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Growth of hatchery-reared sea trout (*Salmo trutta trutta*) on the Finnish coast of the Baltic Sea

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The marine growth of approximately 20 000 tagged and recaptured sea trout (*Salmo trutta trutta*) smolts was examined following Finnish releases into the Baltic Sea from 1980 to 2010. All these trout smolts were hatchery reared. Due to the low catch length and intensive fishing, a high proportion of the trout were captured in their first and second sea year, i.e. before spawning. Sea trout grew better in the southern Finnish sea area (59°30´–60°30´N) than in its northern parts (60°30´–66°N). The marine growth rate increased in both sea areas from 1980 to 2010, but relatively more in the northern than the southern one, especially among the northern two-sea-winter-old trout. Better annual marine growth was associated with an increase in the sea surface temperature in April, or a high abundance of Baltic herring (*Clupea harengus membras*). The condition factor of trout was higher in the southern than the northern sea area and was positively linked to herring abundance.

Introduction

The status of natural sea trout (*Salmo trutta trutta*) stocks is critically endangered in Finland (Urho *et al*. 2010), and both natural and reared sea trout stocks have suffered from reduced marine survival since the 1980s (Kallio-Nyberg *et al*. 2006, 2007, ICES 2011). However, the factors behind the annual and long-term patterns affecting their marine growth in the Baltic Sea are poorly known (Järvi 1940, Ikonen and Auvinen 1984, Kallio-Nyberg *et al*. 2007, Bartel *et al*. 2010, Degerman *et al*. 2012).

Both in the Atlantic Ocean and the Baltic Sea, the abundance of sea trout and Atlantic salmon (*Salmo salar*) declined during the recent decades, probably due to changes in the marine habitat (Friedland *et al*. 2003, Jonsson and Jonsson 2004a, Kallio-Nyberg *et al*. 2006, Poole *et al*. 2006, Peyronnet *et al*. 2008, Mäntyniemi *et al*. 2012), or in rearing and stocking (Jutila *et al*. 2006, Ford and Myers 2008). In the Baltic Sea, the abundance and composition of plankton has changed simultaneously with the sea temperature (Mackenzie *et al*. 2007), while habitat destruction due to the damming of rivers and overexploitation has caused a decline in the stocks of anadromous fish species (Ikonen, 1984, Jutila *et al*. 2006, Rivinoja *et al*. 2001, Urho *et al*. 2010, ICES 2011).

In the Gulf of Bothnia and the Gulf of Finland, situated in the northern parts of the Baltic Sea, 149 rivers or brooks have been estimated to maintain sea trout populations (ICES 2011).

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However, many of these populations are mixed, their status is uncertain and smolt production is below the potential level (ICES 2013). Most of the twenty remaining Finnish sea trout rivers are situated in the Gulf of Finland area and only three of them in the Gulf of Bothnia. In Finland, almost the entire catch of sea trout is taken in sea fishing, mostly as a by-catch of the gill net fishery. This uses small mesh sizes targeted at other species, mainly whitefish (*Coregonus* sp.), perch (*Perca fluviatilis*) or pikeperch (*Sander lucioperca*) (ICES 2011). The legal catch length of sea trout in Finland was 40 cm until 2008, when it was raised to 50 cm, and in 2014 it was further raised to 60 cm. Most female sea trout in the northern Baltic Sea mature for the first time at a length of over 60 cm (Järvi 1940).

Brood stock rearing and release programmes have been established to conserve weak natural stocks, to compensate for the lost natural production or to increase the number of fish recruiting to the sea fishing stock (Poole *et al*. 2002, Kallio-Nyberg *et al*. 2002, Jutila *et al*. 2006). During the 2000s, 2.6–3.8 million sea trout smolts were annually released into the Baltic Sea (ICES 2013).

Data collected on tagged sea trout released into Finnish coastal waters between 1980 and 2010 and subsequently recaptured have earlier been analysed for survival (Kallio-Nyberg *et al*. 2006, 2007) and to study the feeding migration (Kallio-Nyberg *et al*. 2002). Here, we used partly the same data to examine the factors affecting marine growth, measured as the length increment of individual trout after release until recapture and tag return. After entering the sea as smolts, anadromous sea trout undergo a feeding migration for 2–4 years before their first spawning migration to their home river (Järvi 1940, Haikonen *et al*. 2006). Non-mature sea trout may return annually to freshwater and overwinter in the river or spend the winter at sea (Berg and Berg 1987b, Berg and Jonsson 1990, Olsen *et al*. 2006, Bartel *et al*. 2010). In the northern Baltic Sea, sea trout mostly overwinter in the sea (Kallio-Nyberg *et al*. 2002). Sea trout grow faster at sea than in freshwater (Degerman *et al*. 2012), but during winter they may even lose weight (Berg and Jonsson 1990, Degerman *et al*. 2012). Migratory trout feed partly on the same prey as salmon in the Baltic Sea, but compared with salmon, the feeding of sea trout might be more opportunistic due to the short range of the feeding migration (Haluch and Skóra 1997, Svärdson and Fagerström 1982, Knutsen *et al*. 2001).

The aim of this study was to investigate the factors underlying the annual and long-term variation in the marine growth and condition of sea trout released as smolts on the Finnish coast of the Baltic Sea. We compared growth between release years, and studied temporal changes in marine growth and the condition factor in the 1980s, 1990s and 2000s in the coastal waters of southern and northern Finland. The effects of annually varying environmental factors such as the sea surface temperature (SST) and prey fish abundance were analysed in relation to growth and condition factor.

Material and methods

Study area and tagged sea trout groups

Reared and tagged sea trout smolts were released into Finnish river estuaries of the Gulf of Finland (ICES sub-division SD 32 = GF), Archipelago Sea (ICES SD 29 = AS), Bothnian Sea (ICES SD 30 = BS) and Bothnian Bay (ICES SD 31 = BB) in 1980–2010 (Fig. 1). In this study, we combined the southern (29 and 32, GF and AS) and northern (30 and 31, BS and BB) ICES subdivisions.

The smolts were produced by using brood stocks maintained in several state-owned and private hatcheries (Kallio-Nyberg *et al*. 2002, 2006). Altogether, the stocks were known by 14 different names, and a proportion of them were mixed stocks named after their release site. However, most (64%) of the tagged groups were progeny of the Isojoki sea trout brood stock. The Isojoki discharges into the southern Gulf of Bothnia (GB) (62°30´N, 21°25´E) (Fig. 1). In total, 49% of smolts released in the northern (BS, BB) and 76% in the more southern areas (GF, AS) originated from Isojoki sea trout. The other released stocks in the north were Oulujoki (26%), Iijoki (22%), Tornionjoki (1%), Lestijoki and other sea trout (2%) (Jutila *et al*. 2006). Besides Isojoki trout, Åland mixed stock (17%)

and Ingarskila sea trout (5%), as well as other stocks (2%), were also released in the south.

During the study period, nearly 300 000 two-year-old smolts were individually tagged with Carlin tags. The smolts were released in spring, when the naturally-born smolts begin their sea migration (Haikonen *et al*. 2006). During tagging, the total length (mm) of each fish was measured, and the weight (g) of randomly selected individuals, about 10% of each tagging group (usually 500–1000 individuals), was recorded.

Altogether, 6.7% (n = 19 981) of tags were returned (release SD 32: n = 6127; SD 29: n = 4758; SD 30: n = 4083; SD 31: n = 5013). About half of the individuals of the most commonly released trout stock, Isojoki sea trout, were recaptured in coastal waters (0–50 km from the release site) and the rest came from further coastal waters or the open sea (Kallio-Nyberg *et al*. 2002). Fishermen returned the tags of the captured fish, and the tagging office of the Finnish Game and Fisheries Institute compiled the data from these tags. As only a part of recaptures included full information on the recapture site, time, catch length or catch weight, the number of observations varied in different analyses. We did not analyse spatial distribution, but our earlier study demonstrated that over 90% of recaptures occurred in the home sub-basin of the released juveniles (Kallio-Nyberg *et al*. 2007).

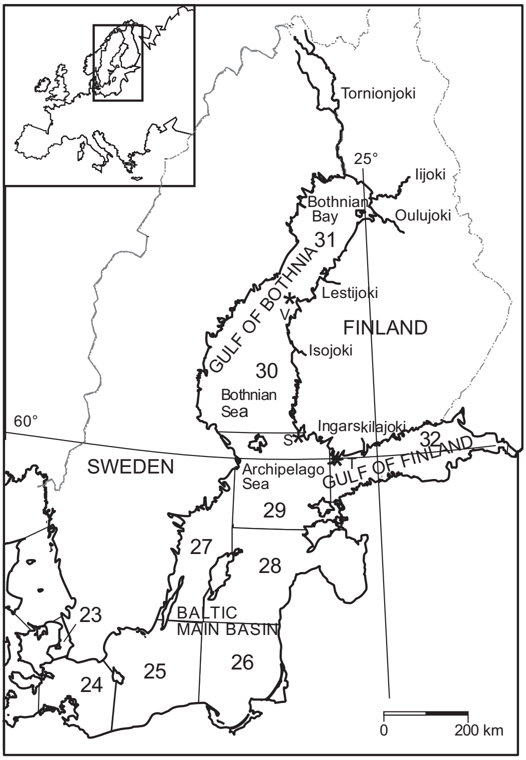

Fig. 1. Map of the Baltic Sea showing the sea areas [Main Basin = ICES sub-divisions 23–28, Gulf of Finland (GF) = 32, Archipelago Sea (AS) = 29, Bothnian Sea (BS) = 30, Bothnian Bay (BB) = 31] and some current and potential trout rivers (Tornionjoki, Iijoki, Oulujoki, Lestijoki, Isojoki and Ingarskilajoki). The locations (*) of Valassaaret (V), Tvärminne (T), Seili (S) stations are shown. In the study, the southern areas were the GF and AS, and the northern areas were the BS and BB.

Variables and statistical analyses

All stocks released in 1980–2010 were included in the analyses. The data and analyses were mainly restricted to fish recaptured 8–25 months after release, i.e. between the beginning of the first winter and the end of the second winter.

Analysis of recapture rates was based on the release groups, and the recapture rate was the number of returned tags per tagged individuals. We compared groups released into different areas (depending on the analysis either four: GF, AS, BS, BB or two: GF + AS = southern area and BS + BB = northern area) or in different periods according to release years (decades 1980s, 1990s and 2000s). Within each of the tagging decades, recapture rates from individual releases were normally distributed, so a t-test could be used to compare mean recapture rates between the areas. However, recapture rates decreased with time towards present, and the yearly recapture rates (calculated by pooling all releases of a year) did not follow the normal distribution anymore. Therefore, to find out whether this decrease in the northern and southern sea areas happened in the same manner, we calculated Spearman's correlation (SAS CORR) of the annual means.

The sea age before recapture and mean recapture length and weight at age were classified into eight time categories: summer months S1 = 1–7, S2 = 14–19, S3 = 26–31, S4 = 38–43 or winter months W1 = 8–13, W2 = 20–25, W3 = 32–37, W4 = 44–49. The mean (± SD) recapture length and weight at age were estimated for the four sea areas (GF, AS, BS, BB) and for the 6–7-month periods. The age of the trout at the time when it was caught (i.e. S1–S4, W1–W4), was compared among the four sea areas (GF, AS, BS, BB) and different decades using a χ^2-test.

We were interested in changes and factors associated with trout growth, which was defined as the length at capture, minus the smolt length of individual trout. Annual means calculated from individual lengths were used in analyses in which growth was examined separately in catches of one-sea-winter-old (1SW) (8–13 months) and two-sea-winter-old (2SW) (20–25 months) sea trout using predictors at the year level. Annual trends in smolt length, and growth were analysed using linear regression (SAS REG). The annual growth (length increment means) between the sea areas (south, north) was compared, separately in the first and second sea winter. As there was an increasing trend in annual mean growths in 1980–2010, we used Spearman's correlation to verify whether this trend in the southern sea area was parallel to the one in the northern sea areas.

The condition factor (CF) was calculated with Fulton's equation: $\mathrm{CF} = 1000W/(L^3) \times 100$, where W is weight (g) and L is body length (mm) (Bolger and Connolly 1989). Fulton's equation was selected because the slopes (b) of the regression equation between ln(length, mm) and ln(weight, g) were close to 3 in the data from the north (ln[weight] = –11.334 + 2.985 × ln[length]; $F_{1,3838} = 17\,094, p < 0.001, r^2 = 0.82$) and the south (ln[weight] = –11.689 + 3.059 × ln[length]; $F_{1,7439} = 48\,273, p < 0.001, r^2 = 0.87$) when fish between 50 g and 10 kg were included. Only individuals with a CF between 0.70 and 1.30 were included in the analysis. The limits of CF were applied because the relationship between reported length and weight for individual fish varied considerably, and some of the length measurements were based on estimates by fishermen.

Growth and trout condition (CF) were likely to depend on the geographic area, study decade and the age of the trout (months at sea). These variables were included in more detailed linear regression models (SAS MIXED). Long-term trends in growth (classified into three decades: 1980–1989, 1990–1999, 2000–2010), and differences between the northern and southern sea areas were used as predictors for the length increment of trout that had spent 8–25 months at sea after release. The analysis was done using the individual data. Length increment was log-transformed to achieve normality. To account for non-linear trends, the time spent at sea was also included in the squared form (month × month) in the models. The same analyses were conducted on CF of trout individuals that spent 8–25 months at sea. To achieve normality, the individual CF values were log-transformed.

Annual growth means in the southern and northern sea areas were explained by year (continuous variable; 1980–2010) and sea surface temperature as predictors in linear regression models (SAS MIXED). We examined separately growth of one-sea-winter-old (1SW) (8–13 months) and two-sea-winter-old (2SW) (20–25 months) sea trout.

Year, as such, may only reveal trends in growth, but we aimed at finding underlying environmental factors. So, we continued to models, where year was replaced by two more obvious year-related factors, temperature and herring abundance as measure of prey fish abundance.

The monthly sea surface temperature (SST) was measured at a depth of 1 m by the Finnish Institute of Marine Research at the field stations of Seili and Valassaaret in the BS and at the station of Tvärminne in the GF (Fig. 1). In 1980–2007, the April mean SST was 2.0 ± 1.9 °C at Tvärminne and 1.3 ± 0.7 °C at the Seili station. In May, SST was 6.6 ± 1.6 °C at Tvärminne, 6.4 ± 1.6 °C at Seili, and 3.5 ± 1.4 °C at Valassaaret. The monthly SST correlated positively between stations (Tvärminne & Seili in April and May: $r = 0.63, n = 24, p < 0.01$ and $r = 0.82, n = 24, p < 0.001$). We had no information on SST after the year 2007.

We used 0+ herring abundance in the Bothnian Sea at the end of the release year (ICES 2012), because previous studies (Kallio-Nyberg *et al.* 2007) have linked it to the marine survival of sea trout in both the Gulf of Finland and the Bothnian Sea. The abundance of 0+ herring was estimated by using the abundance estimate of 1+ herring for the previous year. The annual estimates of herring abundance were transformed by applying the natural logarithm. The environmen-

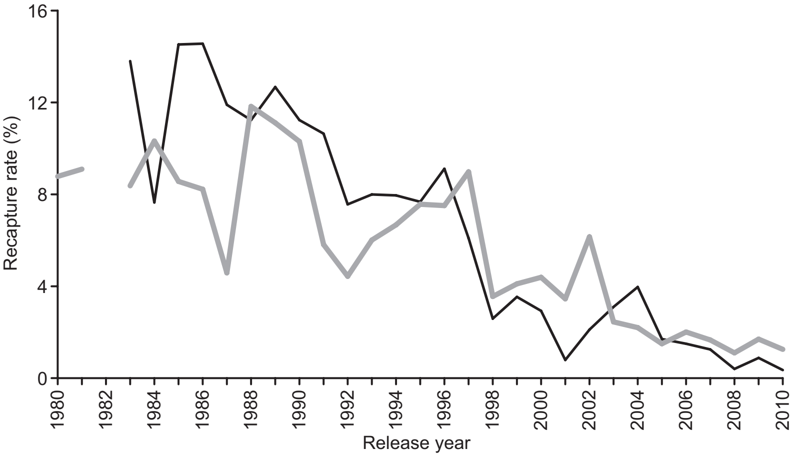

Fig. 2. The recapture rates of tagged sea trout in the southern sea area (black line; Gulf of Finland and Archipelago Sea) and in the northern sea area (grey line; Bothnian Sea and Bothnian Bay) in 1980–2010.

tal explanatory variables during the post-smolt period were used, because the natural mortality of sea trout due to marine factors was assumed to be highest soon after release during the first sea summer (Salminen *et al*. 1995, Kallio-Nyberg *et al*. 2007). The effect of increasing smolt size was tested in the environmental models, but it was omitted, as the environmental factors turned out to be better predictors.

We studied the effects of annual temperature (SST) and herring abundance, and release area (south, north) on SW1 and SW2 growth and the annual CF in linear regression models (SAS MIXED). The mean annual CF was calculated separately for both sea areas and the analyses were conducted for mean CF for trout that had spent 14–25 months at sea. Interactions between predictors were studied in all models, but they are only reported when they were among the models with the lowest AIC (Akaike information criterion).

Results

Recapture rate

The mean recapture rate per tagging group in the 1980s was higher in the southern sea area (mean ± SD: 12.0% ± 5.6%, $n = 51$) than in the northern sea area (8.9% ± 4.5%, $n = 57$) (t-test: $t_{106} = 3.1$, $p < 0.01$), but this difference later disappeared (1990s: GF and AS $n = 57$, 7.9% ± 4.9% $n = 57$ and GB 7.0% ± 4.1%, $n = 68$; 2000s: GF and AS: 2.0% ± 1.7%, $n = 49$; GB: 2.6% ± 2.4%, $n = 37$). The annual recapture rates for trout released in the south and north showed parallel fluctuations ($r_S = 0.79$, $p < 0.001$, $n = 29$) (Fig. 2).

Size, age and condition at recapture

The tags of the sea trout smolts released in 1980–2010 were mainly returned before their third sea summer, i.e. within 1–25 months at sea (GF: 88%; AS: 79%; BS: 89%; BB: 92% of recaptures; Fig. 3). During 1980–2010, the highest mean catch weight and length at recapture (mean ± SD: 2.3 ± 1.6 kg and 54 ± 13 cm) were recorded in the south (AS) and the lowest (0.8 ± 0.8 kg and 39 ± 0.8 cm) in the north (BB) (Table 1). At the same time, an average time at sea of recaptured trout was about 7 months longer in the AS as compared with that in the BB (Table 1).

Growth was slower in the northern sea area (BB and BS in Fig. 4). During the first winter (8–13 months), the highest weights recorded in the GF (mean ± SD: 1.2 ± 0.5 kg, $n = 1436$) and in the AS (1.1 ± 0.5 kg, $n = 1015$) were nearly twice as high as the values in more northern areas in the BS (0.8 ± 0.4 kg, $n = 941$) and the BB (0.6 ± 0.2 kg, $n = 670$). The second winter followed the same pattern: the GF trout weighed on average 3.2 ± 1.2 kg ($n = 798$) and the BB trout 1.4 ± 0.7 kg ($n = 238$). The weight difference between trout released in different sea areas increased as a function of the time spent at sea. In the second winter, the mean length of captured sea trout

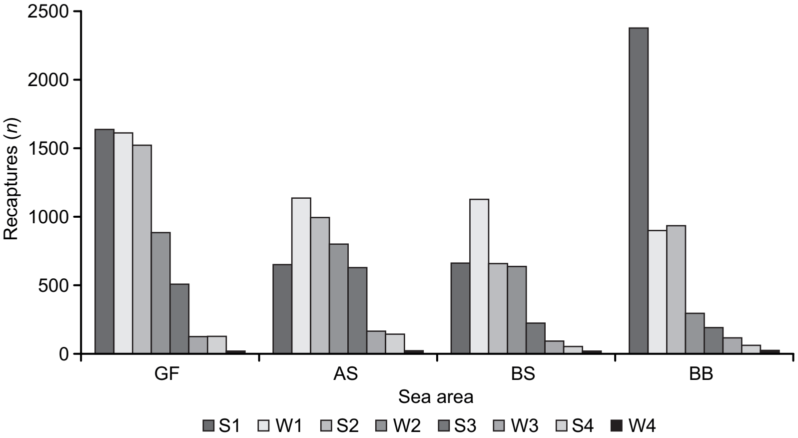

Fig. 3. Temporal distribution of recaptured sea trout released in the four sub-divisions of the Baltic Sea (GF = Gulf of Finland, AS = Archipelago Sea, BS = Bothnian Sea, BB = Bothnian Bay) during summer months (S1 = 1–7, S2 = 14–19, S3 = 26–31, S4 = 38–43) and winter months (W1 = 8–13, W2 = 20–25, W3 = 32–37, W4 = 44–49).

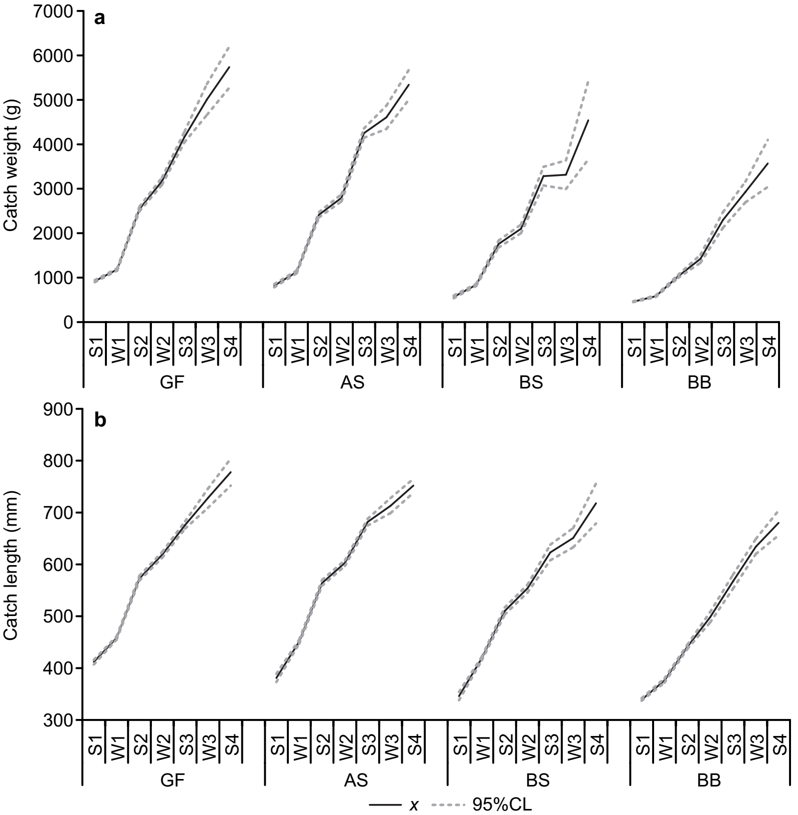

Fig. 4. The mean catch (**a**) weight and (**b**) length of sea trout in the summer (S1 = 1–7, S2 = 14–19, S3 = 26–31, S4 = 38–43) and winter (W1 = 8–13, W2 = 20–25, W3 = 32–37, W4 = 44–49) months in the Gulf of Finland (GF), Archipelago Sea (AS), Bothnian Sea (BS) and Bothnian Bay (BB) over the years 1980–2010.

Table 1. The mean recapture length, weight, and time at sea before recapture in four sea areas (GF = Gulf of Finland, AS = Archipelago Sea, BS = Bothnian Sea, BB = Bothnian Bay) for sea trout released in 1980–2010.

Sea area	*n*	Length (mean ± SD, cm)	Weight *n*	Weight (mean ± SD, kg)	Time at sea (mean ± SD,month)
GF	4567	52 ± 12	5314	2.2 ± 1.5	15.2 ± 8.9
AS	3482	54 ± 13	4015	2.3 ± 1.6	17.6 ± 10.7
BS	2346	47 ± 11	2729	1.4 ± 1.2	14.9 ± 8.6
BB	3945	39 ± 8	4176	0.8 ± 0.8	10.9 ± 10.0

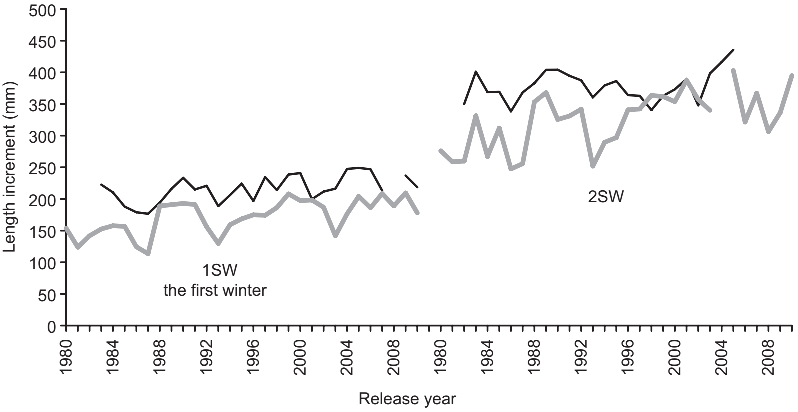

Fig. 5. The mean length increment of sea trout released in 1980–2010 in the first (1SW) and second (2SW) sea winters in the southern (black line) and northern (grey line) sea areas of the Baltic Sea. The annual mean length increment (i.e. growth = length at capture – smolt length) for each sea area was calculated from individual data.

exceeded 60 cm in the GF and AS, but not in the BS (55 cm) or in the BB (49 cm) (Fig. 4). In the third summer (26–31 months), the mean catch length was 68 cm in the GF and AS, 62 cm in the BS and 56 cm in the BB (Fig. 4), when, respectively, 96%, 95%, 81% and 95% of all tags in each area were returned (Fig. 3).

About 90% of sea trout were recaptured within 1–25 months off the south and north coasts of Finland. In the south, a larger proportion of sea trout were caught in the release year in the 2000s (51%) than in the 1990s (28%) or in the 1980s (14%) (χ^2-test: $\chi^2 = 1246.4$, df = 10, $p < 0.001$). In the north, the trend was similar: 53% of recaptures in the 2000s, 47% in the 1990s and 27% in the 1980s occurred within the release year (χ^2-test: $\chi^2 = 545.7$, df = 10, $p < 0.001$).

Trends in smolt length and mean marine growth between 1980–2010

The size of released smolts increased by about 1 mm per year during 1980–2010 (linear regression: length (cm) = –182 + 0.103 × year, $F_{1,20568} = 1510.2$, $p < 0.001$), being 22.2 ± 2.3 cm in the 1980s ($n = 8870$), 23.6 ± 2.3 cm in the 1990s ($n = 9550$) and 23.8 ± 2.3 cm in 2000–2010 ($n = 2150$). A larger smolt size was associated with better growth in the first winter both in the north ($r_S = 0.583$, $p < 0.001$, $n = 31$) and in the south ($r_S = 0.379$, $p < 0.05$, $n = 28$), and a greater catch length in the second winter in both sea areas (GB: $r_S = 0.656$, $p < 0.001$, $n = 30$ and GF + AS: $r_S = 0.565$, $p < 0.01$, $n = 27$).

Growth (length increment of annual means) in the first winter increased over the years from 1980–2000 (south: $-2640.8 + 1.43 \times \text{year}$, $F_{1,26} = 13.2$, $p < 0.01$; north: $-3564 + 1.87 \times \text{year}$, $F_{[1,29]} = 18.9$, $p < 0.001$) (Fig. 5). In the second winter, growth increased significantly in the northern areas, but not in the southern sea area (south: $-223.5 + 0.29 \times \text{year}$, $F_{1,25} = 0.2$, $p = 0.705$; north: $-5904.5 + 3.2 \times \text{year}$, $F_{1,28} = 18.7$, $p < 0.001$). The correlation between growth in the south and north was high in the first winter ($r_S = 0.633$, $p < 0.001$, $n = 28$), but no longer in the second winter ($r_S = 0.231$, p = ns, $n = 26$) (Fig. 5).

Changes in marine growth and condition in relation to time spent at sea

The estimated monthly growth of individual trout during months 8–25 after release was slower in the northern sea area, and interaction between the sea area and release period (decade) ($p < 0.001$) indicated improved growth in the north towards the 2000s (Fig. 6a) (Table 2; model M1). The condition of the trout at the time of capture was better in the south (Table 2; model M2) (Fig. 6b) as compared with that in the north (mean condition factor in the south 1.09, SD: ± 0.13, $n = 5153$, and in the north 1.02 ± 0.14, $n = 4837$; t-test: $p < 0.001$). In both areas, the condition factor increased as a function of months at sea during 1980–2000, but during 2000–2010 the best condition was gained during the second summer (months 15–19) (Table 2; model M2; Fig. 6b).

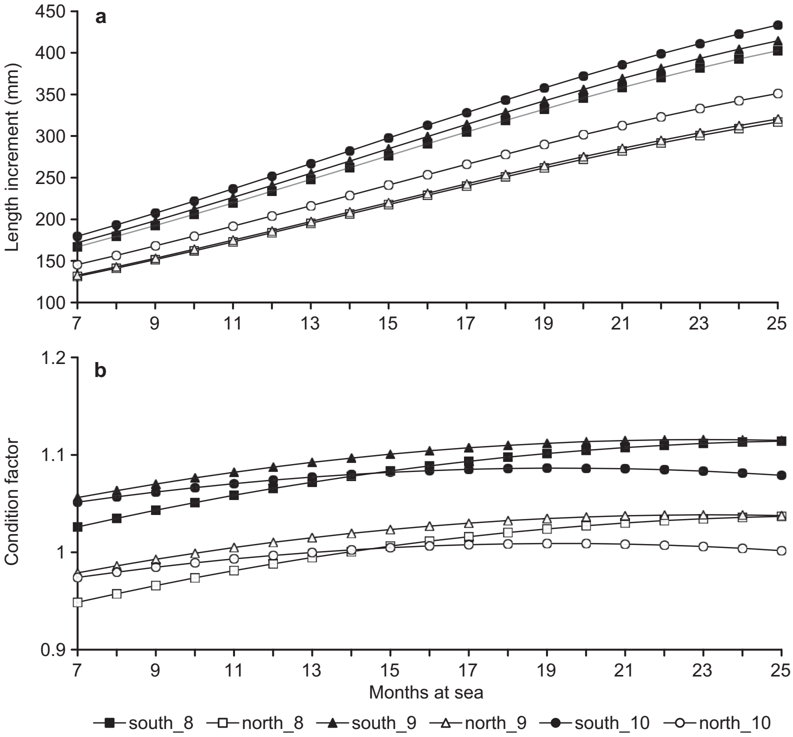

Fig. 6. Predicted length increment of individual sea trout in relation to time (months) spent at sea, release year period (8 = 1980–1989, 9 = 1990–1999, 10 = 2000–2010), and release site (south refers to ICES 32 and 29, and north to ICES 30 and 31; *see* Fig. 1) according to (**a**) the linear regression model (Table 2, M1), and (**b**) predicted condition factor of sea trout in relation to time (months) spent at sea, the release year period and release site according to the linear regression model (Table 2, M2). The sea trout recaptured in the first winter, second summer and the second winter, after 8–25 months at sea, and groups released in 1980–2010 are included in both models. The length increments are log-transformed (natural) in the model, but transformed back to linearity in the figures.

Changes in marine growth and condition in relation to environmental factors

Growth during the first sea winter (1SW) was faster in the south as compared with that in the north, and in years with higher April sea surface temperatures (SST) (Table 3; M3). The growth of 1SW trout improved towards the present years in the same way in the south and in the north (model M3; interaction year × sea area,

Table 2. Models for growth and condition of individual trouts in relation to release site, time (months) spent at sea and release decade (year period) (1980–1989, 1990–1999, 2000–2010). Southern areas are the Gulf of Finland and Archipelago Sea, and northern areas are the Bothnian Sea and Bothnian Bay.

Model	Response	Effect	df	*F*	*p*
M1	Growth	Sea area (south, north)	1, 8708	988.7	< 0.001
		Month	1, 8708	620.8	< 0.001
		Month^2	1, 8708	150.0	< 0.001
		Year period	2, 8708	36.8	< 0.001
		Sea area × year period	2, 8708	3.0	0.048
M2	Condition factor	Sea area (south, north)	1, 6127	451.8	< 0.001
		Month	1, 6127	17.6	< 0.001
		Month^2	1, 6127	8.5	0.004
		Year period	2, 6127	6.8	0.001
		Month × year period	2, 6127	4.1	0.017

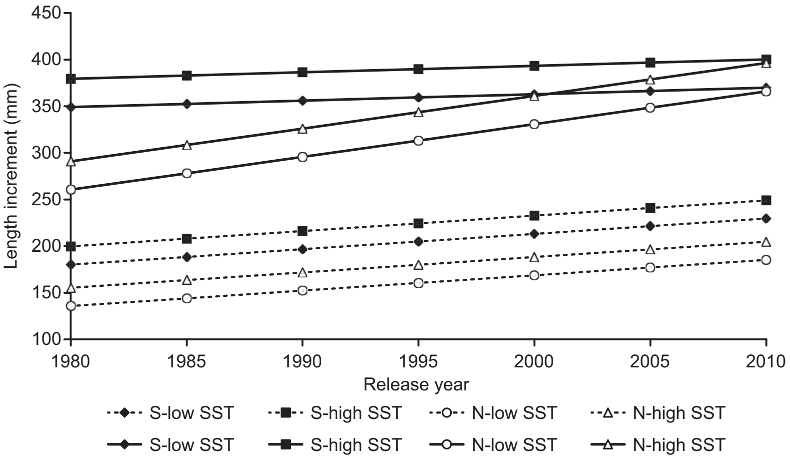

Fig. 7. Predicted length increment of 1SW (dashed line) and 2SW (solid line) sea trout for release sites (south (S) = Gulf of Finland and Archipelago Sea, north (N) = Bothnian Sea and Bothnian Bay) and sea surface temperature in April in the Bothnian Sea (low SST = 0.5 °C, high SST = 2 °C) and release year (1980–2010) according to model M3 (1SW fish) and model M4 (2SW sea trout) in Table 3.

$p = 0.921$, omitted); however, the growth of 2SW trout increased towards the present only in the north (Fig. 7; significant interaction, $p = 0.007$, in M4 of Table 3).

High recruitment of herring in the release year increased the growth rate of 1SW and 2SW sea trout, even when SST was taken into account (M5, M6). Interaction between SST and herring indicates that the growth of 1SW fish was weak when both SST and 0+ herring abundance were low in the BS (Table 3; model M5). For 2SW trout, high herring abundance and high SST had independent effects on growth (Table 3; M6; interaction SST × herring, $p = 0.758$, omitted) (Fig. 8), but high SST was more important than herring abundance for growth in the south (model M6 in Table 3; Fig. 8).

Table 3. Models for the yearly mean growth of sea trout recaptured in the first (1SW growth, 8–13 months) or second (2SW growth, 20–25 months) sea winter, and yearly mean condition factor during the second summer and winter (14–25 months). Predictors are the sea area (south = Gulf of Finland and Archipelago Sea; north = Gulf of Bothnia), year (1980–2010), sea surface temperate (SST in April in BS) or herring abundance in the Bothnian Sea.

Model	Response	Predictor	df	*F*	*p*	AIC
M3	1SW growth	Sea area	1, 24.8	118.80	< 0.001	431.2
		SST	1, 23	9.37	0.006	
Fig. 7		Year	1, 24.8	18.33	0.000	
M4	2SW growth	Sea area	1, 26.5	8.59	0.007	454.0
		SST	1, 24.3	9.11	0.006	
Fig. 7		Year	1, 27.	11.54	0.002	
		Year × sea area	1, 26.5	8.43	0.007	
M5	1SW growth	Sea area	1, 23.5	117.11	< 0.001	419.9
		SST	1, 20.7	6.25	0.021	
Fig. 8		Herring BS	1, 20.5	13.73	0.001	
		SST × herring	1, 20.7	5.48	0.029	
M6	2SW growth	Sea area	1, 23	8.10	< 0.009	449.9
		SST	1, 24	6.91	0.015	
Fig. 8		Herring BS	1, 24.7	6.41	0.0181	
		Herring × area	1, 23	5.90	0.023	
M7	Condition factor	Sea area	1, 24.8	25.79	< 0.001	158.5
	14–24 months	Herring BS	1, 24.6	5.75	0.024	

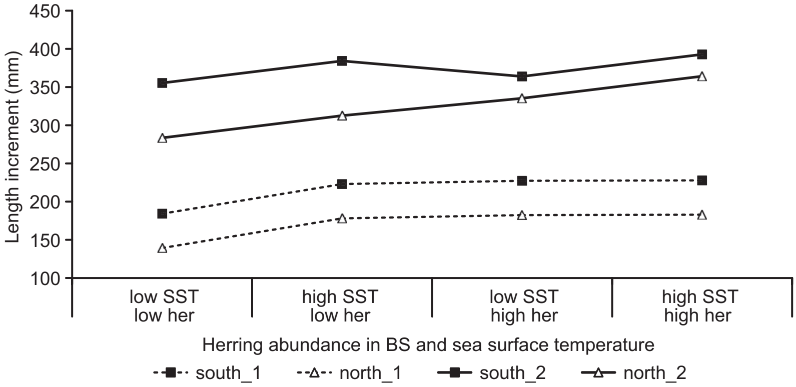

Fig. 8. Dependence of the length increment (marine growth) of 1SW (dashed line) and 2SW (solid line) sea trout on herring abundance in the BS, sea surface temperature (SST) in April and release site (south = Gulf of Finland and Archipelago Sea; north = Bothnian Sea and Bothnian Bay) according to models M5 (1SW fish) and M6 (2SW fish) in Table 3. Herring abundance classes in the BS are low herring abundance (low her, ln-transformed value = 8) and high herring abundance (high her, ln-transformed value = 9.2), and sea surface temperature classes are 0.5 °C (low SST) and 2.0 °C (high SST).

Herring abundance in the BS correlated positively with SST in April ($r_S = 0.367$, $p = 0.059$, $n = 27$) and in May ($r_S = 0.615$, $p = 0.001$, $n = 25$). In both sea areas, the effect of high 0+ herring abundance during the first sea year could be detected as a higher condition factor later in the second summer and winter (Table 3; model M7).

The best model to account for 1SW growth was model M5 (AIC = 419.9), in which unknown factors associated with year were replaced by measured values of SST, 0+ herring abundance and their interaction. The best model to account for 2SW growth was model M6 (AIC = 449.9), in which unknown factors associated with the year were replaced by SST, herring abundance and the interaction between herring abundance and sea area.

Discussion

Effect of marine conditions on growth

Both a long-term trend and annual variation were observed in the growth of sea trout in the Finnish waters of the Baltic Sea. The marine growth of reared sea trout increased during 1980–2010 in both the northern (BS; BB) and southern (GF, AS) parts of the study area. Annual growth was found to be positively associated with the summer sea surface temperature (SST), when smolts migrate to the sea. Growth followed an increasing trend towards the present, which is likely to be associated with the simultaneous rise in the sea surface temperature of the Baltic Sea (Mackenzie *et al.* 2007). The annual SST values used in the study did not increase significantly in 1980–2007, however warm springs induced fast growth. These findings are supported by the studies of Elliott *et al.* (1995) and Elliott and Elliott (2010), who showed that the growth of sea trout is largely controlled by water temperature. According to Friedland *et al.* (2000) and Jonsson and Jonsson (2004b), the growth of one-sea-winter *Salmo salar* was also higher in the years when the water temperature and North Atlantic Oscillation Index (NAOI) in May were high during post-smolt migration. Vainikka *et al.* (2010) recorded an increase in the catch length-at-age of *S. salar* in 1972–1995, which was significantly correlated with the rise in the sea surface temperature of the Baltic Sea.

The growth of the sea trout varied according to the release site; the fish grew faster in the southern than in the northern sea area. L'Abée-Lund *et al.* (1989) and Parra *et al.* (2009) explained the increasing growth of sea trout along the Atlantic coast by its relation to the higher sea temperature in the southern sea areas. Also Degerman *et al.* (2012) reported faster marine growth of the more southern than northern wild sea trout in the Baltic Sea. The sea trout weighed about 2.0 kg in the second winter both in Finnish and Swedish coastal waters in the Bothnian Sea (Degerman *et al*. 2012). In contrast, the anadromous brown trout (*Salmo trutta*), spawning in the rivers flowing to the Atlantic Ocean, may grow slower. According to Jonsson and Jonsson (2011) the three-sea-years old anadromous brown trout were 50 cm or smaller in the Atlantic Ocean, while in the BS and in the Gulf of Finland the trout reached the body length of 50 cm in their second summer. The sea trout grow fast in the Baltic Sea, because in the brackish water they are able to migrate to feed the whole year, while the Atlantic brown trout may commonly return into their home rivers for winter.

According to our study, in the 1980s growth was clearly slower along the Finnish northern coast (BS + BB) than on the southern coast (Gulf of Finland and Åland Sea), while in the 2000s the growth of sea trout was similar in all Finnish coastal waters. The difference in growth rates in different parts of the Baltic Sea suggests that the environmental conditions associated with sea trout growth changed more in the northern areas. Because the sea trout were mainly caught (> 90%) in their own area of release (Kallio-Nyberg *et al*. 2002), the marine conditions in the release area are crucial to the actual growth rate. The low sea temperature in the north probably limited trout growth more in the 1980s than in the 2000s.

The annual variations in fry emergence, smolt migration, marine growth and survival of *Salmo trutta* and *S. salar* are linked to global climatic factors (Elliot and Elliott 2010, Friedland *et al*. 1993, 2009, Jonsson and Jonsson 2004b, 2009, Kallio-Nyberg *et al*. 2004, 2006, 2007). In the Baltic Sea (Huusko and Hyvärinen 2012), the mean weight at age of captured *Salmo salar* is also linked to climatic variation. During marine climate regimes (1902–1938 and 1988–2003), the salmon were larger than during the continental regime (1939–1987). This variation might also affect sea trout via similar environmental factors (Kallio-Nyberg *et al*. 2006).

Effect of food and feeding on growth

Although the feeding areas of sea trout are more restricted as compared with those of salmon (Kallio-Nyberg *et al*. 1999, Degerman *et al*. 2012), their diets overlap (Salminen *et al*. 2001, Rikardsen *et al*. 2006, Haikonen *et al*. 2006), and their post-smolt survival is controlled by densities of the same prey fish (Kallio-Nyberg *et al*. 2006). Both the SST and 0+ herring abundance in the smolt year were positively linked with annual growth in the Bothnian Sea. The observation that a high SST is more important than herring abundance for growth in the south (interaction in model M6 in Table 3; Fig. 8) may be linked to the fact that the abundance used in the analysis was estimated only for the Bothnian Sea. In an earlier study, Kallio-Nyberg *et al*. (2004) found that the annual SST in spring months and 0+ herring abundance may positively correlate.

Since there are few prey fish species in the northern Baltic Sea, herring also dominates the diet of sea trout in the main basin (Haluch and Skóra 1997). An increase in the abundance of herring and smelt (*Osmerus eperlanus*), but not sprat (*Sprattus sprattus*) has been linked with increasing marine survival of both sea trout and salmon in the Baltic Sea (Kallio-Nyberg *et al*. 2006, Kallio-Nyberg *et al*. 2007). The high annual herring recruitment suggests that suitable zooplankton species, namely large copepods, have been abundant (Dippner *et al*. 2001). On the other hand, climatic factors control the zooplankton (Dippner *et al*. 2001) and the abundance of pelagic fauna and benthic organisms (crustaceans or polychaetes). These organisms are also important for sea trout post-smolts, which are not yet large enough to shift their diet from invertebrates to prey fish. Larger brown trout (*Salmo trutta lacustris*), above 30 cm in length, are fully piscivorous, and even the majority of smaller individuals forage on fish (Hyvärinen and Huusko 2006). The 0+ herring abundance was used as a predictor in growth models, because these fish are suitable as food for sea trout in their first sea summer. In the Baltic Sea, 0+ herring are 70–90 mm in length at the end of summer, while one-year-old herring are 90–100 mm in length in the spring (Parmanne 1990). At the beginning of the summer, one-year-old herring are probably too large for sea trout post-smolts, which have an average length of 240 mm (Hyvärinen and Huusko 2006).

The conditions are probably better for sea trout in the southern area of the Baltic Sea, as their condition factor was higher there. Similar seasonal variation in food availability and the condition of trout suggests that condition is linked to food availability (Rikardsen *et al.* 2006). In this study, the abundance of 0+ herring in the smolt year explained the condition of trout in the following year. This is logical, because trout begin to forage on 0+ herring in the smolt year, and the same juvenile 1+ herring are suitable food for 1SW sea trout in the following year.

Effect of fishing, hatchery rearing and genetic origin on growth

The sea trout were exposed to fishing before spawning, as the legal catch length for sea trout was only 40 cm in Finland until 2008. In the southern area, this size was attained during the first summer at sea, and the mean catch size was less than 55 cm. In the north, the mean size during the first summer was 35 cm, and the majority of trout were caught at a size of less than 50 cm (Jutila *et al.* 2006). Tagging experiments in the Gulf of Finland also demonstrated that 80% of the tagged fish are caught before their third sea year (Saura 2001). The young catch age and small size mean that the majority of the sea trout are caught in the sea during their feeding migration. In the northernmost area, the BB, the majority of female sea trout attain maturity after three sea years (Huhmarniemi 2002). Most of the sea trout caught in the northernmost Baltic river, the Tornionjoki (66°–68°N), in 2005 (n = 97) had spent 2 or 3 winters at sea and attained a mean weigh of 2.4 kg (Haikonen *et al.* 2006). In the estuary of another river of that area, the Kemijoki (65°30´–66°N), the mean length of 2SW female sea trout in the 1980s was 58 ± 6 cm (n = 18, 1.8 ± 0.6 kg) and that of the 3SW trout 64 ± 6 cm (n = 79, 2.5 ± 0.8 kg) (Huhmarniemi 2002). The mean catch weight of BB sea trout in this study in the third summer (2.3 ± 1.0 kg, 57 ± 0.7 cm, Fig. 3) corresponded to the size of 2SW sea trout, which might mature for the first time.

Our data were mainly restricted to the first or second sea year (Fig. 3), but sea trout may migrate in the sea for several years and spawn several times during their life (Järvi 1940). The oldest known sea trout ascending the Tornionjoki was seven sea-winters old (Haikonen *et al.* 2006). In the present study, the number of old sea trout was very low. Overlapping generations at spawning maintain genetic diversity, especially in small populations. Anadromous sea trout can, however, also spawn with non-migratory sea trout (Jonsson 1985, Kallio-Nyberg *et al.* 2010). One consequence may be that natural trout populations in the future will be mainly non-migratory, because the anadromous forms have a lower fitness due to the low likelihood of attaining the spawning age.

The catch size of the recaptured fish depends to some extent on the effect of selective fishing. Sea trout with a large smolt length recruit to the fishing stock earlier than trout with a smaller smolt length (Kallio-Nyberg *et al.* 2007). The majority of sea trout, over 80%, were caught with gill nets (Saura 2001, 2002, Kallio-Nyberg *et al.* 2007, ICES 2011). Thus, the proportion of fast-growing trout might be expected to decrease and the mean recapture size to remain smaller than the potential size could be. This result might, however, be somewhat questionable, as the body measures may not be accurate and there is no way of assessing the reliability of the data reported by fishermen concerning the time of capture and the catch size of fish. The proportion of old fish in the catch has decreased (from 1986 to 1996; Saura 2002), which may increase variation in the size estimate of the old fish.

All tagged sea trout smolts were hatchery reared and they were produced using brood stocks with different genetic backgrounds. However, over half of the releases were based on Isojoki trout, which were released along the whole Finnish coast from north to south. The genetically different trout stocks may show different behavioural and phenotypic variation at sea (Kallio-Nyberg *et al.* 2002). In some tagging groups, the genetic origin was unclear or mixed, as private breeders may also produce smolts with an unknown origin. In this study, we did not try to evaluate the effect of a specific stock on growth. The conditions at sea are likely to affect the growth rate of trout more than their genetic origin. For example, comparative studies between anadromous sea trout and non-migratory trout have shown that non-migratory trout can also grow at sea, like migratory sea trout (Kallio-Nyberg *et al*. 2010).

Factors affecting the recapture rate

The recapture rate of tagged sea trout in Finnish coastal waters decreased during 1980–2000, which is consistent with earlier observations of marine survival and abundance in the sea trout and Atlantic salmon populations of the Baltic Sea (Kallio-Nyberg *et al*. 2006, 2011, Mäntyniemi *et al*. 2012) and the Atlantic Ocean (Poole *et al*. 2006, Russell *et al*. 2012). Sea trout and salmon show similar co-variation in annual and long-term survival, and the marine survival decreased in both species during the recent decades (Kallio-Nyberg *et al*. 2006, 2011, ICES 2011, 2013). According to tagging studies in the 1980s, about 8% of the released reared sea trout smolts recruited to fishing, but only about 2% after the year 2000 (Kallio-Nyberg *et al*. 2006). The precise reasons for the decreasing trend in survival are unclear, but the simultaneous decrease in survival of salmon (Kallio-Nyberg *et al*. 2011) suggests that common environmental factors probably determine the survival rate. Kallio-Nyberg *et al*. (2007) reported that an increasing proportion of tagged smolt groups had been released quite early in the spring before the optimal release time. However, this does not explain the long-term decreasing trend in survival. Due to the low legal catch length, the sea trout is recruited to fishing long before reproduction, and most stocks are also overexploited (Saura 2002, ICES 2011), which indicates that the low recapture rate is not due to a decrease in fishing effort.

The long-term trends in the recapture rate differed between the northern and southern release areas. A relatively smaller reduction in recapture rate in the northern sea area (8.9% → 7.0%) than in the southern area (12.0% → 7.9%) might be linked to changes in the sea temperature and food abundance. The sea temperature at the time of sea entry may be critical (Jutila *et al*. 2005), as the abundance of food available for sea trout in the spring and early summer, such as surface organisms (insects and fish larvae), depends on the SST (Dippner *et al*. 2001). The observation that a low SST alone does not reduce annual growth (Fig. 8) may be linked with the ability of sea trout to change their diet according to the conditions. Sea trout may also feed on benthic organisms (crustaceans or polychaetes), the abundance of which is not as tightly linked to a water temperature rise as that of the surface fauna (Knutsen *et al*. 2001). The period of greatest natural mortality might have passed by the time sea trout begin to feed mainly on fish.

The tag return-rate following recapture is likely to represent a minimum value for survival. The tagged fish may suffer higher mortality than un-tagged fish (Berg and Berg 1987a). The length distribution of the recaptured sea trout in the GF suggests that undersized fish (< 40 cm) in the catch are less frequently reported than sea trout of a legal catch length (Kallio-Nyberg *et al*. 2007). However, as the proportion of undersized fish in the catch has gradually increased (ICES 2011), the willingness to return tags might have increased rather than decreased. The recapture rate of sea trout has shown a continued decreasing trend for more than 20 years in both the BS and GF, being 1%–2% in 2002 (ICES 2011). In contrast, in the main basin the tag return-rate was only 0.5% in the 2000s and generally varied in relation to the number of tagged trout. This suggests that the willingness to return tags has varied in the main basin trout catches, but probably not as much as that in case of the Finnish trout.

The majority of the reared smolts were transplanted. The use of local populations in stocking is impossible, because most original populations have been lost (Jutila *et al*. 2006). Lower recapture rates may partly result from the use of non-adaptive populations. Jonsson and Jonsson (2012) found that the population originating from the most distant location from the release site exhibited the poorest survival at sea.

Management of the sea trout stocks

During the past decades, the recapture rate of released sea trout decreased, and sea trout recruited to the fishing stock at a younger age in the 2000s than earlier. At the same time, marine growth increased. An increase in the sea surface temperature in the Baltic Sea is the likely cause of the increase in marine growth in general, and its relatively greater change in the northern sea area as compared with that in the southern one.

In conclusion, the present catch level and the benefit from smolt releases are low. The great majority of sea trout die soon after release, and the remaining trout are recruited to the fishing stock at a small size before spawning, which causes obvious overfishing (ICES 2011, 2013). The economic benefit of hatchery smolt releases was earlier been shown to be low as compared with the costs for Baltic salmon (Kallio-Nyberg *et al.* 2013). Although the aim of the trout releases is to maintain fishing, they actually cause a deterioration in the wild stocks, as fishing is in practice targeted at the critically endangered natural sea trout stocks.

To safeguard the endangered sea trout stocks, Jutila *et al.* (2006) presented various options for reducing gill net fishing with small mesh sizes, thereby reducing the catch of undersized trout. The present minimum legal size of 60 cm is still too low to ensure that the majority of females spawn at least once. To effectively protect wild sea trout, reared smolts should have their adipose fins removed before stocking which would enable fisherman to distinguish between reared and wild trout, and release the latter after capture. Reducing the proportion of young sea trout caught at sea as a by-catch in gill net fishing and raising the minimum legal size to 65 cm are, besides serious evaluation of the sense of hatchery rearing, means that might rescue the natural sea trout populations.

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