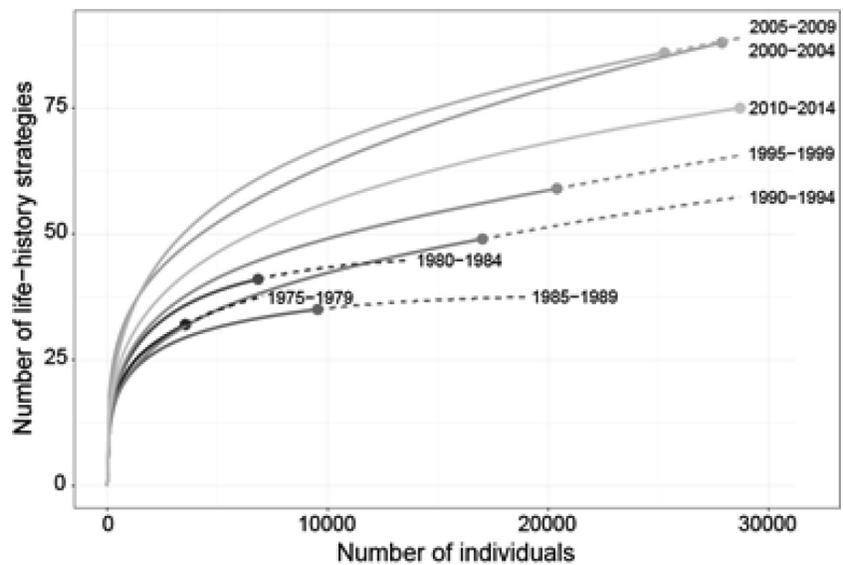
Rarefaction and extrapolation analysis revealed changes in the richness of life history strategies throughout the 40-year period studied (Fig. 4). Curves for the first 20 years (1975–1989) were similar, and strategies accumulated less rapidly than during the last 20 years (1990–2014), mostly driven by a sharp increase in previously spawned salmon during the latter period (Fig. 5). Rarefaction curves for the later time period show that the highest strategy richness was reached in 2000–2009 before a significant reduction occurred during the last 5-year period (2009–2014).

The number of strategies observed differed greatly among different parts of the River Teno system (Fig. 6), ranging from 15 strategies in Kuoppilasjoki to 116 strategies in the Teno main stem. Scale samples collected in the lowermost Norwegian portion of the Teno main stem did not add much to the total diversity of strategies observed in the river system until the sampling effort increased substantially from 1998. Over the last 17 years, 1998–2014, the number of strategies observed would have been reduced on average by six without samples from the lower part of the main stem (Norway only) and by nine without those from the upper part (Finnish–Norwegian border zone), representing 13% and 18%, respectively, of the annual mean number of strategies characterized during this period. Without the samples from the upper part of the main stem, the total number of life history strategies

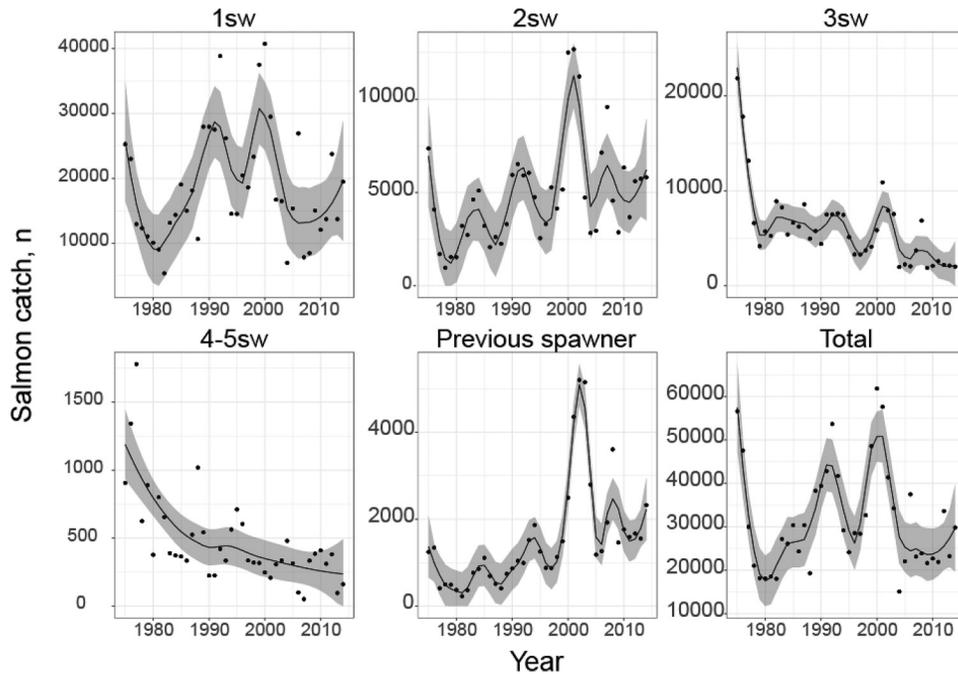
**Fig. 3.** Proportion of each life history strategy of Teno salmon ranked by their frequency in catches (upper panel, triangles: maiden salmon; circles: previous spawners). The most common strategies are indicated for maiden salmon (five strategies; e.g., 4-1: 4 years in fresh water, 1 year at sea) and previous spawners (two strategies; e.g., 4-1S1: 4 years in fresh water, 1 year at sea, first spawning migration, 1 year at sea, second spawning migration). A rarefaction curve of the number of strategies for the 40-year sampling period is shown in the lower panel (shaded area represents 95% unconditional confidence interval).



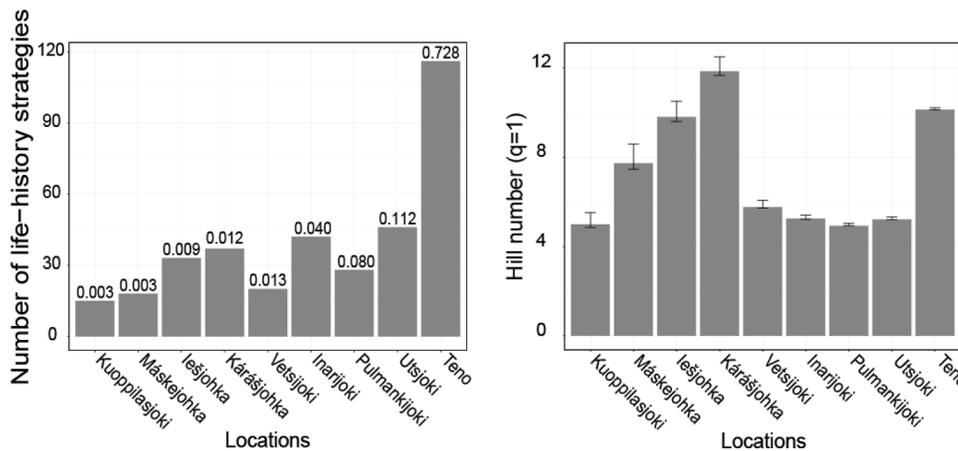
**Fig. 4.** Individual-based rarefaction (solid lines) and extrapolation (broken lines) plot of the life history richness of each 5-year period between 1975 and 2014.



**Fig. 5.** Estimated annual catches of salmon in the River Teno system in different sea-age groups (1–3SW, 4–5SW combined, previous spawners) in 1975–2014. Lines represent LOESS regressions with degrees of smoothing minimizing Akaike information criterion ( $AIC_c$ ); 95% confidence intervals are indicated with shaded areas.



**Fig. 6.** The number of life history strategies described (left graph) and their estimated Hill numbers (right graph; life history strategy diversity corrected for sampling effort) in different locations of the River Teno system. Locations are ordered from left to the right according to the proportion of samples collected (figures above bars on left graph). Error bars on the right graph indicate 95% confidence intervals for the Hill numbers.



observed over the 40-year period would have been 94 instead of 120, and 110 without the lower side. Thus, the bilateral collaboration in sampling has been useful.

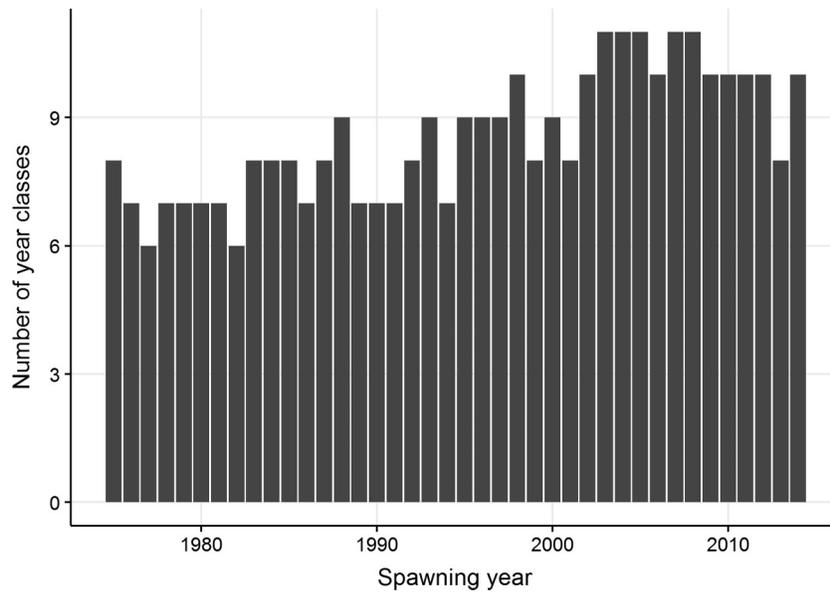
Sampling effort varied considerably between the locations; for instance Kuoppilasjoki and Teno main stem accounted for 0.3% and 73% of the total number of scale samples collected, respectively. Despite the vast differences in sampling effort, Hill numbers of order 1 could be estimated precisely and provided a better view of differences in diversity once rare elements were down-weighted (Fig. 6). The Teno main stem and the large headwater rivers, Kárašjohka and Iešjohka, had the highest diversity with Hill numbers as high as 12, followed by Máskejojha with a Hill number slightly below 8. The other locations showed Hill numbers between 4 and 5, indicating markedly less diversity for those areas compared with that of the Teno main stem, for instance

(Fig. 6). The number of salmon year classes (hatching year) in annual catches increased from 6–8 in 1970s to the late 1980s to 8–11 in 2000s and 2010s (Fig. 7), thus indicating that multiple year classes contribute to reproduction in the Teno system each year.

**Variation in sea age groups**

Annual catches fluctuated greatly between 1975 and 2014, with a maximum as high as 61 800 individuals estimated in catches in 2000 (Fig. 5). However, variation in catches has been lower in the last 10 years. Overall, 59% of the salmon caught were 1SW fish, whereas 5% were previous spawners (PS). There was a marked negative trend in abundances of both 3SW and 4–5SW groups across the time series, whereas 2SW fish and previous spawners showed an increasing trend (Fig. 5).

**Fig. 7.** Number of year classes from individual hatching years in yearly Atlantic salmon catch samples (spawning year) collected from the Teno mainstem fisheries.



**Table 1.** Significance of variables included in the analyses of Atlantic salmon sea-age distribution in the River Teno system.

Quasibinomial models	df	1 sea winter		2 sea winters		3 sea winters		Previous spawners	
		F value	p	F value	p	F value	p	F value	p
<b>Single variables</b>									
Year	1	—	—	—	—	207.1	<0.001	—	—
Location	8	—	—	—	—	172.7	<0.001	—	—
Fishing gear	3	77.7	<0.001	11.1	<0.001	64.4	<0.001	107.0	<0.001
Lag year	1	316.3	<0.001	65.3	<0.001	142.1	<0.001	128.0	<0.001
Sex	—	—	—	—	—	—	—	—	—
Month	—	—	—	—	—	—	—	—	—
<b>Interaction terms</b>									
Year × sex	1	19.7	<0.001	23.5	<0.001	1.4	NS	0.4	NS
Year × location	8	6.3	<0.001	1.1	NS	1.5	NS	3.2	<0.01
Sex × location	8	2.7	<0.01	6.4	<0.001	0.4	NS	2.1	<0.05
Sex × month	2	4.5	<0.05	9.7	<0.001	81.2	<0.001	39.6	<0.001
Year × sex × location	8	0.6	NS	1.1	NS	0.5	NS	1.0	NS

**Note:** Results for single variables included in significant interactions are not displayed. df, degree of freedom; NS, nonsignificant relationship.

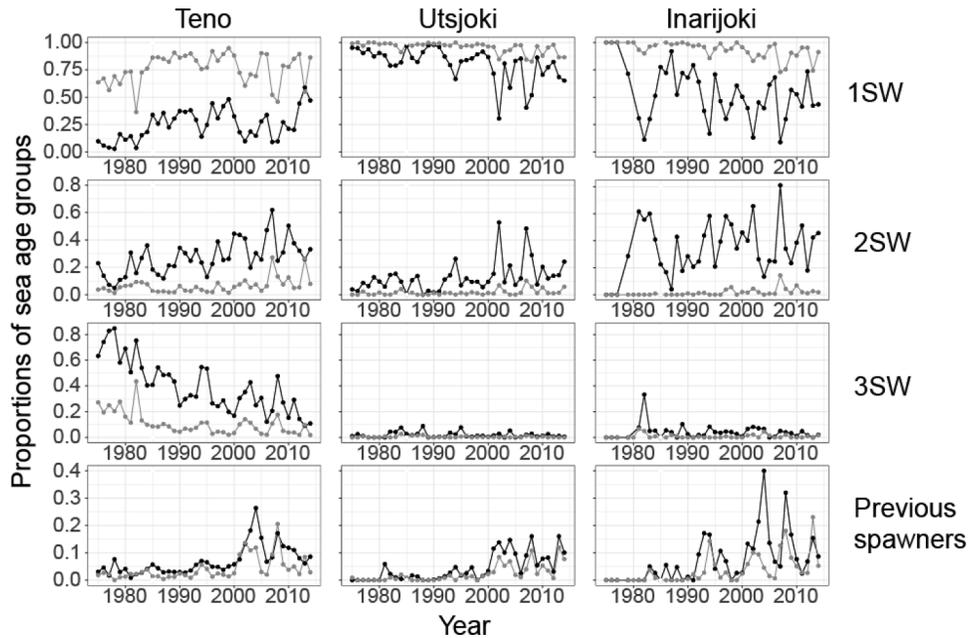
The year, month, location, and method of capture together with the sex of fish significantly influenced the observed sea age proportions in catches, sometimes in complex ways. Most of the explanatory variables and their two-way interactions were significantly associated with the proportions of the four sea age groups analyzed (1–3SW and PS) despite some differences among models (Table 1). The three-way interaction between year, location, and sex was not a significant predictor of sea age proportions in any model (Table 1). The most obvious examples include the strong association between the proportion of 3SW salmon and time (negative trend over the years).

There was considerable temporal variation in the proportions of the different sea age groups in different areas of the River Teno system (Fig. 8). Estimated slopes representing changes in the odds of being 1SW across the 40-year time period were <1 for both sexes in all locations except for females in the Teno main stem (Fig. S1<sup>1</sup>). For the Teno main stem, the proportion of 1SW females significantly increased, whereas it significantly decreased in Inarijoki and Utsjoki. For males, the proportion of 1SW individuals significantly decreased in Inarijoki, Pulmankijoki, Utsjoki, and in the Teno main stem (Fig. 8). The proportion of 2SW individuals

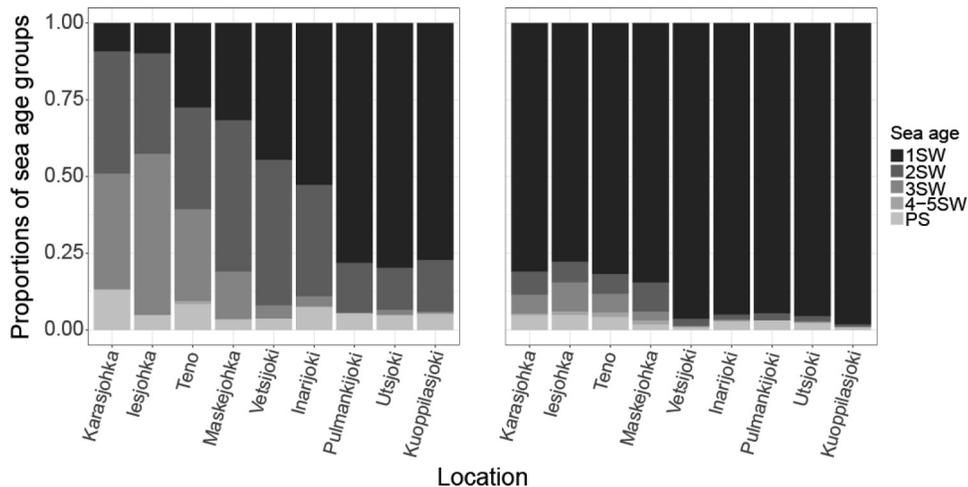
increased across the 40-year time period in all locations, with significantly different slopes between sexes (females: 1.018 with 95% CI = 1.013, 1.023; males: 1.042, 95% CI = 1.033, 1.052). For 3SW individuals, an overall significant decrease was observed (0.970, 95% CI = 0.965, 0.974). Proportions of repeat spawners increased significantly in the Teno main stem, Utsjoki, and Inarijoki, with slopes ranging from 1.034 (95% CI = 1.027, 1.040) in the main stem to 1.059 (95% CI = 1.026, 1.093) in Inarijoki.

Spatial variation in proportions of 1SW was higher for females, although tributaries with the largest proportions of 1SW females also generally had the largest proportions of 1SW males (Fig. 9). Differences in 1SW proportions among locations were large; for instance, the proportions of 1SW females and males in Utsjoki were more than 3 and 1.2 times higher, respectively, than in Iešjohka ( $Z = -3.63$ ,  $p = 0.01$ , and  $Z = -3.32$ ,  $p = 0.03$ , respectively). Considerable proportions of 3SW — mostly female — salmon were found in the main stem and in the large headwater branches, Kárášjohka and Iešjohka, while other large tributaries like Máskejohka, Vetsijoki, and Inarijoki also comprised considerable proportions of 2SW female fish (Fig. 9).

**Fig. 8.** Temporal variation in proportions of one- to three-sea-winter (1–3SW) maiden salmon and previous spawners in two tributaries (Utsjoki and Inarijoki) and in the main stem (Teno) of the River Teno system (see Fig. 1 for locations). Yearly proportions in each river sum up to 1.0 separately for males (grey) and females (black).



**Fig. 9.** Proportions of the different sea ages of females (left) and males (right) in catches from different parts of the River Teno system (see Fig. 1 for details). 1–5SW, one- to five-sea-winter salmon; PS, previous spawners.



The month of fishing season influenced sea age composition in catches: for instance, the proportions of 1SW individuals in July–August were larger than in May–June for both sexes (Fig. 10;  $p < 0.0001$ ). In contrast, the proportion of previous spawners was much higher in May–June than in July–August (4.3- to 3.6-fold more in males and 2.2- to 1.5-fold in females; Fig. 10). Different fishing gear appeared to select for different sea age groups. The highest proportions of 1SW were captured by weir fishing, followed by rod, gillnet, and driftnet fishing (Fig. 11, pairwise  $p < 0.001$ ). The mean proportion of 1SW in rod catches was more than double that in driftnet catches, which in turn captured significantly more 2–3SW salmon and previous spawners than the other methods (Fig. 11).

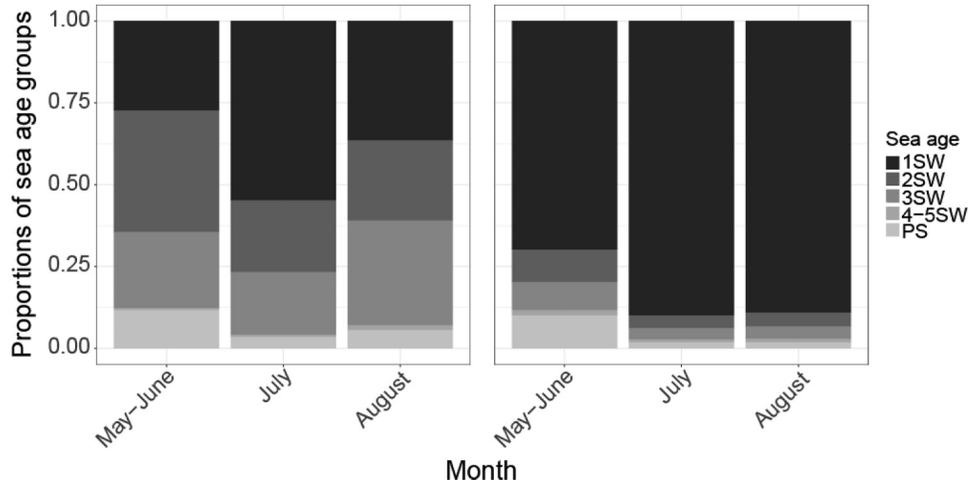
**Variation in river age**

Temporal trends in different river age groups were nonlinear (effective degrees of freedom of smoothers  $> 18$ ,  $p < 0.001$ ). The proportion of 3-year-old smolts decreased over the first 30 years,

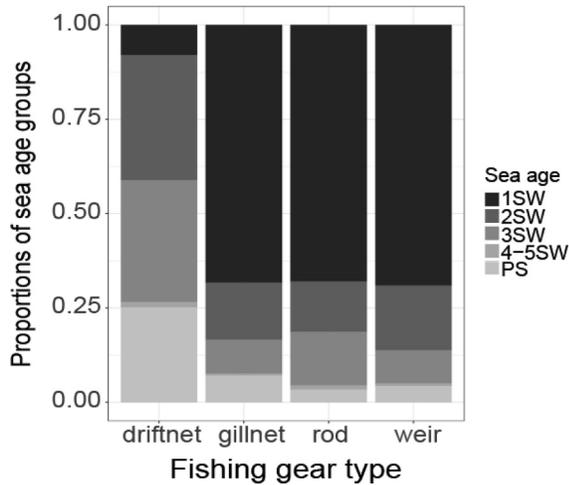
whereas the proportion of 5-year-old smolts increased (Fig. 12). The proportion of 4-year-old smolts fluctuated around its mean, and the magnitude of the smooth function range was low in comparison with the two other river age groups analyzed. Some changes in general patterns were detected: after 2000, the fluctuations in the proportions of age-3, -4, and -5 smolts decreased drastically (Fig. 12). For each analysis, the location within the Teno catchment had a significant influence on proportions of the different age groups ( $p < 0.001$ ; Fig. 13). Individual standard errors were quite high and did not allow locations to be distinguished with respect to age at smoltification except for the River Kuoppilasjoki, where smolts were generally older, with 82% of the salmon caught having smoltified after a minimum of 5 years (Fig. 13).

Proportions of smolt ages differed between sea age groups ( $p < 0.001$ ): a 3-year smoltification age in fresh water was more common in 3SW and 4SW than in 1SW and 2SW (odds for 3SW and

**Fig. 10.** Sea-age distribution of female (left) and male (right) Atlantic salmon in catches obtained in different months in the River Teno system. 1–5SW, one- to five-sea-winter salmon; PS, previous spawners.



**Fig. 11.** Sea-age distribution of Atlantic salmon captured by different fishing gears in the main stem of the River Teno. 1–5SW, one- to five-sea-winter salmon; PS, previous spawners.



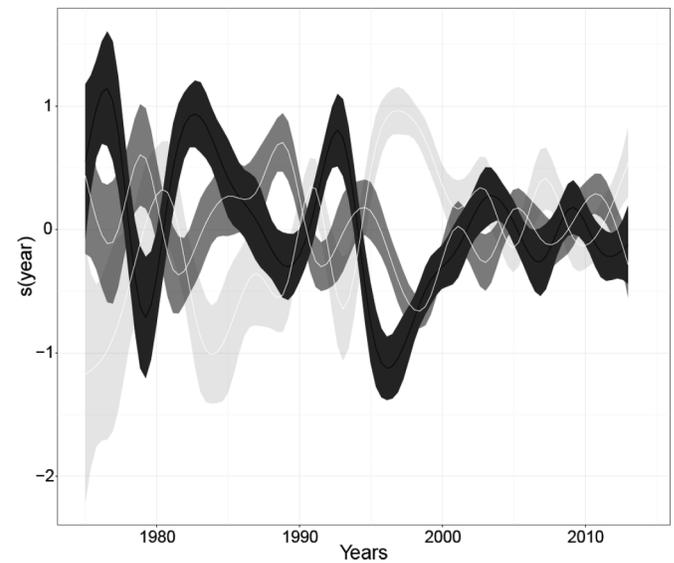
4SW 44% and 84% higher, respectively, than for 1–2SW) groups. The 1–2SW salmon showed the highest odds of having smoltified after 5 years in the river (odds 54% and 101% larger, respectively, than for 3SW and 4SW, Fig. 14). The proportions of salmon smoltifying at the age of 4 years were similar among all sea age groups ( $df = 4, F = 1.36, p = 0.25$ ; Fig. 14).

**Discussion**

The Atlantic salmon population complex of the River Teno show an unusually wide life history variation in combinations of smolt (2–8 years) and sea ages (1–5 years) in maiden fish, and in various forms of alternate and consecutive spawners, comprising 29, 54, and 37 combinations, respectively, totaling 120 different manifestations of the anadromous life history strategy. This diversity is among the widest, if not the widest, reported in a single river system in the distribution area of the species. The oldest salmon recorded was a 14-year-old female (122 cm, 17.0 kg) with four previous spawning migrations and a total of 6 years spent at sea.

There are some areas of the species’ distribution range where Atlantic salmon populations also exhibit wide ranges of life history characteristics. Chaput et al (2006) summarized the phenotype characteristics of more than 100 salmon rivers in eastern

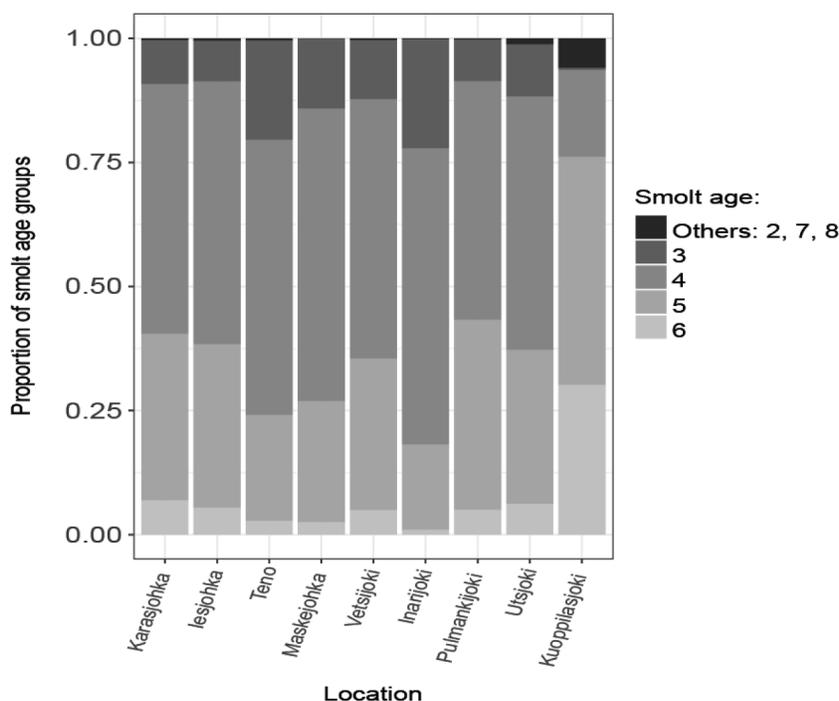
**Fig. 12.** Partial generalized additive model plot representing the effects of years on the proportion of 3-year-old (black), 4-year-old (dark grey), and 5-year-old (light grey) smolts in catch samples from the River Teno. The Y axis represents the contribution of the smoother. The shaded regions are 95% confidence bands around the curve.



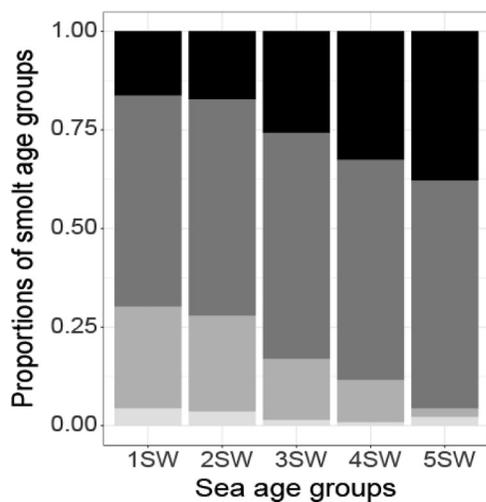
Canada and documented a smolt age range of 1–7 years, sea ages of 1–4 years. Reid and Chaput (2012) reported additional variety of life histories of previously spawned salmon (PS) in that area (see below). In the large Pechora River in northwestern Russia, a total of 24 life history combinations have been reported (Studenov et al. 2008), and many rivers in northwestern Russian include autumn-migrating salmon that spend 1 full year in fresh water before spawning (e.g., Whoriskey et al. 1996; Studenov et al. 2008). The large diversity of life history strategies like that in the Teno system is nevertheless extraordinarily rare or unique in single river systems or areas (e.g., Klemetsen et al 2003; Jonsson and Jonsson 2011).

The vast majority of all life history strategies in the River Teno system were in the diverse PS group. The abundance and proportion of PS is a function of maiden salmon 1 or more years earlier; environmental conditions together with fishing pressure are affecting the survival of spent fish in the river and during their

**Fig. 13.** Proportions of the different smolt ages of adult returning salmon captured from different parts of the River Teno system (see Fig. 1 for locations).



**Fig. 14.** Proportions of Atlantic salmon in the River Teno system that have smoltified after 3 years (black), 4 years (grey), and 5 years (light grey) in relation to their sea age. Other smolt ages (2, 6–8) are indicated by the lightest grey shade.



migration to and at sea, as well as their survival back to fresh water (Klemetsen et al 2003; Chaput and Benoît 2012). The contribution of PS showed a marked increase around the turn of the millennium (Fig. 5). Niemelä et al (2006a) earlier discussed the reasons behind this development. Cessation of the highly size-selective drift net fishery off the northern Norwegian coast in 1988 was followed by an increase in both 2SW and PS salmon in the rivers in the Barents Sea (Jensen et al. 1999). However, despite the large run of 1SW salmon in 1990–1991, the corresponding increase in PS salmon was not especially clear. Yet, the second peak in 1SW abundance in 2000–2001 resulted in an unprecedented abundance of PS salmon in the Teno system (Niemelä et al. 2006a), although the coastal catches were generally higher in the latter period (Niemelä et al. 2012). Since environmental conditions in the Barents Sea are

correlated with the variation in salmon catches in the region (Niemelä et al. 2004; Pasanen et al. 2017), it has been speculated that the increased surface temperature at the Barents Sea between the 1990s and 2000s may have contributed to the better survival of kelts and improved prospects for abundant returns of PS salmon in the early 2000s (Niemelä et al. 2006a). In addition, a general peak in salmon abundance was evident at the turn of the millennium (Anonymous 2017; ICES 2017).

In addition to their population in the Barents Sea, the abundance of PS salmon has also recently increased in the northwestern Atlantic (cf. Klemetsen et al. 2003), especially in the large Miramichi River running to the Gulf of St. Lawrence (Reid and Chaput 2012). At least 20 different PS strategies have been found in the Miramichi River (Reid and Chaput 2012), with more than 50% contribution by consecutive spawners (spawning migration in consecutive years; Chaput and Benoît 2012), whereas the alternate spawners (reconditioning at sea for 1 full year or more) comprise ~98% of the PS salmon in the Teno (this study; Niemelä et al. 2006a). Consecutive spawners are typically less common in northern areas, e.g., in northern Norway, than further south (Abrahamsen 1968; Jonsson et al. 1991). Schaffer and Elson (1975) showed that probability of spending 1 or more full years between spawnings increases with the age at first spawning migration. Pointing towards a similar pattern, later studies have suggested that consecutive spawning is especially common in populations consisting mainly of 1SW spawners, whereas the proportion of alternate spawners tends to increase in populations with mainly MSW fish (Moore et al. 1995; Klemetsen et al. 2003).

The different sea age groups, including the previous spawners, showed different trends in their long-term variation. The sea age groups including the largest female spawners with the highest fecundity (Erkinaro et al. 1997; Niemelä et al. 2006a), 3–4SW salmon, showed a marked decline over the time series. This is an alarming signal and in line with the estimated stock status of the large headwater tributaries of the Teno system with populations furthest below their conservation limits, likely reflecting a long-term effect of weakening stock status of the early-running MSW salmon in Kárášjohka and Iešjohka (Anonymous 2018). On the

other hand, 2SW salmon and previous spawners (discussed above) showed an increasing trend that can be at least partly attributed to the ban of drift nets off the Norwegian coast in late 1989 (Jensen et al. 1999). There was an increasing trend of 1SW abundance until the early 2000s, but the most recent years have shown lower abundances than 10–20 years earlier. A corresponding large-scale phenomenon has recently been noted in Norway in the form of a decrease in the relative number of 1SW salmon and lowered growth rate. Historically, the proportion of 1SW fish among small salmon (<3 kg) has been very high (92%–97% in the period 1989–2006), whereas in the last decade, the corresponding percentage of 1SW fish among salmon <3 kg has been 71%–87% (Anonymous 2017). Partly in contrast to the trends in the northeastern Atlantic, a recent review of Chinook salmon populations in the Pacific Northwest, from Alaska to California, showed that the proportions of older sea age classes have decreased over time and that the length-at-age of older fish has declined, while that of fish in younger sea age groups has increased (Ohlberger et al. 2018).

Jonsson et al. (2016) reported recently that the proportion of 1SW Atlantic salmon in a southern Norwegian river was lower both in the 1970s and after 2000 than in the 1980s and 1990s, a change that was associated with a gradual decline in postsmolt growth and smaller amounts of reserve energy in the fish. An increase in age at maturity after 2000 has also been reported from other Norwegian salmon populations (Otero et al. 2012), suggesting that this has wider relevance in eastern Atlantic populations of the species (see also ICES 2017). The recent (since early 2000s) decreasing abundance of 1SW salmon in the Teno system appears to be in line with this overall trend. An increase in the proportion of female 1SW salmon in the mixed-stock catch of the Teno main stem might reflect the improving stock status of some tributary populations consisting mostly of 1SW spawners (cf. Anonymous 2018).

Variability in years spent in fresh water and years spent in the ocean by Atlantic salmon has been suggested to be the result of combined, complex effects of environment and genetics (e.g., Hutchings and Jones 1998; Klemetsen et al. 2003; Jonsson and Jonsson 2011). Age at smoltification is likely strongly under the control of environmental factors; there is a demonstrated inverse relationship between smolt age and either latitude or growth rate of juveniles (Metcalf and Thorpe 1990; Strothotte et al. 2005). In contrast, sea age at maturity has been suggested to be strongly influenced by parental stock, as also indicated by the relationship between ovarian development of migrating smolts and age at maturity of adult spawners (Chadwick et al. 1987). In addition, intentional selection for late maturation has proven successful both in breeding of hatchery broodstock (Glebe and Saunders 1986) and in developing cultivated strains for commercial aquaculture (e.g., Gjøen and Bentsen 1997). Recent research has confirmed the strong genetic basis for age at maturity in Atlantic salmon; a single gene has been shown to account for ~40% of the variation in sea age in a large number of Fennoscandian wild salmon populations (Barson et al. 2015). The temporal variation in age at maturity and iteroparity of Teno salmon could result from adaptive changes and (or) phenotypic plasticity following temporal differences in fishing selection and (or) environmental conditions. Further studies are needed to disentangle the effects of these different factors and evaluate their potential consequences for the dynamics and genetic diversity of the Teno salmon subpopulations.

Anadromous fish may show both short-term phenotypic responses to changes in ecosystems and climate (Jonsson et al. 2016) and long-term genetic changes in traits such as smolt age and size–age at maturity (Jonsson and Jonsson 2011; Bal et al. 2017). Increased ocean temperatures have been particularly evident in boreal and Arctic areas over the past several decades (Hoegh-Guldberg and Bruno 2010), causing marked changes in food webs and ecosystem functioning (Kortsch et al. 2015; Frainer et al. 2017). Changes

in ocean temperatures and related shifts in other physical conditions have altered marine ecosystems and resulted in distribution shifts among oceanic fauna (Perry et al. 2005; Hátún et al. 2009). In Atlantic salmon, recent studies show that changes in the ocean environment may have affected the 1SW salmon more than the 2SW salmon, suggesting more critical changes in feeding conditions for young fish that have recently entered the ocean from fresh water compared with those for later phases of larger salmon at sea (e.g., Bal et al. 2017 and references therein). Jonsson et al. (2016) documented a decrease in the proportion of 1SW salmon in the River Imsa, southwestern Norway, after levels peaked around 2000, in parallel with trends in the present study (Fig. 8). They concluded that the long-term change in Imsa salmon life history was mainly driven by changes in the oceanic ecosystem with the rebuilding of pelagic fish abundance, together with a decrease in abundance of large zooplankton and an increase in sea surface temperature in the Norwegian Sea. Further, size-selective harvesting, where larger individuals are targeted in fishing, can result in fishery-induced evolution (Jørgensen et al. 2007; Uusi-Heikkilä et al. 2015), which may have undesirable effects on population productivity and resilience (Law and Grey 1989; Olsen et al. 2004; Laugen et al. 2014). However, predicting such changes is difficult owing to a lack of data on the strength of selection, heritability, and genetic linkages among the traits affected (Crozier et al. 2008; Kuparinen et al. 2016).

Diverse population complexes provide more temporally stable ecosystem services, a phenomenon also referred to as the “portfolio effect” (Greene et al. 2010; Schindler et al. 2010; Moore et al. 2014). Schindler et al. (2010) showed that the portfolio effect in sockeye salmon (*Onocorhynchus nerka*) resulted in a twofold increase in catch stability in Bristol Bay, Alaska, and — despite variability in environmental conditions — enabled the fishery to maintain high productivity. This effect occurs because of asynchrony among populations in this area, where even nearby populations are relatively asynchronous in their abundances and productivity and are presumably influenced by differential responses to local environmental conditions (Rogers and Schindler 2008). The highly diverse salmon population complex in the River Teno can potentially have experience such an effect. This argument is in line with the suggestion put forward by Vähä et al. (2007) to explain the positive relationship between genetic diversity and the proportion of MSW salmon in Teno subpopulations. They proposed that larger generation overlap, i.e., a higher proportion of MSW individuals could reduce the impact of environmental fluctuations on a population (see also Gaggiotti and Vetter 1999). The high number of Teno salmon cohorts spawning simultaneously each year that has increased together with the increase in previous spawners over the past 20 years (up to 10–11) is also reflecting a strong generation overlap, which is suggested to maintain genetic diversity and thereby resilience (cf. Gaggiotti and Vetter 1999). It should be noted that the sampling effort increased well before the increase in simultaneous year classes (Table S1<sup>1</sup>; Fig. 7), and therefore the increase of previous spawners in the Teno populations (Fig. 8) likely contributed to the strong cohort overlap spawning each year.

The potential bias in a long time series of samples from diverse fisheries must be addressed, as there is a risk in changes over time. For example, changes in gear proportions could potentially bias observed trends, since there are differences in size selectivity among gear types (cf. Jensen et al. 1999). We addressed this potential bias by modeling the trends in the proportions of sea age groups to account for such temporal variation in fishing season and gear types. The traditional net fisheries in the River Teno did not change greatly over the study period in terms of mesh size or net materials, for instance; it is therefore unlikely that there have been large temporal changes in gear-specific selectivity that could have affected the observed trends in sea age proportions. Typically, rod catches are considered less size selective than net

catches of Atlantic salmon (e.g., Harvey et al. 2017), and the majority of both catches and samples are from rod fisheries (Anonymous 2016; this study). Although some changes have taken place in the River Teno fishing effort — for example, the number of recreational anglers has varied with a general increasing trend (Erkinaro et al. 2017) and the number of nets has decreased (Johnsen 2010) — there is no long-term change in catch proportions among the gear types (Niemelä et al. 2009; Anonymous 2016). We therefore conclude that the general picture of the catch composition and its representativeness have changed minimally over the decades and that covering the different fishing gears and times of the fishing season should provide a reasonably accurate overall picture of the life history variation in the population.

The large variation in the Teno salmon life histories offers opportunities and a safeguard for the genetic contribution of each year class over a number of subsequent spawning years. Successful management is of vital importance in enabling and conserving this diversity. Targeted measures, including regulations governing the early season fishery, can be used to conserve specific groups (e.g., 2–4SW fish) that primarily consist of large, high-fecundity females (Niemelä et al. 2006b); these females potentially produce offspring with higher survival rates owing to their eggs having a higher lipid content (Heinimaa and Heinimaa 2004). Early season regulations also safeguard previous spawners that often make up a substantial proportion of the large female spawners in small tributaries dominated by 1SW salmon (Fig. 9; Niemelä et al. 2006b). Such tailored management measures have already been applied in the recent bilateral agreement on the Teno salmon fishery between Finland and Norway (Anonymous 2018); managers make use of detailed information on spatial and temporal variability in populations, life history groups, and selectivity of different fishing gear in the mixed stock catches in the Teno main stem (Vähä et al. 2017).

Long-term monitoring programs of large, variable population complexes, like those of Atlantic salmon in the River Teno system, require a representative coverage of different parts of the river system, times of the fishing season, and various fishing methods. Our results clearly indicate that covering the entire fishing season is necessary for capturing the large diversity in early running, previously spawned salmon (cf. Niemelä et al. 2006b). In addition, the genetically distinct subpopulations with variable life history combinations have specific run times (Vähä et al. 2011), which further adds to the necessity to cover all run times. The variety of different fishing gear types in use in the Teno system is also a source of variability. Combined with the specific peak seasons for most gear types (e.g., drift nets only permitted in the early season), covering all fishing methods should be linked with the temporal considerations in planning a strategy for monitoring and sampling. Finally, the combined sampling efforts of both countries sharing the catchment seems to ensure good representation of the various life history types in the population.

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