Changes in growth and migration patterns of sea trout before and after the introduction of Atlantic salmon farming

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Marine growth has strong implications for reproductive potential and ultimate fitness of sea trout. Hence, the effects of anthropogenic factors on marine growth are important when evaluating population responses and implementing management measures. Temporal changes in growth patterns of sea trout from three Norwegian and two Irish watercourses were examined, covering time spans of 25–65 years. Elemental chemistry Ba:Ca profiles and visual reading of fish scales were used to estimate smolt length and lifetime growth after first sea entry. Reduced growth after the first sea entry coincided with periods of nearby (<14 km) salmon-farming activity in impacted watersheds in both countries. Increased Ba:Ca levels were also recorded during these periods, likely indicating reduced residency in marine habitats caused by premature return to freshwater and estuaries. An increase in estimated length at first sea entry coinciding with salmon-farming activity, for groups of fish sampled after sea migration, suggests a size-selective marine mortality, with the smallest individuals experiencing a larger mortality.

Keywords: anadromous, aquaculture, body size, brown trout, LA-ICP-MS, Lepeophtheirus salmonis, Salmo trutta, salmon lice, salmonid, smolt size

Introduction

Anadromy is a migratory strategy common among many salmonid fish species, which is characterized by spawning in freshwater and marine feeding migrations. Brown trout *Salmo trutta* (L.) is a highly adaptable salmonid species. Populations in watercourses with access to the sea may consist of both freshwater-resident individuals and individuals migrating to the sea (hereafter termed sea trout) (Jonsson and Jonsson, 1993; Klemetsen *et al.*, 2003). Migratory individuals exploit the richer feeding opportunities at sea to gain a larger body size, higher female fecundity, competitive advantages on the spawning ground, and ultimately a potentially greater fitness than their freshwater-resident conspecifics (Thorstad *et al.*, 2016). However, marine migrations may also expose the individuals to higher risks of predation and being infected by pathogens or parasites (Jensen *et al.*, 2019). As anadromy is considered a quantitative threshold trait, the proportion of anadromous individuals in a populations is thought to be partly governed by the relative fitness of resident vs. migratory individuals of previous generations (Ferguson, 2006; Ferguson *et al.*, 2019). Reduced marine growth and increased marine

mortality reduce the ultimate fitness benefits of marine migrations and may result in selection against anadromy if the cost exceeds the benefits of migration (Thorstad *et al.*, 2015; Archer *et al.*, 2019).

While at sea, sea trout commonly reside in coastal areas within 100 km from their natal river, which may be areas heavily influenced by human activities, such as Atlantic salmon farming and other aquaculture activities, marine traffic, habitat alterations by industrial infrastructure, power production, and fishing (Aldvén and Davidsen, 2017; Nevoux *et al.*, 2019). The negative impacts on sea trout by Atlantic salmon aquaculture have attracted particular attention (Thorstad *et al.*, 2015; Gargan *et al.*, 2016; Moore *et al.*, 2018). Open net pen farming, normally with up to 200 000 individuals per pen in Norway, and 20 000–50 000 individuals per pen in Ireland, involves a major increase in host density and elevated levels of the parasite salmon louse *Lepeophtheirus salmonis* K., which negatively affect wild salmonids in areas with intensive salmon farming (Costello, 2009; Jansen *et al.*, 2012; Thorstad *et al.*, 2015). For sea trout, salmon lice infestations can cause increased mortality, with smaller individuals being more vulnerable than larger individuals (Skaala *et al.*, 2014; Taranger *et al.*, 2015; Serra-Llinares *et al.*, 2020). Hence, it can be expected that larger post-smolts will have better survival than smaller post-smolts in periods with a high salmon lice infestation pressure. Salmon lice infestation can also negatively affect the growth of surviving individuals by causing osmoregulatory problems, negative stress responses, reduced feeding activity, and interrupted feeding migrations (e.g. Birkeland and Jakobsen, 1997; Bjørn and Finstad, 1997; Wells *et al.*, 2007). Indeed, some studies have documented reduced body mass and condition factor of infested individuals compared to control fish (Bjørn and Finstad, 1997; Dawson *et al.*, 1998; Shephard *et al.*, 2016).

Scale reading is a commonly applied method for examining the life history and growth of fish (e.g. Dahl, 1911; Haraldstad *et al.*, 2016). Due to the variable and complex life history and habitat use of sea trout (Thorstad *et al.*, 2016; Birnie-Gauvin *et al.*, 2019), interpretation of growth patterns based on scale reading can be difficult and often subjective (Elliott and Chambers, 1996; Campbell *et al.*, 2015; Ryan *et al.*, 2019). The interpretation of growth patterns of fish moving between freshwater and seawater habitats can be considerably improved by validating scale reading with chemical analyses of the scales, because the elemental composition of scales is affected by the chemical properties of the water where the fish reside and grow (Wells *et al.*, 2000; Hutchinson and Trueman, 2006). Strontium (Sr) and barium (Ba) levels in calcified structures are commonly used to determine whether individuals have migrated between freshwater and the sea, because there are low Sr levels and high barium levels in freshwater compared to the sea (Tzadik *et al.*, 2017). Chemical stability may be lower for fish scales than for otoliths, but the advantages of using scales include non-lethal sampling methods, labour-effective preparation of samples, and possible use of existing fish scale collections (Courtemanche *et al.*, 2006; Campbell *et al.*, 2015; Tzadik *et al.*, 2017). For sea trout, it has been shown that chemical analyses of Ba:Ca profiles in scales are more accurate and reproducible than visual scale readings for evaluating body length at sea entry and marine growth (Ryan *et al.*, 2019).

Sea trout commonly utilize fully marine habitats with high salinity during their marine feeding migrations (Thorstad *et al.*, 2016). However, heavily salmon lice-infested sea trout have been observed to increasingly reside in estuaries and freshwater during times when they would be expected to be in marine habitats (Tully *et al.*, 1993; Birkeland, 1996). Estuarine waters and freshwater habitats have significantly higher levels of available barium for incorporation into calcified structures compared to marine water bodies (Walther and Limburg, 2012). Therefore, it is likely that sea trout that reside in estuarine habitats as opposed to marine habitats, or spend prolonged periods in freshwater because of premature return to freshwater, will exhibit elevated Ba:Ca values in the part of the scales that reflects the lifetime growth after the first sea entry.

In this study, we had access to historic and recent scale samples from sea trout in three rivers in Norway and two rivers in Ireland, covering periods of 25–65 years. The main aims were to examine if sea trout in populations with nearby salmon farms would have (i) increased length at first sea entry in periods with salmon-farming activity compared to periods without activity at the farming sites, which would indicate a size-selective mortality until they were sampled in freshwater later in life, (ii) increased Ba:Ca levels in the section of the scale after first sea entry, and (iii) reduced growth after first sea entry. The methods developed by Ryan *et al.* (2019) were used to identify the first freshwater–marine transition, by analysing scale Ba:Ca profiles obtained by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). This was combined with traditional scale reading to determine length at first sea entry (hereafter referred to as smolt length), lifetime growth after the first sea entry, and number of marine migrations and to measure average Ba:Ca levels during their lifetime after the first sea entry.

Material and methods

Study area

Sea trout (body length 25–51 cm) were collected for scale sampling in three rivers in Norway and two rivers in Ireland. In Norway, sea trout were collected in River Straumsvassdraget at Hitra Island outside the Trondheimsfjord and in the River Nidelva and River Levangerelva within the Trondheimsfjord (Figure 1). The salmon-farming industry in Norway started in the early 1970s on the coast outside the Trondheimsfjord and has since then become a major industry. There were no active salmon-farming sites within the Trondheimsfjord during the historic sampling years in River Nidelva and River Levangerelva. Hence, the historic samples from River Straumsvassdraget (1953) were sampled before any salmon farming was established, while the distance to the nearest aquaculture site for River Nidelva and River Levangerelva was >50 and >100 km, respectively, during the period of historic scale sampling. In recent years, there have been numerous salmon-farming sites along the coast outside the fjord. The Trondheimsfjord has recently not been used for open cage salmon farming, because the fjord was protected as a "Norwegian salmon fjord" in 2002, leading to the liquidation of existing salmon farms (established after the historic sampling years in River Nidelva and River Levangerelva) and banning of future salmon farming within the fjord. Hence, the distance from the nearest salmon-farming sites in recent sampling periods for the Norwegian rivers was 12, >50, and >100 km for River Straumsvassdraget, River Nidelva, and River Levangerelva, respectively. The salmon farms within 30 km from the river mouth of River Straumsvassdraget slaughtered their fish during early spring 2017 and were largely fallow during the summer, while there was more activity at these sites in 2018 (Barentswatch,
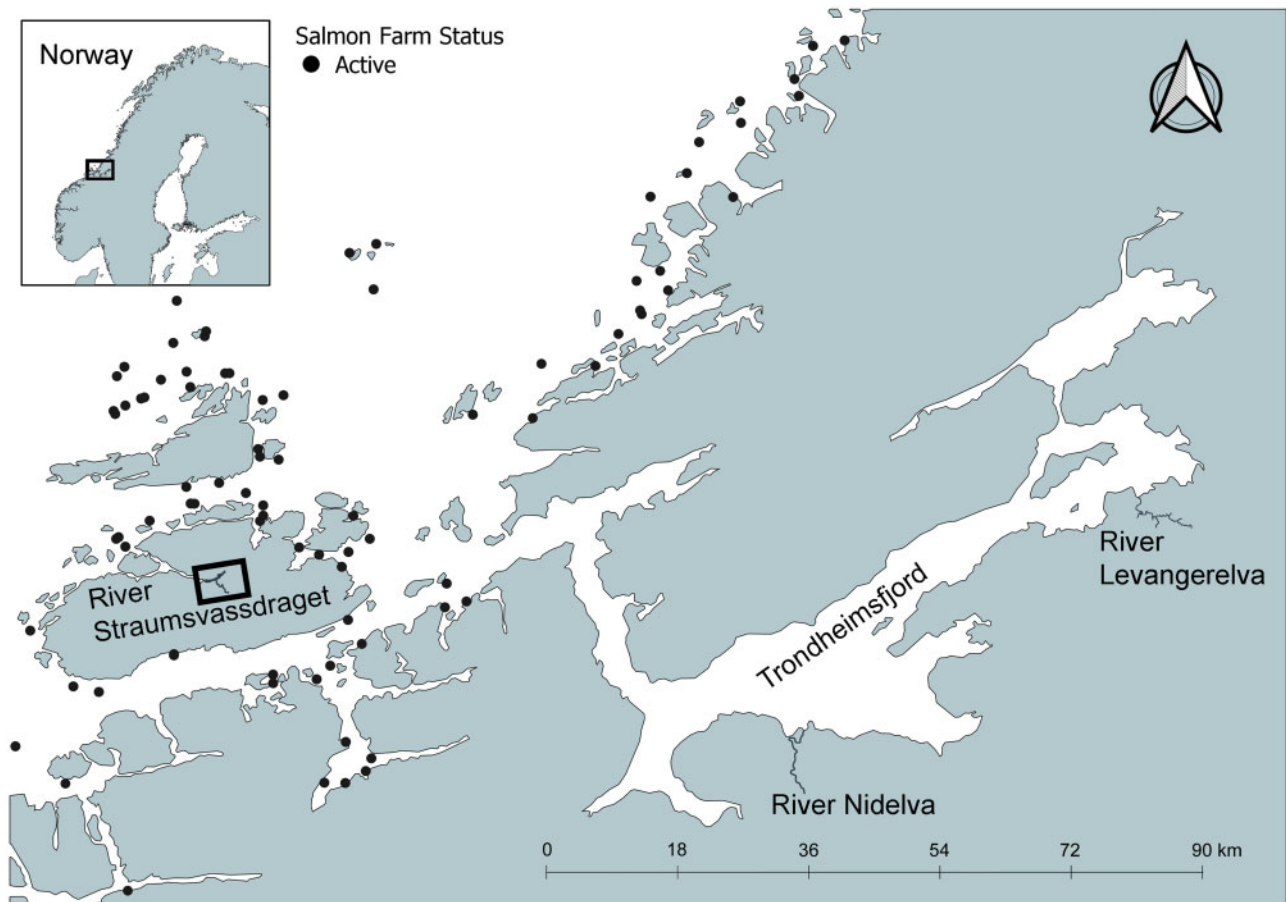
Figure 1. Study area with the River Straumsvassdraget, River Nidelva, and River Levangerelva in Central Norway. Black dots denote active open cage salmon-farming sites that reported salmon lice counts to the authorities in 2017 and/or 2018.

2020). However, the model of salmon lice larva densities developed by the Institute of Marine Research, Norway, indicated elevated infestation pressure in the areas around River Straumsvassdraget both in 2017 and 2018. The same models also indicate periodically increased salmon lice infestation levels within the Trondheimsfjord in recent years due to salmon farming, including areas close to both River Nidelva and River Levangerelva, although with lower intensities than the areas outside the fjord (IMR, 2020). Actual salmon lice counts on sea trout from the study sites were not available for the rivers in Norway.

In Ireland, samples were collected from the River Erriff in County Mayo and the River Cashla in County Galway (Figure 2). The River Erriff drains into the 15-km-long fjord of Killary Harbour, where open cage salmon-farming sites at Rosroe and Inishdeighil are located just inside the mouth of the fjord and outside the fjord, respectively. Farming of Atlantic salmon in Killary Harbour in proximity to the River Erriff started in 1986; hence, after the historic scale samples were collected. During April and May 2015, the inner site at Rosroe held large one sea winter farmed salmon with an average salmon lice load of 8.1 mobile lice per fish. In the same period in 2016, the outer Inishdeighil site was the only active site and held farmed salmon smolts with an average salmon lice load of 0.3 mobile lice per farmed fish, indicating that the farmed salmon lice infestation pressure in Killary was significantly greater during the 2015 sea

trout smolt run. It should be noted that another farmed salmon site, Clare Island smolt site, was active during the April and May period in 2016, located 24 km to the north of Killary Harbour. Data on salmon lice levels on sea trout captured migrating upstream in the Aasleagh trap on the River Erriff were available in 2015 and 2016. Average salmon lice load (all life stages) on sea trout in 2015 was high at 27.5 per fish ($n = 11$) in May, 11.8 ($n = 20$) in June, and 25.0 ($n = 34$) in July. Salmon lice levels on sea trout were significantly lower in 2016, at 5.8 ($n = 241$) in June, 4.4 ($n = 268$) in July, and 1.0 ($n = 51$) in August. Because of the reported differences in farming activity and observed salmon lice infestation rates between the sampling years 2015 and 2016 in the areas of River Erriff, the among-year differences were specifically evaluated for this watercourse.

The River Cashla drains into Cashla Bay (Figure 2). In the late 1980s when the historic scale samples were collected, salmon farming was active in the neighbouring Greatman's Bay 13 km away, and at numerous sites in Kilkieran Bay, 16–20 km from the River Cashla. In recent years, the nearest active salmon farm was located 26 km from the River Cashla in Kilkieran Bay (Figure 2).

Scale sampling

Scales were obtained from the collections at the Norwegian University of Science and Technology University Museum, the
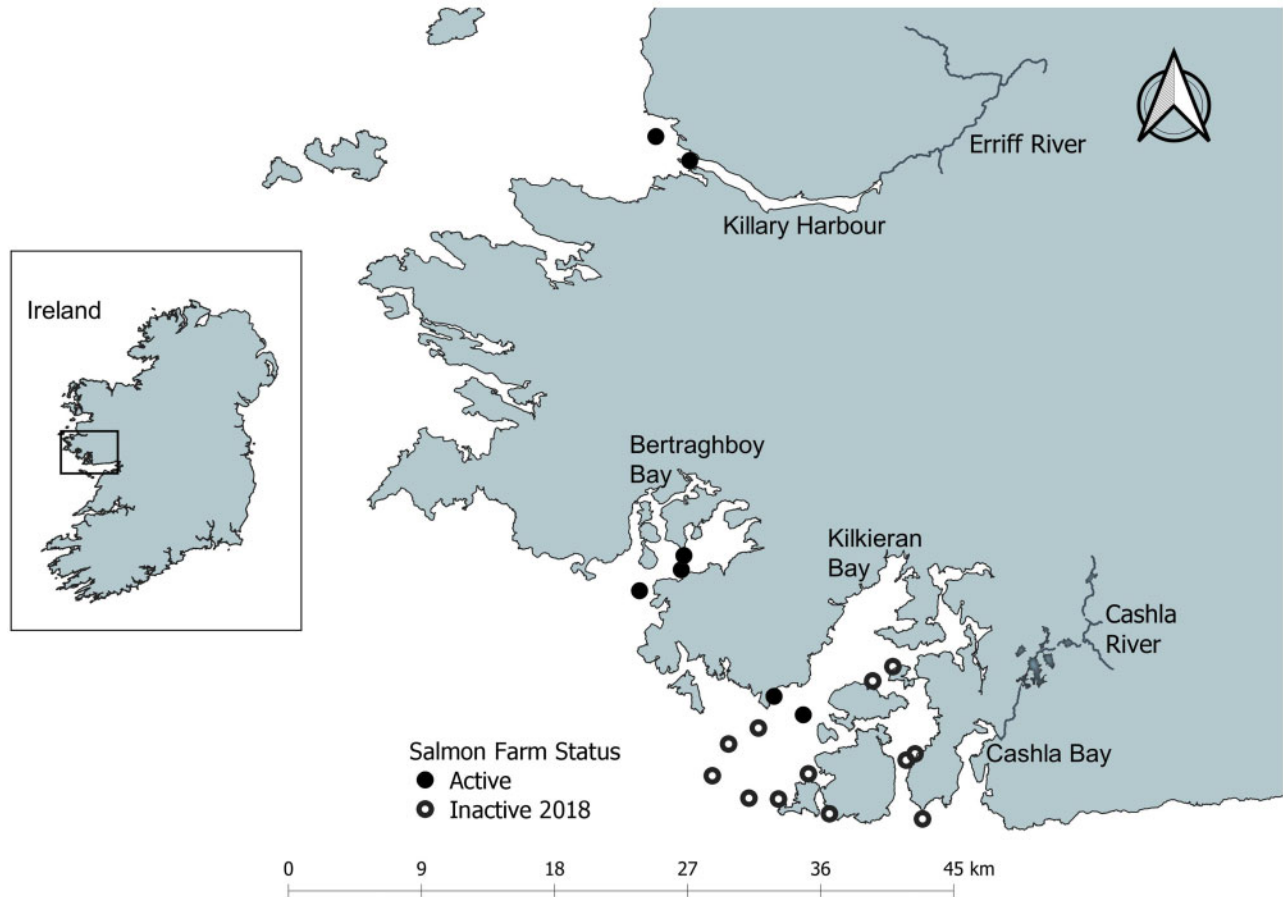
Figure 2. Study area with the River Erriff and River Cashla in Western Ireland. Black dots denote open cage Atlantic salmon-farming sites that were active during recent years when sea trout were sampled. Black circles denote Atlantic salmon-farming sites that were active during historic sampling of sea trout but inactive in 2018.

Norwegian Institute for Nature Research, and the Inland Fisheries Ireland (Table 1). Additional fish were collected and sampled from River Straumsvassdraget at Hitra Island and River Levangerelva during 2017 and 2018 (Table 1). The samples from River Straumsvassdraget were caught by gill net fishing in Lake Hustadvatnet. In River Nidelva, the historic samples were collected by recreational anglers, while the samples from 2011 to 2013 were collected by scientific personnel using rods and gillnets in the river. The samples from the 1980s from River Levangerelva originated from recreational rod fisheries in the river, while the samples from 2017 to 2018 were collected by the authors using rods and light fishing with landing nets in the river and estuary, and a bag net in the estuary. In River Erriff, the samples from 1983 were collected in the recreational rod angling fisheries, while the samples from 2015 and 2016 were collected from fish in the Aasleagh Falls fish trap, where all up-migrating fish are captured immediately upstream of the tidal interface. For the River Erriff, the data included in this study were a randomized sub-sample from a larger collection of scales, while from all other rivers all available and relevant samples were analysed. The samples from River Cashla originated from the recreational rod fisheries. Scales from trout scales that did not exhibit Ba:Ca profiles indicating that the fish had been at sea were excluded from further analyses.

Scale preparation and LA-ICP-MS analysis

One non-regenerated scale from each of the sampled trout was selected and manually cleaned using an acid-washed nylon brush prior to ultrasonically cleaning for 4 min in element grade 3% hydrogen peroxide followed by triple rinsing in 18.2 MΩ deionized water. The cleaned scales were mounted on petrographic slides with the basal plate facing down. Linear transects were analysed from the nucleus of the scale towards the edge of the scale along the midline of the anterior axis using an NWR213 New Wave Research laser ablation system, coupled to a Perkin Elmer DRC-e inductively coupled plasma mass spectrometer (LA-ICP-MS). The concentrations of the stable isotopes ^{43}Ca, ^{23}Na, ^{24}Mg, ^{55}Mn, ^{66}Zn, ^{88}Sr, and ^{138}Ba were analysed for every 9.01 μm along the scale transect. Raw LA-ICP-MS data were processed using the Iolite data reduction software with reduction scheme "Trace Elements" (Paton et al., 2011) using a ^{43}Ca concentration of 374 000 ppm as an internal standard. The concentration of ^{138}Ba was selected as the element to describe the transaction from freshwater to saltwater because Ryan et al. (2019) found this to be the element measured that was the least affected by post-depositional change. The ^{138}Ba elemental concentration values were converted to molar concentrations and standardized to calcium (Ba:Ca) prior to further analyses. Further details of the LA-ICP-MS method are described by Ryan et al. (2019).

Table 1. Overview of sea trout sampling groups, time of sampling, sample sizes (*n*), sampling method, owner of scale collection, NINA, NTNU, and IFI, and distance to nearest active salmon farm in years of sampling.

Study site	Sampling period	Sampling years	Sampling dates (dd.mm)	n	Scale collection	Sampling method	Distance to salmon farm
River Straumsvassdraget	Historic	1953	16.09–28.10	27	NINA	Gillnets in Lake Husvatnet	No farming
River Straumsvassdraget	Recent	2017–2018	25.09–10.10	50	NTNU	Gillnets in Lake Husvatnet	12 km
River Nidelva	Historic	1983–1986	05.06–25.08	23	NTNU	Recreational rod fisheries	>50 km
River Nidelva	Recent	2011–2013	16.04–14.09	29	NTNU	Rod fishing/Gillnets in river	>50 km
River Levangerelva	Historic	1987–1991	03.07–31.08	25	NTNU	Recreational rod fisheries	>100 km
River Levangerelva	Recent	2017–2018	29.08–02.11	20	NTNU	Rod fishing/Bag net in River and Estuary	>100 km
River Erriff	Historic	1983	08.08–11.10	39	IFI	Recreational rod fisheries	No farming
River Erriff	Recent	2015	09.07–20.09	31	IFI	Aasleagh Falls Trap	14 km
River Erriff	Recent	2016	01.07–18.08	29	IFI	Aasleagh Falls Trap	17 km
River Cashla	Historic	1988	07.07–07.09	47	IFI	Recreational rod fisheries	13 km
River Cashla	Recent	2018	10.07–27.09	39	IFI	Recreational rod fisheries	26 km

Freshwater-resident trout and fish with more than three seasonal marine migrations are excluded.
IFI, Inland Fisheries Ireland; NINA, Norwegian Institute for Nature Research; NTNU, Norwegian University of Science and Technology University Museum.

Determining smolt length

The Ba:Ca profiles derived from the LA-ICP-MS analysis were characterized by three distinct regions: a region representing the juvenile phase until first sea entry with high Ba:Ca values, a transition region with decreasing Ba:Ca values, and a zone representing lifetime growth (both marine and potential freshwater growth) after the first sea entry (Ryan *et al.*, 2019).

A freshwater threshold value was defined as the fifth percentile of Ba:Ca values from a freshwater growth region for each scale starting 50 μm after the start point in the scale nucleus until 50–100 μm before the start of the transition region (Figure 3). The first of greater than two consecutive Ba:Ca values in the scale transects below this threshold value was defined as the point of first sea entry (Figure 3). Smolt length was calculated as the number of Ba:Ca measurements before the transition point divided by the total number of measurements and multiplied by the body length (mm) of the fish at the time of scale sampling, assuming a linear relationship between body length and scale length. Further details of the method used to estimate growth are described by Ryan *et al.* (2019).

Estimating smolt length and lifetime growth after first sea entry by LA-ICP-MS scale chemistry is a rule-based method that can be an alternative to traditional scale reading, or be used in combination with traditional scale reading for increased scale interpretation confidence (Ryan *et al.*, 2019). Traditional scale reading is based on visual interpretation and/or morphometrical measurements, identifying the points of significant changes in distance between deposited annuli or circuli (Dahl, 1911; Elliott and Chambers, 1996; McCarthy *et al.*, 2008). Poor growth in the marine habitat or growth stagnation in periods during summer can lead to scale patterns that are difficult to interpret by traditional scale reading (Beamish and McFarlane, 1983). Failing to interpret scales with abnormal growth patterns might potentially lead to bias in analyses by excluding fish with certain behaviours or growth patterns.

Determining lifetime growth and Ba:Ca levels after first sea entry

Estimated growth after first sea entry was calculated as the body length at the time of scale sampling minus the estimated smolt
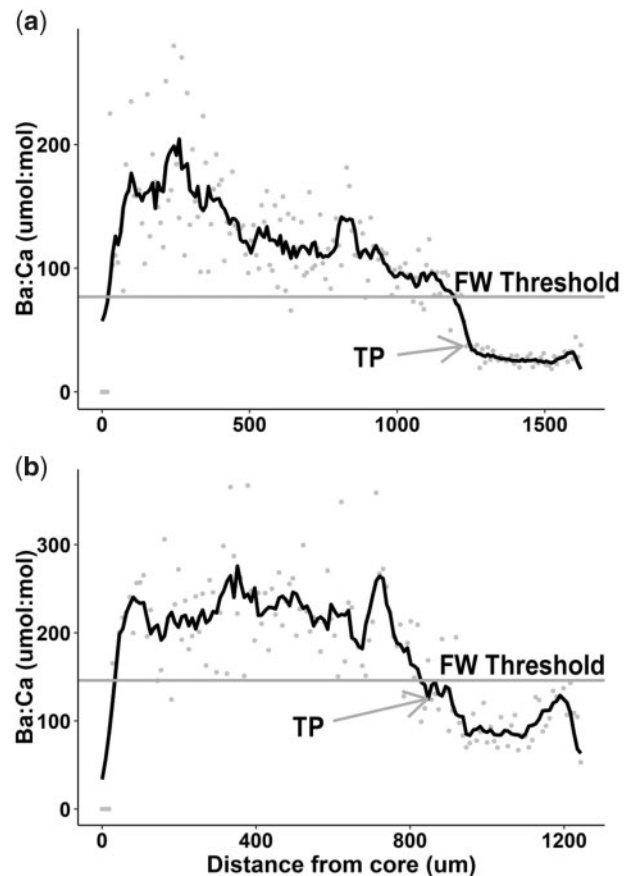
Figure 3. Examples of Ba:Ca profiles of (a) fish id 83_111 (sampled in 1983, body length 303 mm, smolt length 232 mm, one marine migration) and (b) fish id 15_14 (sampled in 2015, body length 280 mm, smolt length 193 mm, one marine migration) from River Erriff, Ireland. Grey points denote the data points along the scale transect. The black lines denote the three-point running average of the data points. Freshwater threshold value denotes the fifth percentile of Ba:Ca values from the freshwater growth region, "TP" denotes point of first sea entry.

length. An average Ba:Ca value for the growth after first sea entry was calculated for each fish. The mean value was calculated for all the measurements in sections of the scale starting 50–100 µm after end of the Ba region of transition from freshwater to saltwater to 50 µm before the transect end point (Ryan *et al.*, 2019).
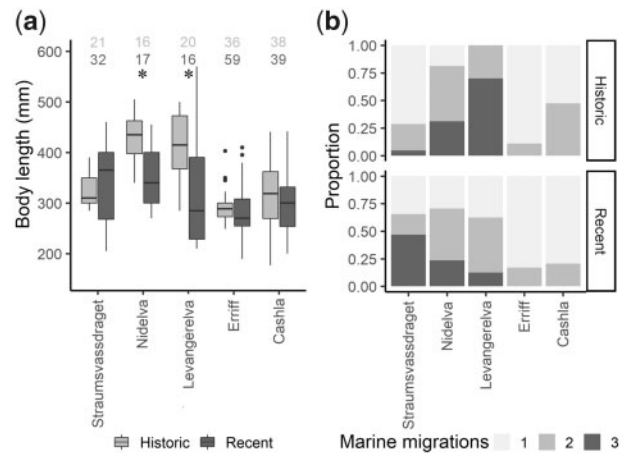
Determining the number of marine migrations

Sea trout with various numbers of marine migrations were included, but the scale chemistry analysis was not sufficiently refined to determine short-time periods of freshwater re-entry and multiple transitions between freshwater and saltwater habitats. Therefore, it was necessary to combine the chemistry analyses with ordinary scale reading to classify the number of annual marine migrations the sea trout had conducted. Combining scale chemistry analyses, which provided an estimate of smolt length, with ordinary scale reading of the number of growth seasons after smoltification provided more objective results compared to traditional scale reading alone. Scales from the Norwegian fish were pressed against Lexan plates, and their imprint was photographed using a Leica M165C and Leica MC170HD. Scales from the Irish fish were photographed using an Olympus BX51 and Q-imaging Micro-publisher 5.0. Using the information about the smolt length derived from the Ba:Ca profiles as a reference point, the number of marine migrations was determined by experienced scale reading personnel by visual interpretation. The number of marine migrations could not be confidently determined for 16% ($n = 59$) of the sampled sea trout, and these individuals were excluded from further analysis.

Statistical analyses

Statistical analyses were conducted by using RStudio version 1.2.1355 (RStudio Team, 2020) and R version 3.5.3 (R Core Team, 2020). Figures were made by using the R package ggplot 2 (Wickham, 2016). For statistical comparisons between two groups, we used two-sided *t*-tests, or two-sided Wilcoxon tests for non-normally distributed data checked by using a Shapiro–Wilk test. Analysis of variance (ANOVA) and Tukey HSD were used for statistical comparisons of three groups. For comparisons among three groups with non-normally distributed data and/or heterogeneous variance, Kruskal–Wallis rank sum tests and Dunn's tests were applied (Ogle *et al.*, 2020). Sea trout caught in River Nidelva in 1983–1986 with one marine migration were excluded from statistical analyses because of possible bias in the recreational fisheries towards fast-growing individuals in this sea age class. Statistical comparisons of Ba:Ca levels in the growth after the first sea entry zone were not conducted for River Levangerelva because of differences in the timing and method of sampling between the historically and recently collected fish. Fish that had four or more marine migrations prior to sampling were excluded from further analysis because of a low number of observations in this age group and uncertainty regarding their spawning history.

Results

In River Straumsvassdraget in Norway, sea trout with ≤3 marine migrations sampled in 2017–2018 did not differ in body length (Wilcoxon test; $n = 53$, $p = 0.14$) but had performed a higher number of marine migrations (Wilcoxon test; $n = 53$, $p = 0.002$) compared to the fish sampled in 1953 (Figure 4). In River Nidelva, the fish sampled in 2011–2013 had a shorter body length

Figure 4. Body length (a) and distribution (proportions) of number of marine migrations (b) for sea trout with ≤3 marine seasons captured and analysed using LA-ICP-MS. The box plots (a) show the interquartile range (boxes), median (horizontal line in boxes), the 5th and 95th percentiles (whiskers), and outliers (dots). The stacked bar plot (b) shows the relative numbers of marine age classes among sampled groups for the historic samples (upper panel) and recently sampled fish (lower panel). Number of observations in each group is denoted above the boxes; * above boxes indicates a significant difference in body length between the groups of historic and recent samples ($p < 0.05$).

(*t*-test; $n = 33$, $p < 0.001$ but did not differ in the number of marine migrations (Wilcoxon test; $n = 33$, $p = 0.48$) compared to fish sampled in 1983–1986 (Figure 4). In River Levangerelva, the fish sampled in 2017–2018 had a shorter body length (*t*-test; $n = 31$, $p = 0.007$) and fewer marine migrations (Wilcoxon test; $n = 31$, $p < 0.001$) than fish sampled in 1987–1991 (Figure 4).

In River Erriff in Ireland, sea trout with ≤3 marine seasons sampled in 2015–2016 did not differ in body length (Wilcoxon test; $n = 95$, $p = 0.066$), or number of marine migrations ($n = 95$, $p = 0.44$) compared to fish sampled in 1983 (Figure 4). In River Cashla, fish sampled in 2018 did not differ in body length (*t*-test; $n = 77$, $p = 0.15$) but had fewer marine migrations (Wilcoxon test; $n = 77$, $p = 0.014$) compared to fish sampled in 1988 (Figure 4).

In River Straumsvassdraget, Norway, sea trout that had performed one marine migration were shorter, had poorer growth after first sea entry and had higher Ba:Ca levels in the scale section after first sea entry in 2017–2018 (a period with nearby salmon farming) than in 1953 (pre-salmon farming, Table 2 and 3). Moreover, fish that had performed two marine migrations had a larger smolt length in 2017–2018 than in 1953 (Table 2 and 3). In River Nidelva, sea trout that had performed two marine migrations had larger Ba:Ca levels in the scale section after first sea entry in 2011–2013 than in 1983–1986 (Table 2 and 3). In River Levangerelva, there were no differences in growth patterns between fish sampled in 2017–2018 and 1987–1991 (Table 2 and 3).

In River Erriff, Ireland, sea trout that had performed one marine migration were shorter, had poorer growth after first sea entry, and had higher Ba:Ca levels in the scale section after first sea entry in 2015–2016 (a period with nearby salmon farming) than in 1983 (pre-salmon farming, Table 2 and 3). In River Cashla, sea trout that had performed one marine migration had higher growth after first sea entry, lower Ba:Ca levels in the scale section

Table 2. Summary statistics of sea trout sampled during historic and recent periods from the study rivers in Norway and Ireland.

Historic samples

Watercourse/year		River Straumsvassdraget 1953			River Nidelva 1983–1986			River Levangerelva 1987–1991			River Erriff 1983		River Cashla 1988	
Number of marine migrations		1	2	3	1	2	3	1	2	3	1	2	1	2
Number of samples	n	15	5	1	3	8	5	0	6	14	32	4	20	18
Body length (mm)	Mean	316	342	360	397	425	459	na	391	419	284	361	272	368
	SD	21	35	na	38	50	36	na	80	59	18	28	38	25
	Range	285–350	305–390	na	370–440	340–500	410–505	na	285–480	310–500	249–323	345–403	177–320	333–441
Growth after first marine entry (mm)	Mean	107	182	220	187	247	270	na	240	272	98	172	74	152
	SD	17	42	na	29	63	22	na	79	61	18	47	37	39
	Range	70–149	128–230	na	170–221	180–333	239–299	na	123–336	143–344	68–150	102–201	20–191	67–209
Ba:Ca after first marine entry	Mean	6.9	7.3	4.7	12.3	9.6	12.2	na	2.7	3.1	37.1	65.0	55.7	67.2
	SD	2.5	3.2	na	4.2	4.8	8.0	na	0.9	1.0	19.1	9.4	20.6	19.2
	Range	2.5–11.7	2.8–10.2	na	8.2–16.7	5.6–18.6	6.6–26.2	na	1.2–3.9	1.9–4.9	11.8–80.5	54.4–74.0	13.9–93.6	30.2–95.4
Smolt length (mm)	Mean	209	160	140	210	178	189	na	151	146	186	189	199	216
	SD	15	24	na	61	38	29	na	22	25	25	75	41	31
	Range	188–239	135–186	na	149–270	125–239	144–224	na	131–190	92–193	145–232	144–301	104–273	169–296

Recent samples

Watercourse/year		River Straumsvassdraget 2017–2018			River Nidelva 2011–2013			River Levangerelva 2017–2018			River Erriff 2015–2016		River Cashla 2018	
Number of marine migrations		1	2	3	1	2	3	1	2	3	1	2	1	2
Number of samples	n	11	6	15	5	8	4	6	8	2	49	10	31	8
Body length (mm)	Mean	263	348	403	316	376	355	248	317	530	269	343	281	373
	SD	39	54	34	46	80	44	48	81	57	33	50	39	41
	Range	205–360	240–380	340–460	275–380	270–455	300–400	210–340	210–420	490–570	190–350	235–410	200–334	331–442
Growth after first marine entry (mm)	Mean	60	131	161	110	193	190	114	202	343	70	131	106	168
	SD	24	34	45	49	64	44	15	53	41	31	57	19	24
	Range	21–100	96–172	87–252	53–167	102–281	128–229	104–143	123–272	314–372	6–158	39–215	78–155	131–207
Ba:Ca after first marine entry	Mean	19.5	15.3	14.1	15.6	15.7	16.3	9.2	12.5	8.5	52.1	46.9	29.0	33.3
	SD	8.9	8.5	6.1	8.1	4.6	8.3	5.2	7.6	2.8	42.4	24.5	13.5	13.8
	Range	4.5–33.5	7.7–31.3	6.3–29.7	6.8–25.8	6.8–21.7	4.2–22.8	3.7–15.9	3.3–28.9	6.6–10.5	5.0–206.2	13.0–82.9	12.0–65.3	14.4–54.0
Smolt length (mm)	Mean	202	217	243	206	184	165	134	115	187	199	212	175	205
	SD	29	45	58	72	45	17	33	46	15	29	28	30	26
	Range	166–260	144–281	108–341	133–327	112–267	139–176	103–197	54–187	176–198	103–297	180–276	121–229	158–235

Number of marine migrations indicate the number of feeding growth seasons (summers) the sea trout had spent in saline waters.

Table 3. Statistical comparisons between sea trout sampled during historic and recent periods from the study rivers in Norway and Ireland.

Change from historic to recent samples	Number of migrations	River Straumsvassdraget			River Nidelva			River Levangerelva			River Erriff		River Cashla	
		1	2	3	1	2	3	1	2	3	1	2	1	2
Number of samples	n	26	11	na	8	16	na	na	14	16	81	14	51	26
Body length (mm)	Estimate	**−54**	6	na	na	−49	na	na	−74	111	**−15**	−18	9	5
	t-test/Wilcoxon test[a]	**p < 0.001[a]**	p = 0.65[a]	na	na	p = 0.17	na	na	p = 0.12	p = 0.18	**p = 0.010**	p = 0.54[a]	p = 0.58[a]	p = 0.78
Growth after first marine entry (mm)	Estimate	**−47**	−51	na	na	−55	na	na	−38	70	**−28**	−41	**32**	16
	t-test/Wilcoxon test[a]	**p < 0.001**	p = 0.49	na	na	p = 0.11	na	na	p = 0.33	p = 0.10	**p < 0.001**	p = 0.30[a]	**p < 0.001[a]**	p = 0.20
Ba:Ca after first marine entry	Estimate	**12.62**	8.01	na	na	**6.11**	na	na	na	na	15.07	−18.04	**−26.69**	**−33.35**
	t-test/Wilcoxon test[a]	**p < 0.001[a]**	p = 0.074	na	na	**p = 0.020**	na	na	na	na	p = 0.19[a]	p = 0.070	**p < 0.001[a]**	**p < 0.001**
Smolt length (mm)	Estimate	13	**8**	na	na	6	na	na	10	5	**15**	−18	**−27**	−34
	t-test/Wilcoxon test[a]	p = 0.51[a]	**p = 0.030**	na	na	p = 0.79	na	na	p = 0.09	p = 0.082	**p = 0.023[a]**	p = 0.19[a]	**p = 0.032**	p = 0.37

Values in bold indicate statistically significant ($p < 0.05$) differences between historical and recent samples. Number of marine migrations indicate the number of feeding growth seasons (summers) the sea trout had spent in saline waters. Na-values indicate categories where statistical comparisons could not be made.

after first sea entry, and shorter smolt length in 2018 (when nearby salmon farming had ceased) than in 1988 (a period with nearby salmon farming). No other differences between groups when comparing historic and recent samples were found for these variables in any of the rivers in Norway and Ireland (Table 2 and 3).
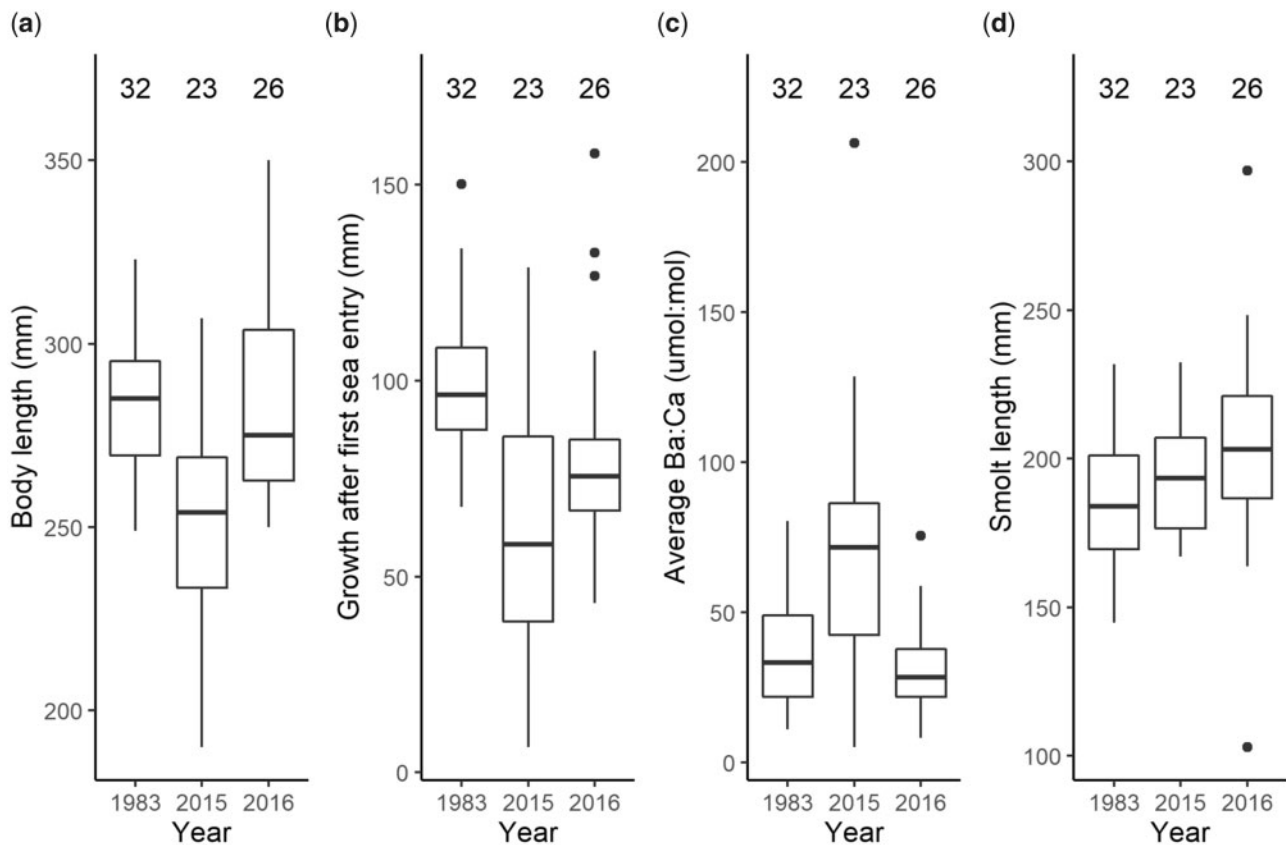
For fish sampled in the River Erriff, the body length (ANOVA, $n = 81$, $p < 0.001$), growth after first sea entry (Kruskal–Wallis test; $n = 81$, $p < 0.001$), Ba:Ca levels in the scale section after first sea entry (Kruskal–Wallis test; $n = 81$, $p < 0.001$), and smolt length (Kruskal–Wallis test; $n = 81$, $p = 0.018$) differed among years for the sea trout that had performed one marine feeding migration (Figure 5). Here, the fish sampled in 2015 were shorter (Tukey HSD, $p < 0.001$) and had poorer growth after first sea entry (Dunn's test; 1983–2015; $p < 0.001$, 2015–2016; $p = 0.048$) and higher Ba:Ca levels in the scale section after first sea entry (Dunn's test; 1983–2015; $p = 0.002$, 2015–2016; $p < 0.001$) than the fish sampled in 1983 and 2016 (Figure 5). Furthermore, the growth after first sea entry was poorer (Dunn's test; $p < 0.001$) and smolt length larger ($p = 0.014$) when comparing fish sampled in 2016 to fish sampled in 1983 (Figure 5). No other differences in these variables were found among years for the sea trout from River Erriff that had performed one marine migration prior to sampling (Figure 3, Tukey HSD/Dunn's tests; $p > 0.18$).

Discussion

Significant differences in growth and chemical composition of the scales were observed when comparing the historic and recently sampled fish both from populations in Norway and Ireland. In the populations with nearby aquaculture locations (<14 km, River Straumsvassdraget, River Erriff, and River Cashla), reduced lifetime growth and increased Ba:Ca levels after first sea entry coincided with periods of salmon-farming activity. This suggests that the sea trout had reduced marine growth and spent increased time in estuarine and freshwater habitats in the periods with active nearby salmon farms. The observed reduction in growth is consistent with previous studies comparing growth of sea trout before and after introduction of intensive salmon-farming activity in nearby areas (Poole et al., 1996; Butler and Walker, 2006; Fjørtoft et al., 2014). Using scales, Fjørtoft et al. (2014) compared the growth of sea trout in River Etneelva over a 25-year period and found that the marine growth was significantly reduced after the introduction of salmon farming in the fjord and estimated a 20–40% reduction in body mass after the first summer at sea. Butler and Walker (2006) documented a gradual decrease in marine growth rates of sea trout in River Ewe in Scotland after introduction of nearby marine salmon farming in 1987. In Ireland, Poole et al. (1996) observed a reduction in marine growth for sea trout in the River Burrishole after 1990 and concluded that it was likely linked to premature return of salmon lice-infested fish. Previous studies have found that increased salmon lice larva densities in the water and increased infestation rates on sea trout are typically found <30 km from salmon farms (reviewed by Thorstad et al., 2015). In River Erriff, lower lifetime growth and higher Ba:Ca levels in the scales after first sea entry were observed in 2015 compared to 2016, coinciding with larger salmon lice production at the nearby farm and higher salmon lice levels on sea trout collected in the nearby River Aasleagh trap in 2015 than in 2016.

Overall, the data in the present study suggest that the presence of farmed salmon farms in close proximity to the sampled rivers

Figure 5. Comparison of body length (a), growth after first sea entry (b), Ba:Ca levels in the scale section after first sea entry (c), and smolt length (d) among sampling years for fish with one marine migration in the River Erriff. The *x*-axis indicates the year of sampling for the fish. No aquaculture was established in 1983. Nearby salmon farms were active in 2015, and merely fallow in 2016. Box plots show the interquartile ranges (boxes), medians (horizontal line in boxes), the 5th and 95th percentiles (whiskers), and outliers (dots). Number of observations in each group is denoted above the boxes.

likely contributed to the observed reduction in lifetime growth after first sea entry. However, isolating the effect of salmon farming and associated increase in infestation pressure by salmon lice on the growth and survival of wild salmonids can be difficult due to multiple factors that can influence the sea trout growth over the study periods (Thorstad *et al.*, 2015; Shephard and Gargan, 2017), which is also the case in this study. Variation in the marine growth of sea trout among years has previously been observed in areas without salmon farming and has been suggested to be influenced by climatic conditions and variation in marine prey availability (Berg and Jonsson, 1990; Kallio-Nyberg *et al.*, 2015). Important pelagic prey species, such as sprat *Sprattus sprattus*, herring *Clupea harengus*, and small sandeel *Ammodytes tobianus* (Knutsen *et al.*, 2001; Rikardsen and Amundsen, 2005; Davidsen *et al.*, 2017), can vary greatly among years (ICES, 2020). Climate change and anthropogenic factors, such as overfishing of key marine species, can lead to regime shifts in marine ecosystems (Möllmann and Diekmann, 2012), which can also influence the marine growth of sea trout. However, the importance of such factors for the observed sea trout growth patterns was not possible to evaluate in this study.

No differences in lifetime growth after first sea entry were found between old and new samples from the River Nidelva and River Levangerelva, which are situated in the Trondheimsfjord system where no open cage salmon-farming sites were active during the periods of sampling in these rivers. However, the number of samples for each sea age group from these rivers is small leading to low statistical power to detect differences. Although the distance from the river mouth to the nearest active farms was large for the River Nidelva (>50 km) and River Levangerelva (>100 km), the salmon lice models run by the Institute of Marine Research suggest that salmon farming can periodically lead to increased salmon lice infestation rates within the Trondheimsfjord and in the areas close to both River Nidelva and River Levangerelva in some years (IMR, 2020). Also, although most sea trout seem to remain within 100 km of their watercourse of origin (Thorstad *et al.*, 2016), some can migrate substantially longer distances (Birnie-Gauvin *et al.*, 2019). It is therefore likely that some sea trout from River Nidelva and River Levangerelva migrate to the outer areas of Trondheimsfjord, where the modelled salmon lice infestation pressure is periodically high (IMR, 2020). It should also be noted that the time period between historic and recent samples varies among the watercourses, with the samples from River Straumsvassdraget watercourse representing the longest time interval. Moreover, it cannot be excluded that climate change has impacted the populations in different ways, because their freshwater, estuarine, and marine habitats near the rivers have different characteristics.

The elevated Ba:Ca levels in the scale section after first sea entry that coincided with periods of salmon-farming activity in

River Straumsvassdraget, River Erriff, and River Cashla suggest that the sea trout sampled during high salmon-farming activity to a greater extent resided in estuarine water and freshwater habitats after their first migration to the marine environment compared to fish sampled in periods when the nearby farming sites were inactive. Elevated Ba:Ca levels were also observed for sea trout that had performed two marine migrations in River Nidelva when comparing fish sampled in 2011–2013 to fish sampled in 1983–1986. Freshwater and estuarine water bodies have higher concentrations of available barium for absorption in the fish scales (Walther and Limburg, 2012; Tzadik et al., 2017). Previous studies have documented that sea trout heavily infested with salmon lice tend to seek estuaries and freshwater (Tully et al., 1993; Birkeland, 1996; Birkeland and Jakobsen, 1997), likely to regain osmotic balance, but which also result in reduced lice loads because salmon lice do not survive in freshwater and has a poor survival in brackish water. A recent telemetry study showed that sea trout spent more time close to the river mouth in years with active salmon farms in the area compared to years when the farm was fallow (Halttunen et al., 2018). Combining telemetry and artificial infestation, Serra-Llinares et al. (2020) documented that sea trout infested with salmon lice had higher mortality, remained closer to the estuary, and returned to freshwater earlier than the non-infested control group. Although the reason for the observed trends in Ba:Ca levels remains obscure, previous studies on the effect of salmon lice on sea trout behaviour may suggest a behavioural response to salmon lice infestation of the sea trout in periods with nearby aquaculture in the present study.

Studies linking scale Ba:Ca levels to the behaviour of sea trout need to be performed to verify causes for the observed differences in Ba:Ca concentrations and to quantify the effect of estuarine and freshwater residency on the overall Ba:Ca levels. Ba:Ca levels in the juvenile zone of the scales (before the smolt migration to the sea) were generally decreasing with increasing seasons at sea, suggesting a gradual degradation of the freshwater Ba:Ca signal over time when residing in the marine habitat. Similarly, the overall Ba:Ca levels after the point of first freshwater entry are likely elevated by post-depositional change when the fish reside in estuarine or freshwater habitats, even though it may have initially migrated to fully marine habitats. Chemical post-depositional change in scales has been documented in previous studies (Tzadik et al., 2017). However, there may be several causes for this, including diffusion of the deposited barium to saltwater, active reabsorption of the fish in response to a requirement for barium in biological processes, and secondary growth of the scale leaving a thin layer of saltwater-deposited material over the part of the scale grown in freshwater (Metz et al., 2014; Seeley et al., 2015).

The observed increase in estimated length at first sea entry coinciding with salmon-farming activity for groups of fish sampled after sea migration may suggest an increased size-selective marine mortality in these periods, with the smallest individuals experiencing a larger mortality. Previous studies have documented that smaller individuals are more vulnerable to both salmon lice infestation and predation (Taranger et al., 2015; Thorstad et al., 2015; Serra-Llinares et al., 2020). However, smolt length may also be influenced by changes in climate, river productivity, and/or density-dependent competition in the freshwater habitat (Klemetsen et al., 2003).

As body size is strongly correlated with fecundity (Elliott, 1995), reduced marine growth due to anthropogenic factors is likely to have negative impact on the reproductive capacity of the spawning populations of sea trout and reduce the population's productivity. In one of the rivers included in this study, River Erriff, Gargan et al. (2016) documented significant decreases in the number and length of post-spawned sea trout, the estimated number of eggs deposited, sea trout rod catches, the proportions of older sea trout, and the frequency of repeat spawners in the period following establishment of the nearby salmon farm in 1986. Reduced marine growth and increased risk of mortality at sea can ultimately lead to selection against anadromy and lower proportions of marine migrants in partially migratory populations (Gargan et al., 2006; Thorstad et al., 2015; Archer et al., 2019). Methods for monitoring the growth of sea trout and incorporating sustained marine growth as a conservation aim in the management for sea trout populations are therefore crucial to maintain anadromy as a common migratory strategy within coastal brown trout populations.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

References

Aldvén, D., and Davidsen, J. 2017. Marine migrations of sea trout (Salmo trutta). In Sea Trout: Science & Management: Proceedings of the 2nd International Sea Trout Symposium, pp. 288–297. Ed. by G. Harris. Troubador Publishing Ltd, Dundalk.

Archer, L. C., Hutton, S. A., Harman, L., O'Grady, M. N., Kerry, J. P., Poole, W. R., Gargan, P., et al. 2019. The interplay between extrinsic and intrinsic factors in determining migration decisions in brown trout (Salmo trutta): an experimental study. Frontiers in Ecology and Evolution, 7: 1–18.

Barentswatch. 2020. Norwegian Fish Health Database. Barentswatch, Tromsø. https://www.barentswatch.no/en/fishhealth (last accessed 8 July 2020).

Beamish, R. J., and McFarlane, G. A. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society, 112: 735–743.

Berg, O. K., and Jonsson, B. 1990. Growth and survival rates of the anadromous trout, Salmo trutta, from the Vardnes River, northern Norway. Environmental Biology of Fishes, 29: 145–154.

Birkeland, K. 1996. Consequences of premature return by sea trout (Salmo trutta) infested with the salmon louse (Lepeophtheirus salmonis Krøyer): migration, growth, and mortality. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2808–2813.

Birkeland, K., and Jakobsen, P. J. 1997. Salmon lice, Lepeophtheirus salmonis, infestation as a causal agent of premature return to rivers and estuaries by sea trout, Salmo trutta, juveniles. Environmental Biology of Fishes, 49: 129–137.

Birnie-Gauvin, K., Thorstad, E. B., and Aarestrup, K. 2019. Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. Reviews in Fish Biology and Fisheries, 29: 749–766.

Bjørn, P., and Finstad, B. 1997. The physiological effects of salmon lice infection on sea trout post smolts. Nordic Journal of Freshwater Research, 73: 60–72.

Butler, J., and Walker, A. 2006. Characteristics of the sea trout *Salmo trutta* (L.) stock collapse in the River Ewe (Wester Ross, Scotland), in 1988-2001. *In* Sea Trout: Biology, Conservation and Management, pp. 45–59. Ed. by G. Harris and N. Milner. Blackwell Publishing Ltd, Oxford.

Campbell, L. A., Bottom, D. L., Volk, E. C., and Fleming, I. A. 2015. Correspondence between scale morphometrics and scale and otolith chemistry for interpreting juvenile salmon life histories. Transactions of the American Fisheries Society, 144: 55–67.

Costello, M. J. 2009. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. Proceedings of the Royal Society B: Biological Sciences, 276: 3385–3394.

Courtemanche, D. A., Whoriskey, J. F. G., Bujold, V., and Curry, R. A. 2006. Assessing anadromy of brook char (*Salvelinus fontinalis*) using scale microchemistry. Canadian Journal of Fisheries and Aquatic Sciences, 63: 995–1006.

Dahl, K. 1911. Age and Growth in Salmon and Trout as Shown by Their Scales (in Norwegian). Landbruksdepartementet, Kristiania. 115 pp.

Davidsen, J. G., Knudsen, R., Power, M., Sjursen, A. D., Rønning, L., Hårsaker, K., Næsje, T. F., *et al.* 2017. Trophic niche similarity among sea trout *Salmo trutta* in central Norway investigated using different time-integrated trophic tracers. Aquatic Biology, 26: 217–227.

Dawson, L. H. J., Pike, A. W., Houlihan, D. F., and McVicar, A. H. 1998. Effects of salmon lice *Lepeophtheirus salmonis* on sea trout *Salmo trutta* at different times after seawater transfer. Diseases of Aquatic Organisms, 33: 179–186.

Elliott, J. M. 1995. Fecundity and egg density in the redd for sea trout. Journal of Fish Biology, 47: 893–901.

Elliott, J. M., and Chambers, S. 1996. A Guide to the Interpretation of Sea Trout Scales. National Rivers Authority R&D Report 22. National Rivers Authority, Bristol. 63 pp.

Ferguson, A. 2006. Genetics of sea trout, with particular reference to Britain and Ireland. *In* Sea Trout: Biology, Conservation and Management, pp. 155–182. Ed. by G. Harris and N. Milner. Blackwell Publishing Ltd, Oxford.

Ferguson, A., Reed, T. E., Cross, T. F., McGinnity, P., and Prodöhl, P. A. 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. Journal of Fish Biology, 95: 692–718.

Fjørtoft, H. B., Borgstrøm, R., and Skaala, Ø. 2014. Differential changes in growth patterns of anadromous brown trout and Atlantic salmon from the River Etneelva over a 25-year period. Marine Biology Research, 10: 301–307.

Gargan, P. G., Kelly, F. L., Shephard, S., and Whelan, K. F. 2016. Temporal variation in sea trout *Salmo trutta* life history traits in the Erriff River, western Ireland. Aquaculture Environment Interactions, 8: 675–689.

Gargan, P. G., Roche, W., Forde, G., and Ferguson, A. 2006. Characteristics of the sea trout (*Salmo trutta* L.) stocks from the Owengowla and Invermore fisheries, Connemara, Western Ireland, and recent trends in marine survival. *In* Sea Trout: Biology, Conservation and Management, pp. 60–75. Ed. byG. Harris and N. Milner. Blackwell Publishing Ltd, Oxford.

Halttunen, E., Gjelland, K.-Ø., Hamel, S., Serra-Llinares, R.-M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., *et al.* 2018. Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. Journal of Fish Diseases, 41: 953–967.

Haraldstad, T., Haugen, T. O., Borgstrøm, R., and Jonsson, B. 2016. Increased precision of growth data gained by reading multiple scales from each individual of Atlantic salmon (*Salmo salar*). Fauna Norvegica, 36: 1–7.

Hutchinson, J. J., and Trueman, C. N. 2006. Stable isotope analyses of collagen in fish scales: limitations set by scale architecture. Journal of Fish Biology, 69: 1874–1880.

ICES. 2020. ICES Stock Assessment Database. ICES, Copenhagen. http://ices.dk/data/assessment-tools/Pages/stock-assessment-graphs.aspx (last accessed 8 July 2020).

IMR. 2020. Salmon Lice Map. Institute of Marine Research, Bergen. https://www.hi.no/forskning/marine-data-forskningsdata/lakseluskart/html/lakseluskart.html (last accessed 8 July 2020).

Jansen, P. A., Kristoffersen, A. B., Viljugrein, H., Jimenez, D., Aldrin, M., and Stien, A. 2012. Sea lice as a density-dependent constraint to salmonid farming. Proceedings of the Royal Society B: Biological Sciences, 279: 2330–2338.

Jensen, A. J., Finstad, B., and Fiske, P. 2019. The cost of anadromy: marine and freshwater mortality rates in anadromous arctic char and brown trout in the arctic region of Norway. Canadian Journal of Fisheries and Aquatic Sciences, 76: 2408–2417.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries, 3: 348–365.

Kallio-Nyberg, I., Saloniemi, I., and Jutila, E. 2015. Growth of hatchery-reared sea trout (*Salmo trutta trutta*) on the Finnish coast of the Baltic Sea. Boreal Environment Research, 20: 19–34.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., ÓConnell, M. F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L., and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish, 12: 1–59.

Knutsen, J. A., Knutsen, H., Gjosaeter, J., and Jonsson, B. 2001. Food of anadromous brown trout at sea. Journal of Fish Biology, 59: 533–543.

McCarthy, J. L., Friedland, K. D., and Hansen, L. P. 2008. Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. Journal of Fish Biology, 72: 1572–1588.

Metz, J. R., Leeuwis, R. H. J., Zethof, J., and Flik, G. 2014. Zebrafish (*Danio rerio*) in calcium-poor water mobilise calcium and phosphorus from scales. Journal of Applied Ichthyology, 30: 671–677.

Moore, I., Dodd, J. A., Newton, M., Bean, C. W., Lindsay, I., Jarosz, P., and Adams, C. E. 2018. The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus salmonis* infection of anadromous *Salmo trutta* populations on the isle of Skye, Scotland. Journal of Fish Biology, 92: 1849–1865.

Möllmann, C., and Diekmann, R. 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the northern hemisphere. Advances in Ecological Research, 47: 303–347.

Nevoux, M., Finstad, B., Davidsen, J. G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., *et al.* 2019. Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). Fish and Fisheries, 20: 1051–1082.

Ogle, D. H., Wheeler, P. and Dinno, A. 2020. FSA: Fisheries Stock Analysis. R Package Version 0.8.30. https://github.com/droglenc/FSA (last accessed 8 July 2020).

Paton, C., Hellstrom, J., Paul, B., Woodhead, J., and Hergt, J. 2011. Iolite: Freeware for the visualisation and processing of mass spectrometric data. Journal of Analytical Atomic Spectrometry, 26: 2508 10.1039/c1ja10172b

Poole, W. R., Whelan, K. F., Dillane, M. G., Cooke, D. J., and Matthews, M. 1996. The performance of sea trout, *Salmo trutta* L., stocks from the Burrishoole system western Ireland, 1970–1994. Fisheries Management and Ecology, 3: 73–92.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/ (last accessed 8 July 2020).

Rikardsen, A. H., and Amundsen, P. A. 2005. Pelagic marine feeding of Arctic charr and sea trout. Journal of Fish Biology, 66: 1163–1166.

RStudio Team. 2020. RStudio: Integrated Development for R. RStudio Inc., Boston. http://www.rstudio.com/ (last accessed 8 July 2020).

Ryan, D., Shephard, S., Gargan, P., and Roche, W. 2019. Estimating sea trout (*Salmo trutta* L.) growth from scale chemistry profiles: an objective approach using LA-ICPMS. Fisheries Research, 211: 69–80.

Seeley, M., Miller, N., and Walther, B. 2015. High resolution profiles of elements in Atlantic tarpon (*Megalops atlanticus*) scales obtained via cross-sectioning and laser ablation ICP-MS: a literature survey and novel approach for scale analyses. Environmental Biology of Fishes, 98: 2223–2238.

Serra-Llinares, R. M., Bøhn, T., Nilsen, R., Karlsen, Ø., Freitas, C., Albretsen, J., Haraldstad, T., *et al.* 2020. Increased mortality and altered behaviour of sea trout (*Salmo trutta*) post-smolts infested with salmon lice (*Lepeophtheirus salmonis*). Marine Ecology Progress Series, 635: 151–168.

Shephard, S., and Gargan, P. 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environment Interactions, 9: 181–192.

Shephard, S., MacIntyre, C., and Gargan, P. 2016. Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. Aquaculture Environment Interactions, 8: 597–610.

Skaala, Ø., Kålås, S., and Borgstrøm, R. 2014. Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. Marine Biology Research, 10: 279–288.

Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., Kvamme, B. O., *et al.* 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, 72: 997–1021.

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., *et al.* 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*—a literature review. Aquaculture Environment Interactions, 7: 91–113.

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., *et al.* 2016. Marine life of the sea trout. Marine Biology, 163: 1–47.

Tully, O., Poole, W. R., and Whelan, K. F. 1993. Infestation parameters for *Lepeophtheirus salmonis* (Krøyer) (*Copepoda: Caligidae*) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquaculture Research, 24: 545–555.

Tzadik, O. E., Curtis, J. S., Granneman, J. E., Kurth, B. N., Pusack, T. J., Wallace, A. A., Hollander, D. J., *et al.* 2017. Chemical archives in fishes beyond otoliths: a review on the use of other body parts as chronological recorders of microchemical constituents for expanding interpretations of environmental, ecological, and life-history changes. Limnology and Oceanography: Methods, 15: 238–263.

Walther, B. D., and Limburg, K. E. 2012. The use of otolith chemistry to characterize diadromous migrations. Journal of Fish Biology, 81: 796–825.

Wells, A., Grierson, C. E., Marshall, L., MacKenzie, M., Russon, I. J., Reinardy, H., Sivertsgård, R., *et al.* 2007. Physiological consequences of "premature freshwater return" for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice (*Lepeophtheirus salmonis*). Canadian Journal of Fisheries and Aquatic Sciences, 64: 1360–1369.

Wells, B. K., Bath, G. E., Thorrold, S. R., and Jones, C. M. 2000. Incorporation of strontium, cadmium, and barium in juvenile spot (*Leiostomus xanthurus*) scales reflects water chemistry. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2122–2129.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer Publishing, New York.

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