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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0343.R2
Manuscript Type:	Article
Date Submitted by the Author:	27-Feb-2018
Complete List of Authors:	Erkinaro, Jaakko; Natural Resources Institute Finland, Czorlich, Yann; Natural Resources Institute Finland Orell, Panu; Natural Resources Institute Finland (Luke), Kuusela, Jorma; Natural Resources Institute Finland Falkegård, Morten; Norsk Institutt for Naturforskning, Department for Arctic ecology Länsman, Maija; Natural Resources Institute Finland Pulkkinen, Henni; Natural Resources Institute Finland (Luke) Primmer, Craig; Helsingin yliopisto Matemaattis-luonnontieteellinen tiedekunta, Department of Biosciences, Biotechnology Institute Niemelä, Eero; Natural Resources Institute Finland ,
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	LIFE HISTORY < General, MONITORING < General, SALMON < Organisms, MATURATION < General, BIODIVERSITY < General

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

Jaakko Erkinaro*

Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu, Finland; jaakko.erkinaro@luke.fi

Yann Czorlich*

Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu, Finland; and
Division of Genetics and Physiology, Department of Biology, University of Turku, Finland, Itäinen Pitkätatu
4, Turku FI-20520, Finland; yann.czorlich@luke.fi

Panu Orell

Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu, Finland; panu.orell@luke.fi

Jorma Kuusela

Natural Resources Institute Finland (Luke), FI-99980 Utsjoki, Finland; jorma.kuusela@luke.fi

Morten Falkegård

Norwegian Institute for Nature Research, POB 6606, Langnes N-9296 Tromsø, Norway;
morten.falkegard@nina.no

Maija Länsman

Natural Resources Institute Finland (Luke), FI-99980 Utsjoki, Finland; maija.lansman@luke.fi

Henni Pulkkinen

Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu, Finland; henni.pulkkinen@luke.fi

Craig R. Primmer

Department of Biosciences, Biotechnology Institute, POB 56, FI-00014, University of Helsinki, Finland;
craig.primmer@helsinki.fi

Eero Niemelä

Natural Resources Institute Finland (Luke), FI-99980 Utsjoki, Finland; eero.niemela@luke.fi

Corresponding author: Jaakko Erkinaro, Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu,
Finland; jaakko.erkinaro@luke.fi tel: +358405435929

*Authors contributed equally to this work

Abstract

We used >154000 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 one year at sea following 3-5 years in freshwater. Age at maturity has changed with an increase in two-sea-winter (2SW) salmon and previous spawners (PS), and a decline in 3SW fish. Smolt age distribution showed a decreasing proportion of age-3 smolts while that of age-5 increased. Fishing gear and fishing season times selected for fish differing in life-history strategies. Temporal variation in life histories reflects changes both in fisheries and the changing environment. There was an inverse relationship between years spent in freshwater and sea age. Biocomplexity was manifested by the multiple year classes (6-11) present in annual runs that increased with years, reflecting an increase both in PS and sampling effort. The high number of cohorts spawning simultaneously each year indicates strong generation overlap, which has been suggested to maintain genetic diversity and thereby resilience via the portfolio effect.

Introduction

Bio-complexity in fish populations, i.e. 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 allocating the reproductive effort across multiple years and stabilizing 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 bio-complexity 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, both in time spent in freshwater before the oceanic migration and in duration of the marine feeding migration and connected timing of return migration to freshwater 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 (*O. mykiss*; Thorpe 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 of 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 freshwater at ages between 1-5 in a size range c. 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 freshwater 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 freshwater after few months or one or more years of

reconditioning period at sea after the previous spawning migration (e.g. Niemelä et al. 2006a; Chaput and Benoît 2012).

The abundance of Atlantic salmon has declined markedly throughout the North Atlantic area since the 1970s (ICES 2017). Specific 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). Especially, 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 area (Ohlberger et al. 2018). However, in recent years an opposite trend with a decline in 1SW fish has been evident 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 area (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 threat factors, it is important to assess diversity in river systems that are still relatively intact. The large Teno river 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 sub-populations, 2) assess the long-term trends in this diversity, 3) provide guidelines for monitoring of life history diversity in large diverse population complexes and their components that are subjected to different fisheries.

Material and methods

Study area

The Teno river system (Norwegian: *Tana*, Sami: *Deatnu*) is located in northern Europe (68 - 70°N, 25-27°E) and forms the border between northern Finland and Norway, draining into the Tana fjord at the Barents Sea (Fig. 1). More than 1100 km of the 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 c. 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 support 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 tons, or 20 000–60 000 individual salmon (Niemelä et al. 2006a; Anon. 2018). Typically, the majority (50-60%) of the salmon catch is taken in the recreational rod fishery, the next most

important gears being weir (c. 20%) and stationary gill nets (10-20%), and the smallest proportion (c. 10%) being taken with drift nets (Anon. 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 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 at conserving the wild stocks but also supporting sustainable fisheries. Stocking of reared fish or eggs is strictly forbidden in the 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 Teno river system (Table S1) by recreational tourist anglers and local fishers using various net and rod fishing methods (see above; Fig 2). The scales were collected by a network of trained fisherman, equipped by standard measuring boards and scales, and 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 at covering all fishing methods, the entire fishing season, and different parts of the Teno river system (cf. Niemelä et al. 2005; 2006a). The fishermen measured the length and weight 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, experienced experts, following the internationally agreed guidelines for Atlantic salmon scale reading (ICES 2011). Annually, a small number of escaped farmed salmon are captured and sampled in the Teno river fishery in addition to the wild salmon (Erkinaro et al. 2010). The farmed salmon were distinguished by the external 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 weight of yearly salmon catches was estimated from postal questionnaires sent to fishermen, interviews and logbooks, and 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 lower to the upper part of the system) Máskejohka, Pulmankijoki, Vetsijoki, Utsjoki, Kuoppilasjoki, Inarijoki, Kárášjohka and Iešjohka (Fig. 1). In addition, the samples collected along the c. 210 km long main stem were separated to form two separate groups,

179 termed here lower (from the estuary up to Norwegian-Finnish border; 60 km), and upper (from
180 the border to the junction of Inarijoki and Kárášjohka; 150 km) part of the main stem (Fig. 1).

181 In the absence of catch quotas and monitoring of the total number of salmon entering the Teno
182 river, the total salmon catch is considered to represent a reasonable index of abundance (cf.
183 Niemelä et al. 2005; Thorley et al. 2005). There are significant correlations in the catch between
184 fishing methods, indicating that – in general – environmental conditions are stable enough to
185 allow effective fishing for all fishing methods in different parts of the system throughout the
186 season. In addition, we have detected correlations between run size and catch in monitoring
187 programmes at tributaries of the Teno (Anon 2018; unpublished data). Therefore, we use here
188 catches as indices reflecting run sizes (Niemelä 2004; Niemelä et al. 2009).

189 **Statistical methods**

190 Life-history strategy diversity was quantified by evaluating unique combinations of years spent
191 in freshwater and in the ocean, and the number of reproductive events. An individual-based
192 rarefaction curve with 95% unconditional confidence intervals was used to determine the
193 relationship between the number of strategies described and the number of individuals sampled
194 throughout the 40-year period. After rank-ordering life-history strategies by their frequencies, the
195 proportion of each strategy was plotted against its rank. Temporal variation in numbers of
196 strategies between 1975 and 2014 was visualized by building individual-based rarefaction and
197 extrapolation curves for each 5-year period (cf. Chao et al. 2014). Variation in strategy diversity
198 among rivers was determined by comparing raw richness along with sampling effort and
199 estimated Hill number of order 1 (Hill 1973). Hill number of order 1 represents the exponential of
200 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-winter (1-3SW) and previous spawners (representing more than 99% of individuals), were analyzed with separated generalised 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 one-year lagged dependent variable in order to remove 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 to 5 years; representing more than 96 % of individuals) were analysed separately with generalised additive models (GAM), using the quasibinomial family. The location of capture and age at sea were included as independent variables together with the year of smoltification, inside a smoothing function using cubic regression splines. This allowed determination of eventual non-linear 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 the R software (R Core Team 2015), the INEXT package for the rarefaction curves and the estimations of Hill numbers (Hsieh et al. 2015) and the mgcv package for the generalised 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 period including smolt ages ranging from 2-8, maiden sea ages from 1-5, and a variety of previous spawners. Twenty-nine different strategies were maiden salmon, 54 alternate spawners (two or more years between spawning migrations) and 37 consecutive spawners (spawning migrations in consecutive years), i.e. 69% 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 (15407; 11%), 4-2 (12 280; 9%), 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 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 were 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 strategies richness was reached in 2000-2009 before a significant reduction during the last five-year period (2009-2014).

The number of strategies observed differed largely among different parts of the River Teno system (Fig 6), ranging from 15 in Kuoppilasjoki to 116 in the Teno mainstem. Scale samples collected in the lowermost Norwegian part of the Teno mainstem 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 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 observed over the 40 years 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 a lot 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 quite precisely and provided a better view of differences in diversity once rare elements were downweighted (Fig. 6). The Teno mainstem and the large headwater rivers, Kárášjohka and Iešjohka, had the highest diversity with Hill numbers as high as 12, followed by Máskejohka with a Hill number slightly below eight. The other locations showed Hill numbers between four and five indicating a markedly less diversity for those areas compared to the Teno main stem, for instance (Fig 6). The number of salmon year classes (hatching year) in annual catches increased from 6-8 in

1979s – 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 10 last 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).

The year, month, location and method of capture together with 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 (1-3 SW 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 odds of being 1SW across the 40-year time period were below 1 for both sexes in all locations except for females in the Teno main stem (Fig. S1). For the Teno main stem, the proportion of 1SW female 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 [1.033,1.052]). For 3SW individuals, an overall significant decrease was observed (0.970 [0.965, 0.974]). Proportions of repeat spawners increased significantly in the Teno main stem, Utsjoki and Inarijoki with slopes ranging from 1.034 ([1.027, 1.040]) in the mainstem to 1.059 ([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 had also generally 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 three 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, Kárašjohka and Iešjohka, while other large tributaries like Máskejohka, Vetsijoki and Inarijoki also comprised considerable proportions of 2SW female fish (Fig. 9)

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 (4.3-3.6 fold more in males and 2.2-1.5 fold in females; Fig. 10). Different fishing gear appeared to select for different sea-age groups. The highest proportions of 1SW were captured with weir, followed by rod, gillnet and driftnet (Fig. 11, pairwise p -values < 0.001). The mean proportion of 1SW in rod catches was more than double of 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 non-linear (effective degrees of freedom of smoothers > 18, $p < 0.001$). The proportion of three-year-old smolts decreased over the first 30 years whereas the proportion of five-year-old smolts increased (Fig. 12). The proportion of four-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 could be noticed: 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 values < 0.001 ; Fig. 13). Individual standard errors were quite high and did not allow distinguishing locations with particular 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 three year smoltification age in freshwater was more common in 3SW and 4SW than in 1SW and 2SW (odds for 3SW and 4SW 44% and 84% higher, respectively, than for 1-2SW) groups. 1-2SW salmon showed the highest odds of having smoltified after five years in river (odds 54% and 101% larger, respectively, than for 3SW and 4SW, Fig. 14). The proportions of salmon smoltifying at the age of four 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 six 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 Canada, and documented a smolt age range of 1 to 7 years, sea ages 1-4 years, and 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, northwestern Russia, a total of 24 life history combinations have been reported (Studenov et al. 2008), and many Russian northwest rivers include autumn-migrating salmon that spend one full year in freshwater before spawning (e.g. Whoriskey et al. 1996; Studenov et al. 2008). The large diversity of life history strategies like 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 group of previously spawned salmon (PS). The abundance and proportion of PS is a function of maiden salmon one or more years earlier; environmental conditions together with fishing pressure are affecting the survival of spent fish in the river and during their migration to and at sea, and their survival back to freshwater (Klemetsen et al 2003; Chaput and Benoît 2012). The contribution of PS showed a marked increase around the turn of the millennium (Fig. 5), and Niemelä et al (2006a)

have 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 area (Jensen et al. 1999). However, despite the large run of 1SW salmon in 1990-1991, the corresponding increase of PS salmon was not especially clear, but 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 have shown to be 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 1990s and 2000s may have contributed to the better survival of kelts and improved prospects for abundant returns of PS salmon in early 2000s (Niemelä et al. 2006a). In addition, a general peak in salmon abundance was evident at the turn of the Millennium (Anon. 2017; ICES 2017).

In addition to the Barents Sea region, the abundance of PS salmon has also recently increased in the north-western Atlantic area (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 of consecutive spawners (spawning migration in consecutive years; Chaput and Benoît 2012) whereas the alternate spawners (reconditioning at sea for one full year or more) comprise c. 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 one 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 (Anon. 2018). On the other hand, 2SW salmon and previous spawners (discussed above) showed an increasing trend which can be at least partly attributed to the ban of drift nets off the Norwegian coast in late 1989 (ref. Jensen et al. 1999). There was an increasing trend of 1SW abundance until early 2000s but the latest years have shown lower abundances than 10-20 years earlier. A corresponding large-scale phenomenon has recently been noted in Norway with 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 % (Anon. 2017). Partly in contrast to the trends in the northeastern Atlantic area, a recent review on Chinook salmon populations in the Pacific Northwest, from Alaska to California, showed that proportions of older sea age classes have decreased over time and 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 associated with a gradual decline in post-smolt 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. Anon 2018).

Variability in years spent in freshwater and in the ocean in Atlantic salmon has been suggested to be a result of combined, complex effects of environment and genetic background (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 latitude/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 use (e.g. Gjølén 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 c. 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 effects of these different factors and evaluate potential consequences on dynamics and genetic diversity of the Teno salmon sub-populations.

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 last 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 the change in ocean environment may have affected the 1SW salmon more than 2SW salmon, suggesting more critical changes in feeding conditions for young fish that have recently entered the ocean from freshwater, compared to 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 in 1SW salmon in the River Imsa, Southwestern Norway, after the peak levels around 2000 that is parallel with the trends in the present study (Fig. 8). They concluded that the long-term change in the Imsa salmon life history was mainly driven by the oceanic ecosystem change with the rebuilding of the 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 fisheries 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 due 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 two-fold increase in catch stability in Bristol Bay, Alaska, and – despite variability in environmental conditions – enabled the fishery to maintain a 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, presumably influenced by differential responses to local environmental conditions (Rogers and Schindler 2008). The highly diverse salmon population complex in the River Teno may have a potential for such effect. This 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 multi-sea winter salmon in Teno sub-populations. 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, 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; 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.

It is important to address a potential bias in a long time series of samples from diverse fisheries as there is a risk in changes over time, e.g. in gear proportions as it 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 proportions of sea age groups in order to account for such temporal variation in fishing season and gear types. The traditional net fisheries in the Teno river did not change much over the study period in terms of e.g. mesh size or net materials; it is therefore unlikely that there have been large temporal changes in gear-specific selectivity which 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 (Anon. 2016; this study). Although some changes have taken place in the River Teno fishing effort, e.g. 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 between the gear types (Niemelä et al. 2009; Anon. 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, and targeted measures, e.g. regulations in the early season fishery, can be used to conserve specific groups such

as 2-4SW fish that largely consist of large, high-fecundity females (Niemelä et al. 2006b) that potentially produce offspring with higher survival due to their eggs having higher lipid content (Heinimaa and Heinimaa 2004). Early season regulations also safeguard previous spawners that often make 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 (Anon. 2018) that makes 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 programmes on a large and variable population complexes, like Atlantic salmon from the 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 e.g. in capturing the large diversity in early running previously spawned salmon (cf. Niemelä et al. 2006b). In addition, the genetically distinct sub-populations 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 at 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 early season), covering the 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 seemed to ensure capturing a good representation of the various life history types.

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517 **Acknowledgements**

518 We thank the numerous fishers and their background organizations in the Teno river system who have
519 helped collecting the large data set over the 40 years; Jari Haantie, Jorma Ollila and Matti Kylmäaho for
520 analyzing scale material and two anonymous reviewers for helpful comments. Funding was partly provided
521 by the Academy of Finland (project No. 286334).

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Table 1. Significance of variables included in the analyses of Atlantic salmon sea-age distribution in the River Teno system. Results for single variables included in significant interactions are not displayed. Df, degree of freedom; NS, non-significant relationship; p-values: *<0.05, **<0.01, ***<0.001)

Quasi-binomial models		1 sea winter		2 sea winter		3 sea winter		Previous spawners	
	df	F-value	Significance	F-value	Significance	F-value	Significance	F-value	Significance
Single variables									
Year	1	-	-	-	-	207,1	***	-	-
Location	8	-	-	-	-	172,7	***	-	-
Fishing gear	3	77,7	***	11,1	***	64,4	***	107,0	***
Lag Y	1	316,3	***	65,3	***	142,1	***	128,0	***
Sex	-	-	-	-	-	-	-	-	-
Month	-	-	-	-	-	-	-	-	-
Interaction terms									
Year : sex	1	19,7	***	23,5	***	1,4	NS	0,4	NS
Year : location	8	6,3	***	1,1	NS	1,5	NS	3,2	**
Sex : location	8	2,7	**	6,4	***	0,4	NS	2,1	*
Sex : month	2	4,5	*	9,7	***	81,2	***	39,6	***
Year : sex : location	8	0,6	NS	1,1	NS	0,5	NS	1,0	NS

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

785

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

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). Five and two most common strategies have been indicated for maiden salmon (e.g. 4-1: four years in freshwater, one year at sea) and previous spawners (e.g. 4-1S1: four years in freshwater, one year at sea, first spawning migration, one year at sea, second spawning migration), respectively. Rarefaction curve of the number of strategies for the 40 years sampling period (lower panel, shaded area represents 95% unconditional confidence interval).

Fig. 4. Individual-based rarefaction (solid lines) and extrapolation (dashed 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 Teno river 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 AICc; 95% confidence intervals are indicated with shaded areas

Fig. 6. Barplot of the number of life-history strategies described (left) and the estimated Hill numbers (right; life history strategy diversity corrected for sampling effort) in different locations of the Teno river system. Locations are ordered from the 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.

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

Fig. 8. Temporal variation in proportions of 1-3SW maiden salmon and previous spawners in two tributaries (Utsjoki and Inarijoki) and 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 Teno river system (see Fig. 1 for details). 1-5SW, one- to five-sea-winter salmon; PS, previous spawners.

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.

Fig. 12. Partial GAM plot representing the effects of years on the proportion of three- (black), four- (dark grey), and five- (light gray) year-old smolts in catch samples from the River Teno. Y-axis represents the contribution of the smoother. The shaded regions are 95% confidence bands around the curve.

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

Fig. 14. Proportions of Atlantic salmon in the River Teno system that have smoltified after three (black), four (grey) and five years (light grey) in relation to their sea-age. Other smolt ages (2, 6-8) are indicated by the lightest grey.