

# Atlantic salmon abundance and size track climate regimes in the Baltic Sea

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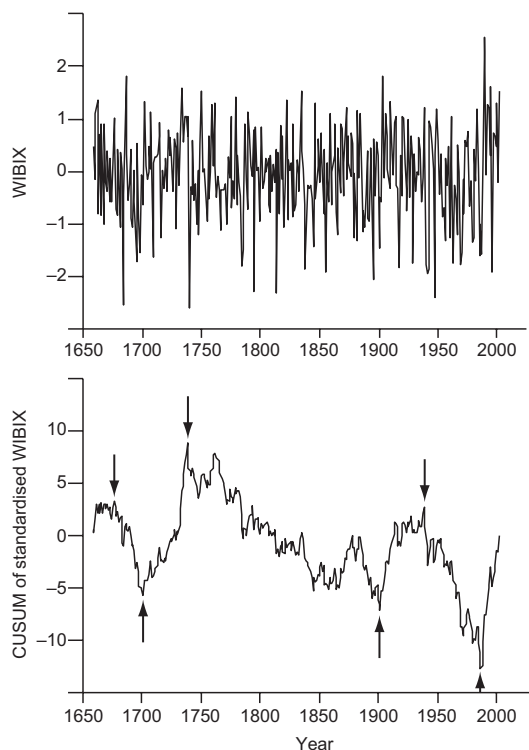
Atmospheric variations on multi-decadal time scales, or climate regimes, can cause significant alterations throughout the physical environment, often with remarkable consequences for animal populations and ecosystems. Here we report that the climate regimes in the Baltic Sea area, which are based on the North Atlantic Oscillation and two more regional oceanographic variables, account for the observed dynamics of Atlantic salmon abundance and size in the sea. The changes in the salmon abundance and size followed changes in the climate regimes in the Baltic Sea area, indicating that high amplitude shifts in the Atlantic salmon performance are closely associated with longer-term patterns in the climate. During maritime, temperate regimes salmon were larger in size but low in abundance, with contrasting characteristics during continental, cold climate regimes. Therefore, Atlantic salmon seem to provide a very sensitive indicator of the biological effects of climate-forced changes in the aquatic environment.

## Introduction

Understanding the responses of animal populations to climate modes and environmental forcing represents a fundamental ecological challenge. However, mechanisms to describe how climate induced environmental change translate into animal population changes, are poorly understood (Ådahl *et al.* 2006). For much of the last century scientists were puzzled by the periodic variations in animal populations in terrestrial and aquatic environments, but only recently have large-scale spatial synchrony of population oscillations been associated with global climate patterns, such as the North Atlantic Oscillation (NAO). Furthermore, regional climate types (maritime-continental) have been shown

to account for low frequency, high amplitude changes in population abundance (Stenseth *et al.* 1999, Drinkwater *et al.* 2003, Mysteryd *et al.* 2003, Straile *et al.* 2003). Such long-term co-variations between population characteristics and climate indices provide evidence for climate dependence of organisms.

The effects of climate change on aquatic environments, both marine and freshwater, are expected to vary from place to place. Changes in climate are likely to impact water temperature, quantity and quality and thus alter the biological composition, production, and function of aquatic ecosystems. The Baltic Sea climate varies greatly in many parameters such as precipitation, river runoff, salinity, sea level, and sea-ice cover (Feistel *et al.* 2008). The main reason for



**Fig. 1.** Winter Baltic Climate Index (WIBIX; upper panel) for 1659–2002, and corresponding cumulative series (CUSUM) of the standardized WIBIX (lower panel), with arrows indicating turning points between subsequent climate regimes. Modified from Hagen and Feistel (2005).

such variation is the location of the Baltic Sea between the North Atlantic and Eurasian weather systems, which lead to large seasonal and inter-annual variation in the low- and high-pressure systems (Omstedt *et al.* 2004). Thus, the Baltic Sea can be expected to be very sensitive to climatic and environmental changes. The recently derived Winter Baltic Climate Index (WIBIX) (Hagen and Feistel 2005; *see* Fig. 1) combines a large-scale climate system, the NAO, with two other local oceanographic variables: sea surface level and maximum winter ice cover in the Baltic Sea, providing a measure that describes the climate driven physical nature of the Baltic Sea area for the years 1659–2002. The beauty of this index is that it integrates relatively local hydrographic variability with a global-scale climate index resulting in a highly-tuned

regional measure of climatic patterns (Stenseth *et al.* 2002, Stenseth *et al.* 2003). Over the last 300 years, six regime shifts between three mild (maritime) and three severe (continental) climate modes were defined in the Baltic Sea area, with estimated transitions from one mode to another taking place in the years 1701, 1739, 1902, 1939 and 1987 (Fig. 1; *see* also Hagen and Feistel 2005). Both modes were observed to cause changes in the functioning of the Baltic Sea ecosystems, affecting all trophic levels (MacKenzie *et al.* 2007, MacKenzie and Köster 2004, Alheit *et al.* 2005, Köster *et al.* 2005, Möllmann *et al.* 2005, Möllmann *et al.* 2009).

Atlantic salmon (*Salmo salar*) is a pan-Atlantic species, being one of the valuable North Atlantic and Baltic Sea fish resources for which fishery records date back several hundreds of years. The salmon life cycle, from their freshwater birthplace to estuarine and open-sea habitats and back again, exposes salmon to a variety of potential effects resulting from climate change and forcing. It has become increasingly appreciated that numerous Atlantic salmon populations are in decline, especially at mid-latitudes of both sides of the Atlantic Ocean (Friedland 1998, Hawkins 2000, Voellestad *et al.* 2009). This is happening despite fairly restrictive management measures and a reduction in fisheries and exploitation rates. However, low frequency variations, though dramatic in magnitude, in the abundance of Atlantic salmon populations in the Baltic Sea area have been known for a long time, even under the relatively low harvesting rates (Järvi 1948a, Lindroth 1964, 1965). Here we demonstrate, using an analysis of a time series of up to 200 years, that Atlantic salmon population dynamics track climate driven regime shifts in the Baltic Sea area, giving evidence of climate-forcing associated variability in the Atlantic salmon populations. Our approach is to use *a priori* interventions, determined by the transition years of the WIBIX regimes, to test whether abundance and size of Atlantic salmon in the Baltic Sea indicates the same pattern. The study adds to earlier, mainly circumstantial evidence that Atlantic salmon variability is linked to the global climate modes (Dickson and Turrell 2000, Beaugrand and Reid 2003).

## Material and methods

### Regime shifts in the Baltic Sea area

A regime shift is a rapid and considerable transition from one persistent climate mode or regime to another (Lees *et al.* 2007). Here the origin of the shift is considered to be a climate change or forcing. We used the Winter Baltic Climate Index (WIBIX) to describe the large-scale climate in the Baltic Sea area (Hagen and Feistel 2005). WIBIX is based on the North Atlantic Oscillation (NAO) (differences in the sea-level air pressure between Gibraltar and Reykjavik), sea level anomalies on the Swedish coast of the Baltic Sea, and maximum sea-ice coverage of the Baltic Sea, during the years 1659–2002. Applying the cumulative-sum plots of standardized anomalies (zero mean, and unit standard deviation) of the WIBIX, six regime shifts can be determined in the time series, separating three mild (maritime) from three severe (continental) winter modes in the Baltic Sea area, with transitions between the modes in the years 1701, 1739, 1902, 1939 and 1987 (Fig. 1; *see also* Hagen and Feistel 2005). The maritime modes are characterized by enhanced NAO with pronounced prevailing westerly winds over western Europe that are responsible for mild winters over the Baltic Sea area, with decreased peak values during maximum Baltic Sea ice cover. In addition, a high NAO index is associated with high precipitation in the Baltic Sea catchment, followed by higher river discharges and increased sea level in the main basin of the Baltic Sea. The continental modes are in contrast with these (Hagen and Feistel 2005).

### Atlantic salmon data

#### Abundance

The 200 years (1804–2003) time series of abundance data for Atlantic salmon in the Baltic Sea is based on the all-nation total yield statistics derived from McKinnell and Karlström (1999) and FGFRI (2004). Indirect measures of population abundance, such as harvest data of game

(Ranta *et al.* 1997, Forchhammer *et al.* 1998, Stenseth *et al.* 1999) and fish (Scarnecchia 1984, Chadwick 1985, Mills 1989, Gudjonsson *et al.* 1995, Beaugrand and Reid 2003, Post *et al.* 2004, Niemelä *et al.* 2004, Boylan and Adams 2006, Voellestad *et al.* 2009) are often used as a surrogate of abundance to make inferences on long term population dynamics when direct observational data are not available (Cattadori *et al.* 2003, Ranta *et al.* 2008). However, a major concern over the use of such data is that harvesting records tend to underestimate low densities and overestimate high densities as a consequence of variation in harvesting effort. Here we assume that harvest records provide an index of Atlantic salmon populations that scales with population size. This is based on the premises that, first, annual yield caught from a salmon weir in the Oulujoki — the weir set into the river for the same two-month period each year — during the years 1870–1919 (Järvi 1948b), was significantly correlated with the all-nation-yield estimate (Pearson's product moment correlation:  $r = 0.85$ ,  $p < 0.001$ ), indicating that river-specific yield per effort is in accordance with the abundance estimate. Second, Atlantic salmon yields taken from the Baltic Sea area are a large fraction of the estimated total population (Karlsson and Karlström 1994), and Atlantic salmon populations in the Baltic Sea area fluctuate in synchrony, with spatial correlation among populations being greater than reported for other anadromous salmonids (McKinnell and Karlström 1999). These facts lend support to the view that all-nation (or all-salmon-populations) harvesting records provide a reliable estimate of the total abundance of Atlantic salmon in the sea.

Mainly Finnish and Swedish hatcheries have released Atlantic salmon smolts since the 1950s to compensate for the effects of hydropower developments in the salmon spawning rivers (Karlsson and Karlström 1994). In the 1950s, the number of stocked fish was small, but in the early 1960s, over one million smolts were already released, rising to 5–7 million smolts per year in 1980–2003 (FGFRI 2004). As compared with natural fish, hatchery-released fish may have different survival patterns in the sea (Ruggerone *et al.* 2007), and thus may also display

different responses to climate regimes and their variations. In order to refine the total Atlantic salmon yield to only include catches containing fish of natural origin, we calculated the yield from the stocked Atlantic salmon smolts for the period 1960–2003, using the procedure described in Hyvärinen and Huusko (2005). The calculation was based on the recapture data of Carlin-tagged smolts released by Finnish hatcheries (1099 release groups including 948 138 smolts aged 1–3 years (mainly 2-year-olds) in 1960–2003) (unpublished archives of the release and recapture data of tagged Atlantic salmon smolts released by Finnish hatcheries, databases compiled and provided by the tagging office of the Finnish Game and Fisheries Research Institute (FGFRI), Helsinki, Finland), and the total number of smolts released by all nations in the Baltic sea area (FGFRI 2004). The recovery of fishery tags was based on the engagement of fishermen, with rewards offered as an incentive to return tags. The proportion of tags recovered for any release year provides only a minimum estimate of the true survival rate as most factors affecting the tag recovery, such as tagging imposed additional smolt mortality, tag shedding, and caught but not reported tagged salmon, result in an underestimate of the true survival rate. Here, we used no corrective measures to adjust the reported rates. Thus, the estimate of Atlantic salmon yield from stocked salmon smolts is a lower bound of the true yield. Finally, an estimate of Atlantic salmon yield originating from natural reproduction was calculated by subtracting the total yield of stocked fish from the all-nation salmon yield, resulting in higher bound yield estimate of naturally produced Atlantic salmon than the true yield.

### Atlantic salmon size

We derived two different long-term data sets of Atlantic salmon size from literature and the archives of the Finnish Game and Fisheries Research Institute. First, the mean mass of Atlantic salmon in commercial catches from the four rivers (rivers Oulujoki, Kemijoki and Torniojoki in Finland and Ångermanälven in Sweden) flowing into the Gulf of Bothnia, Baltic Sea, span-

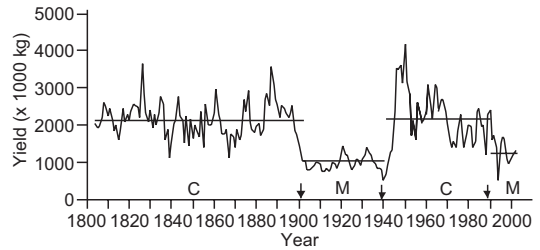
ning the years 1869–1961, was derived from the literature (Järvi 1948a, 1948b, Lindroth 1965). These two data sets of Atlantic salmon mass overlapped in the period 1916–1943. During this joint period the average mass of Atlantic salmon in the catch did not differ between the data sets (Mann-Whitney  $U$ -test:  $U = 1.02$ ,  $p = 0.312$ ), indicating that Atlantic salmon size in mass followed common dynamics in the Gulf of Bothnia regardless of the data source. Second, the sea-winter-age-specific data of Atlantic salmon mass, collected from literature (Järvi 1938, 1948b, Larsson 1984) and the archives of FGFRI (unpublished scale archives of Atlantic salmon, sampled from the Baltic Sea salmon fisheries, compiled, determined and provided by the FGFRI, Helsinki, Finland) over the years 1917–2003 were applied. Here, the sea-winter-age of fish is determined by the number of winters the salmon has spent in the sea after smoltification and out-migration from the river. The literature-derived data set (Järvi 1938, 1948b, Larsson 1984) includes the average mass-at-sea-winter-age of Atlantic salmon sampled on their way up into three large rivers flowing into the Gulf of Bothnia over the years 1917–1944. The data set of FGFRI is based on fish mainly sampled from a coastal professional fishery. To keep the FGFRI data set comparable to the literature derived data set (Järvi 1938, 1948b, Larsson 1984), only data from the Atlantic salmon caught and sampled in the Gulf of Bothnia, i.e. near the spawning rivers, were accepted ( $n = 7487$  in total, annual mean number of samples 170). In addition, the FGFRI data set includes individuals from both wild and hatchery origin, but there is evidence indicating no difference in growth whatever the origin of fish (Larsson 1984).

According to the WIBIX index (Hagen and Feistel 2005), there were regime shifts in 1902 (from continental to maritime), 1939 (from maritime to continental), and 1987 (from continental to maritime) in the period for which Atlantic salmon yield and size data are available (1804–2003). Here, we used these estimated transition years as *a priori* interventions to test the hypothesis that Atlantic salmon abundance and size tracked the WIBIX regime patterns observed in the Baltic Sea area. The expected effects of a year-based climatic intervention would be to

produce a more or less step-like change in the Atlantic salmon abundance or fish size parameters. However, it can be assumed that changes in the abiotic environment and biotic variables, originating from climatic forcing, occur in a sequence of events, accumulating during a certain transition period. Indeed, recent analyses of tens of abiotic and biotic variables of the central Baltic Sea ecosystem from the years 1974–2005 by Möllmann *et al.* (2009) indicated a climate-induced regime shift in 1987, followed by a five-year transition period during which the ecosystem variables adjusted to the new state. Thus, it is possible that data adjacent to a transition year still include dampening signals from the previous regime. To avoid this, a solution would be to remove the data of the estimated transition period, and use only ‘cleaned’ data in the analysis. For the other WIBIX regime shift years than 1987, i.e. 1902 and 1939, determination of such transition periods is not possible due to the lack of data on corresponding biotic and abiotic variables. To this end, we recognized the possibility of transition periods entangled in the transition years of the WIBIX regimes, but for the sake of uniformity applied step changes between the regimes when analyzing our data sets. In our analysis, we applied the outlines presented in Steward-Oaten *et al.* (1992) and Stewart-Oaten and Bench (2001) to compare before and after regime-shift parts of time series values. A Mann-Whitney *U*-test was used instead of a parametric *t*-test because a Durbin-Watson test, ran for *a priori* diagnostic checks, indicated slight serial correlation in the time series (Gastwirth & Rubin 1975, Steward-Oaten *et al.* 1986).

## Results

Atlantic salmon abundance in the Baltic Sea has undergone high amplitude, low frequency changes during the past 200 years (Fig. 2). The abundance of Atlantic salmon matched with the climate regimes (WIBIX regimes) in the Baltic Sea area, indicating that high amplitude shifts in the Atlantic salmon abundance were closely associated with longer-term patterns in the climate. During the continental regimes (in the 1800s, and 1939–1987), Atlantic salmon abun-

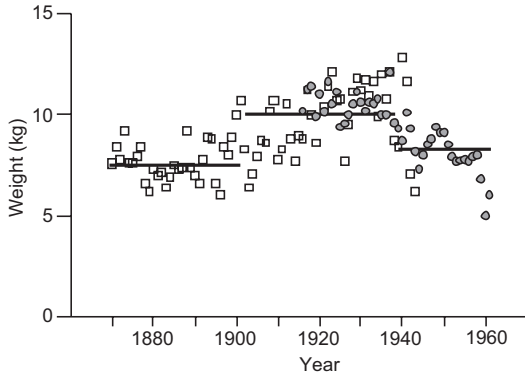


**Fig. 2.** Time-series of the annual all-nation yield of Atlantic salmon in the Baltic Sea, derived from McKinnell and Karlström (1999) and FGFRI (2004). The arrows indicate the years when the climate regime shifts, based on the WIBIX index, occurred. The letters indicate the type of the regime (C = continental, M = maritime). The straight lines show the average yield level during the regimes.

dance was high, and during maritime regimes (1902–1938, and 1988–2003) it was low (Fig. 2). All variation in abundance between the periods outlined by the WIBIX transition years were statistically significant (comparison between the periods before and after the regime shift; 1902:  $U = 78.06$ ,  $p < 0.001$ ; 1939:  $U = 44.47$ ,  $p < 0.001$ ; 1987:  $U = 10.61$ ,  $p = 0.001$ ). The time-series also indicated that there was high frequency, low amplitude periodic variability in the abundance fluctuations, but these were on a minor scale compared with the shifts between climate regimes (Fig. 2).

During the continental climate period in the years 1939–1987, there was a clear decline in the Atlantic salmon abundance in the late 1960s (Fig. 2, difference between the time periods before and after 1970:  $U = 6.45$ ,  $p = 0.011$ ) which was most obviously connected to the development of intensive offshore fisheries in the main basin of the Baltic Sea, in addition to hydropower construction in the rivers running into the Gulf of Botnia, both reducing the size of reproductive populations (McKinnell and Karlström 1999). Even so, there was a significant difference in the mean level of abundance between the latter period of the continental regime and the following maritime regime ( $U = 9.46$ ,  $p = 0.002$ ) indicating that maritime climate conditions in the Baltic Sea area still strongly affected Atlantic salmon success.

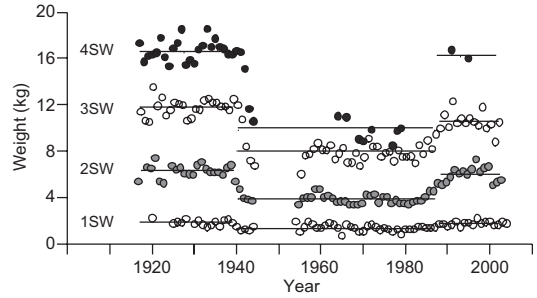
In addition to Atlantic salmon abundance, the two data sets on Atlantic salmon size in



**Fig. 3.** Average mass of salmon in the commercial catches in the four rivers flowing into the Gulf of Bothnia, Baltic Sea. Straight lines indicate the average size of salmon during the climate regimes (during the years 1902–1938 maritime regime, others continental). Squares: data sampled from catches from in the Finnish rivers Oulujoki, Kemijoki and Torniojoki; gray dots: from catches in the Swedish river Ångermanälven.

the 20th century showed comparable regime patterns to abundance data. Firstly, during the period 1869–1961, the differences in the average mass of Atlantic salmon in the catch between the WIBIX regimes were highly significant (comparison between the periods before and after the regime shift; 1902:  $U = 28.04$ ,  $p < 0.001$ ; 1939:  $U = 16.17$ ,  $p < 0.001$ ). During the maritime climate period, the average mass of Atlantic salmon in the catch was larger than during the continental climate regime. At the end of the 19th century, the mean mass in the catch was  $7.78 \pm 1.08$  kg (mean  $\pm$  SD) (Fig. 3). After the regime shift in 1902, the average size of Atlantic salmon increased reaching over 10 kg in the 1920s. Over the whole maritime regime, the mean mass of Atlantic salmon in the catch was  $9.82 \pm 1.39$  kg (mean  $\pm$  SD) (Fig. 3). The mean mass of Atlantic salmon in the catch dropped rapidly at the end of 1930s, following the climate regime change. The average mass during this continental climate period was  $8.10 \pm 1.32$  kg (mean  $\pm$  SD) (Fig. 3). The average size between the two continental regimes (before 1902 and after 1939) did not differ ( $U = 1.73$ ,  $p = 0.189$ ) from each other.

Secondly, the more detailed data on the Atlantic salmon size in the sea from the years 1918–2003 indicated that during maritime climate regimes Atlantic salmon at the age of 1–4 sea-



**Fig. 4.** Annual average mass of salmon after spending 1–4 winters in the sea. Age of fish are expressed in sea winters (SW), 1SW and 3SW salmon by open dots (no overlap), 2SW salmon by gray dots, and 4SW salmon by black dots. The straight lines indicate the average mass of fish during the climate regimes (during the years 1939–1987 continental regime, others maritime).

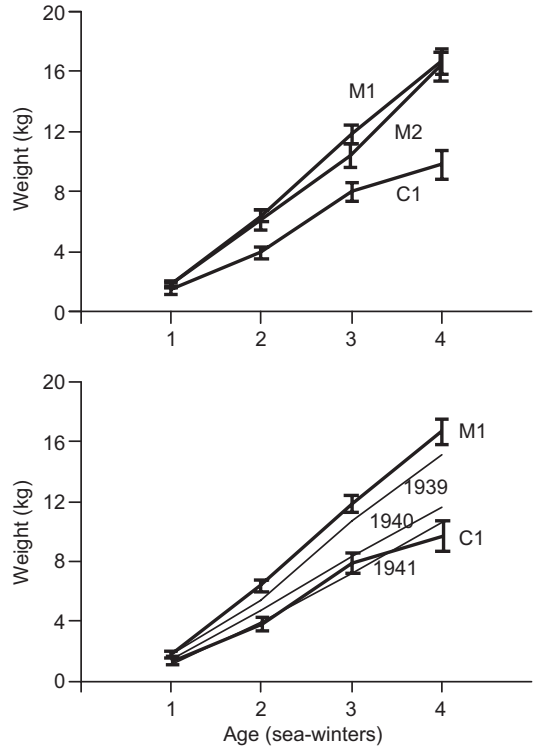
winters (SW) were clearly larger than during the continental climate regimes (Fig. 4). The average size of 1SW Atlantic salmon in the maritime regime (1902–1938) was  $1.83 \pm 0.24$  kg (mean  $\pm$  SD) and in the later maritime regime (1988 onwards)  $1.75 \pm 0.19$  kg (mean  $\pm$  SD), with no difference between the periods ( $U = 0.93$ ,  $p = 0.336$ ). In the continental regime (1939–1987), the average size of 1SW Atlantic salmon was only  $1.36 \pm 0.27$  kg (mean  $\pm$  SD), being significantly smaller than during both maritime periods (1902–1938 maritime period;  $U = 22.12$ ,  $p < 0.001$ ; 1988–2003 maritime period;  $U = 21.38$ ,  $p < 0.001$ ). The corresponding figures for 2SW Atlantic salmon are:  $6.30 \pm 0.5$  kg (mean  $\pm$  SD),  $5.94 \pm 0.65$  kg (mean  $\pm$  SD) ( $U = 3.27$ ,  $p = 0.070$ ), and  $3.91 \pm 0.47$  kg (mean  $\pm$  SD) (1902–1938 maritime period;  $U = 39.61$ ,  $p < 0.001$ ; 1988–2003 maritime period;  $U = 32.08$ ,  $p = 0.001$ ); for 3SW Atlantic salmon are:  $11.77 \pm 0.74$  kg (mean  $\pm$  SD),  $10.52 \pm 0.81$  kg (mean  $\pm$  SD) ( $U = 15.42$ ,  $p < 0.001$ ), and  $7.99 \pm 1.07$  kg (mean  $\pm$  SD) (1902–1938 maritime period;  $U = 39.01$ ,  $p < 0.001$ ; 1988–2003 maritime period;  $U = 25.95$ ,  $p < 0.001$ ), and for 4SW Atlantic salmon are:  $16.69 \pm 0.81$  kg (mean  $\pm$  SD),  $16.36 \pm 0.51$  kg (mean  $\pm$  SD), and  $9.71 \pm 0.93$  kg (mean  $\pm$  SD) (1902–1938 maritime period;  $U = 17.63$ ,  $p < 0.001$ ; other periods not tested due to too few data points, see Fig. 4). Thus, all the differences in the Atlantic salmon mass-at-sea-winter-age between the opposite climate regimes were highly significant. Between the maritime climate regimes there

was no significant difference in growth during the first two years in the sea, but the 3SW fish were smaller in the latter maritime regime. This may be due to differences in the data sets: the Atlantic salmon size data for the maritime regime before the year 1938 were from the three rivers flowing into the Gulf of Bothnia while the data for the maritime period 1988 onwards was from a coastal fisheries, and probably included fish on their way up to several rivers flowing into the Gulf of Bothnia. Salmon may show river-specific growth while in the sea in Baltic Sea area (Järvi 1948b, Lindroth 1964, 1965).

Atlantic salmon growth in the sea was smolt-year-class (i.e. the year when the smolts entered the sea) specific (Fig. 5). In addition, Atlantic salmon size and growth responded rapidly to the regime shifts (Figs. 4 and 5). In 1938, at the regime shift, Atlantic salmon growth followed the pattern typical to the maritime regime. However, the first smolt-year-class (1939) after the shift from maritime to continental regime clearly grew more slowly than the former year-classes, while the 1940-year-class already followed the pattern typical for the smolt-year-classes of the continental regime (Fig. 5). Interestingly, e.g. the smolt-year-class of 1939 continued to grow throughout the whole period of four sea-winters according to its own trajectory, and their growth continued at the same rate even when the climate regime shifted, and the following smolt-year-classes responded to this shift with slower growth. This indicates that Atlantic salmon seemed to follow the growth pattern that started during their first year in the sea. Correspondingly, comparable rapid growth changes were observed when the continental regime changed to maritime regime in the end of 1980s (Fig. 4).

## Discussion

Low frequency, high amplitude shifts in abundance and growth reported here are not unique to Atlantic salmon in the Baltic Sea. For example, Pacific salmon (*Oncorhynchus* spp.) undergo marked shifts in abundance that have been attributed to climate variation (Beamish and Bouillon 1993, Beamish *et al.* 1997). Atlantic salmon populations in the Baltic Sea area fluctuate in



**Fig. 5.** Smolt-year-class specific average mass (including SD) of Atlantic salmon. Upper panel: Average mass of salmon by sea-winter age during climate regimes (M1: maritime regime during years 1902–1938, M2: maritime regime during years 1988–2003; C: continental regime during years 1939–1987). Lower panel: average mass of salmon of smolt-year-classes 1939–1941 together with corresponding average values for the maritime regime (M1) and the continental regime (C1; years 1939–1941 excluded from the averages).

synchrony, with spatial correlation among populations being greater than reported for other anadromous salmonids (McKinnell and Karlström 1999). Thus, it is not surprising that when a relatively restricted area such as the Baltic Sea is compared with e.g. the Atlantic Ocean, the joint response of synchronous populations leads to clear and even dramatic patterns in relation to regional factors affecting the area. Atlantic salmon population complex in the Baltic Sea area may not be buffered against large-scale climate forcing or against human induced impacts, and thus they perform as all-in-one in a single market, being a sensitive indicator of the effects of climate forcing on the ecosystem (Köster *et al.* 2005, Möllmann *et al.* 2005). This provides a

contrast to asynchronous stock complexes, such as e.g. Bristol Bay sockeye salmon (*Oncorhynchus nerka*) stocks, where the buffering effects even on strong shifts in climatic conditions are derived from the weakly synchronous population dynamics among the components of the stock complex (Schindler *et al.* 2010, Moore *et al.* 2010).

Here, we described clear patterns of Atlantic salmon population dynamics in the Baltic Sea as a whole. Based on the present data, however, we can only speculate as to how climate driven abiotic conditions work their way through the ecosystems to Atlantic salmon populations causing abundance or growth trajectory change, and whether such change ultimately takes place in the sea or in the freshwater phases of the salmon life history. Recent international research on the sea phase of the Atlantic salmon life history has identified that marine-based factors strongly influence salmon abundance and catches in various rivers and regions (Todd *et al.* 2008, Friedland *et al.* 2009). A comprehensive study by Möllmann *et al.* (2009) indicated that following the year 1987 regime shift in the Baltic Sea there was a five-year transition period during which the ecosystem variables adjusted to the new state, with changes also in the composition of prey species assemblage and prey quality available for Atlantic salmon (Ikonen 2006, Vuori & Nikinmaa 2007). For example, a low nutritional value of prey has been suggested to cause the M74 syndrome in Atlantic salmon (Vuori & Nikinmaa 2007), leading to highly reduced reproductive success (Karlström 1999, Ikonen 2006, Vuori & Nikinmaa 2007). Interestingly, Atlantic salmon smolt-year-classes entering the sea during the years 1988–1994, just after the 1987 regime shift, showed the highest frequency of occurrence of the M74 syndrome later in their spawning run during the M74 monitoring period of 1985–2007 (Keinänen *et al.* 2008). Although a pathway from climate forcing through sea ecosystem and food web change to low reproductive performance of Atlantic salmon could serve as a route to regime-shift induced changes in Atlantic salmon abundance, the available data, due to limited time series on M74 covering only one regime shift, provide only a fragile leg to stand on and warrants more research. Still, there

also is evidence that variations in survival rates during the freshwater phase of Atlantic salmon are important e.g. in some Irish rivers (Potter and Crozier 2000, Clews *et al.* 2010). Further, on the Norwegian coast of the Atlantic Ocean, the synchrony of catch-based abundance index of Atlantic salmon between rivers is short-ranged, indicating strong local-scale or even river-specific effects (Voellestad *et al.* 2009). Taken together, these data suggest that Atlantic salmon might be threatened by climate effects in both their marine and freshwater stages. Due to high long-ranged synchrony between populations (McKinnell and Karlström 1999), mechanisms at work in both river and sea phases can operate in the Baltic Sea, i.e. macroclimatic changes that may impact adult growth at sea, reproductive success, and survival act in the same way on populations utilizing the same region.

Atlantic salmon in the Baltic Sea showed signs of density-dependent growth during its sea journey. During the maritime regimes, with low abundance, size of Atlantic salmon returning to spawning rivers, i.e. fish that have survived the sea phase of the life history, were clearly larger than during the continental regime with high abundance. Thus, the last decades decline in the abundance of Atlantic salmon is simultaneous with fish of larger size in the Baltic Sea, being opposite to what has been reported for Atlantic salmon in the Atlantic Ocean, i.e. smaller fish with low abundance (Jonsson and Jonsson 2004, Peyronnet *et al.* 2007, Friedland *et al.* 2009). In the Atlantic stocks of salmon, the post-smolt growth during summer is positively correlated with later survival and recruitment, growth appearing to mediate survival by the functional relationship between post-smolts and their predators (Peyronnet *et al.* 2007, Friedland *et al.* 2009). However, McKinnell and Lundqvist (2000), based of their release-recapture experiments with hatchery-reared fish in the Baltic Sea, reported that large smolts are not immune to the effects of a poor oceanic environment. The growth performance of Atlantic salmon in the Baltic Sea deserves a more detailed analysis, e.g. whether only the individuals showing high growth rate will survive under maritime regimes, leading to sparse population with large individuals.



Our analyses provide an important insight into the general patterns of the Atlantic salmon dynamics in the Baltic Sea area. We documented that the low frequency, high-amplitude up and down swings in the Atlantic salmon abundance and size in the Baltic Sea area can be attributed to climatic factors, but also to human induced impacts such as hydropower construction (Karlsson and Karlström 1994). Atlantic salmon performance seems to provide a very sensitive indicator of the biological effects of climate-forced changes in the aquatic environment. Our observations underline the importance of regime shifts because they reflect the fact that the sea environment is heavily impacted by climate forcing (Rothschild and Shannon 2004). The knowledge whether Atlantic salmon stocks are in an optimal or less-optimal environment in relation to abundance and growth would be a powerful tool for fisheries managers in their quest to conserve Atlantic salmon stocks or modulate fishing effort. For example, a key issue would be to identify the regime shifts towards unproductive phase as soon as they have happened to prevent serious overexploitation of the stocks. Nevertheless, contemporary management of Atlantic salmon stocks in the Baltic Sea does not account for variability in the sea environment or how this variability affects Atlantic salmon recruitment and stock abundance. In this sense, thanks to the long-term data on Atlantic salmon and environmental characteristics available for the area (Feistel *et al.* 2008), the Baltic Sea may provide a powerful template for further analysis and interpretation of Atlantic salmon performance under changing climate. Further, more detailed biological and socioeconomic interpretation of both historic (Järvi 1938, 1948a, 1948b) and present data would generate insights required to assess the impacts of past, current, and future climates and their consequences on Atlantic salmon populations, with the results enabling us to learn from the past and to adapt future resource management.

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