



Original Article

Post-smolt survival of Baltic salmon in context to changing environmental conditions and predators

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The survival of Baltic salmon *Salmo salar* during the first year at sea (post-smolt stage) has declined since the beginning of the 1990s. In this analysis, we complement previous studies on possible causes of this decline by considering a suite of environmental parameters, potential change in predation pressure, and post-smolt growth. Marine survival estimates were found to be negatively correlated with temperature, indicating that warming conditions have not favoured survival. Survival was also found to be positively correlated with dissolved oxygen levels and regionally related to shifts in salinity. These relationships were further studied in context to the potential predation on post-smolts by one of the main piscivores in the Baltic, Eastern Baltic cod (*Gadus morhua callarias*). Concomitant with changes in environmental conditions, Baltic cod has changed its latitudinal range, moving northward in the Baltic, possibly in response to warming conditions. These changes lead us to hypothesize that predation pressure on salmon may have increased in recent years as cod has now occupied habitats used by salmon post-smolts during their southward feeding migrations. This predation may have been intensified as a result of anoxic conditions in the central basin by concentrating predation interactions in coastal waters and/or the upper water column typically occupied by salmon post-smolts. Indicators of post-smolt growth were applied to test the alternate hypothesis that mortality is growth-mediated; these indicators lacked a time series trend, which supports the contention that shifting predation pressure rather than feeding opportunities is responsible for the decline in post-smolt survival in Baltic salmon.

Keywords: Atlantic salmon, Baltic, post-smolt survival, recruitment, temperature.

Introduction

Atlantic salmon (*Salmo salar*) populations in the Baltic Sea have been negatively impacted by an increase in natural mortality during the marine phase, more commonly shown as a decline in survival rates. In spring, young salmon are called smolts when they transition from their freshwater juvenile rearing habitats in rivers and begin their migration to the sea. After they enter the marine environment they are called post-smolts. The first weeks and months at sea is considered the critical period

for the survival of young salmon (Hansen and Quinn, 1998; Potter and Crozier, 2000; Friedland *et al.*, 2009a), though the exact length of this high-mortality period is poorly known. Typically, the first indications of the success of a cohort are received when the salmon start to recruit to fisheries. The post-smolt phase is commonly considered to cover the whole period at sea prior to recruitment to fisheries, i.e. either most of or the full first year at sea (Potter *et al.*, 2004; Michielsens *et al.*, 2008).

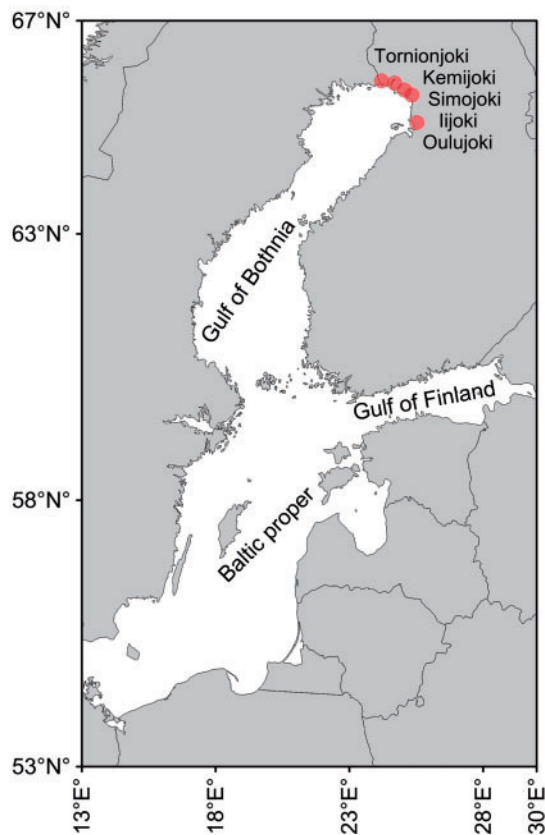


Figure 1. Map of the Baltic Sea with location of rivers used in tagging studies, marked with red circles.

The results from stock assessment analyses provide estimates of post-smolt survival and indicate that survival conditions for Baltic salmon began to erode during the early 1990s, reaching exceptionally low levels a decade ago (ICES, 2015). Wild Baltic salmon stocks were, however, in a stressed condition already during the 1980s because of high levels of exploitation in offshore fisheries. Despite the decline in sea survival observed since then, dramatic reductions in fishing pressure have resulted in some positive net effects on populations as seen in increasing abundances of wild salmon returns, particularly in northern rivers. Populations from smaller rivers in the Baltic Proper (Figure 1) have so far shown no, or only weak signs of recovery, suggesting a spatial aspect to the survival mechanism affecting Baltic salmon.

The main production of wild Baltic salmon takes place in a few large rivers in Gulf of Bothnia in the northern part of the Baltic Sea (ICES, 2015). The wild productivity is augmented by the release of hatchery-reared salmon in this area. Reared salmon are released mainly as compensation for the loss of natural production in rivers impacted by hydropower development. After leaving their natal rivers in the spring, wild and reared post-smolts from these populations migrate south and mix with other salmon populations in the southern segments of the Baltic Proper (Ikonen, 2006). During the early phase of their sea migration, salmon post-smolts feed mainly on insects (Juttila and Toivonen, 1985), but switch to a fish diet consisting mainly of young-of-the-year herring by autumn (Salminen, 1997; Salminen *et al.*, 2001). During the time salmon remain at sea their diet is mainly

composed of herring and sprat (Christensen and Larsson, 1979; Hansson *et al.*, 2001; Salminen *et al.*, 2001).

The historical development of Baltic salmon populations has been affected by multiple factors, including natural mortality, fishing, exploitation of river environments, and disease. The salmon disease M74 (Mikkonen *et al.*, 2011) has periodically been an important source of mortality; however, it is not considered a factor patterning trends in recruitment. River restorations and reduced fishery exploitation has enabled the recent recovery of northern populations, but modelling exercises clearly show that natural mortality during the post-smolt phase has been a key parameter affecting the dynamics and recruitment of Baltic salmon populations in recent decades (ICES, 2015). Knowledge about factors affecting survival at sea is of central importance when assessing stock status and for advice provided to fishery management.

In the Baltic, a host of factors have been shown to affect post-smolt survival at sea, including the size and physiological status of smolts (Virtanen *et al.*, 1991; Salminen *et al.*, 1995; Saloniemi *et al.*, 2004), predator occurrence (Larsson, 1985; Mäntyniemi *et al.*, 2012), and the availability of suitable food items (Salminen *et al.*, 2001; Kallio-Nyberg *et al.*, 2006). The problem has also been addressed through assessment analyses which brought particular attention to the role of herring and sprat as post-smolt prey items, seal abundance, and intraspecific competition (ICES, 2008, 2009). Following from this preliminary work, Mäntyniemi *et al.* (2012) found that salmon post-smolt survival was positively correlated with the abundance of herring recruits in the Gulf of Bothnia, whereas a negative correlation was found between survival and seal abundance. A closer examination of these relationships revealed that herring recruitment was able to explain a large proportion of the annual variation, but not the declining trend in post-smolt survival; whereas, the increase in the seal population coincided with the declining time series trend in salmon survival. It remains unknown to what extent these relationships arise from direct causalities (Mäntyniemi *et al.*, 2012).

In recent decades, the Baltic Sea ecosystem has gone through dramatic changes, manifesting in shifts in species composition at several trophic levels (Möllmann *et al.*, 2009; Diekmann and Möllmann, 2010; Lindegren *et al.*, 2010; Gårdmark *et al.*, 2015). Climate-change, fishery exploitation, eutrophication, saltwater inflow, and spatial variation in abundance of important predators have all been mentioned as important drivers behind these regime shifts (Gustafsson *et al.*, 2012; Fisher *et al.*, 2015). We believe that when studying survival of salmon in the marine environment, it is important to take into account all aspects of the marine ecosystem to effectively identify possible mechanisms behind putative correlations between survival and various biotic and abiotic factors.

In this study, we complement previous work by analyzing the relationships between a suite of environmental parameters and sea survival of Baltic salmon, in particular the temporal and spatial variation in these parameters. We further focus our analyses on potential mechanisms behind the observed environmental correlations by analyzing scale growth and size at age in an attempt to evaluate the role of post-smolt growth. We also analyze the distribution of one of the main piscivores in the Baltic, Eastern Baltic cod (*Gadus morhua callarias*), which constitutes a potential predator on salmon post-smolts, in an attempt to evaluate the role of changing predation pressure. Our correlative approach is intended to assist in the development of new

hypotheses and contribute to the accumulation of evidence to either support or reject these ideas, while recognizing that developing a mechanistic understanding of early life stage survival is a challenge across all areas of fisheries research.

Methods

Migration of Baltic salmon post-smolts

The post-smolt feeding migration of Baltic salmon post-smolts was characterized with tag recovery data for fish emigrating from rivers in the Gulf of Bothnia. Carlin-type external tags were attached to both hatchery-reared and migrating wild smolts captured at smolt traps in the Tornionjoki, Kemijoki, Simojoki, Iijoki and Oulujoki rivers (Figure 1). Tags recovered by fishermen were reported to the Finnish Game and Fisheries Research Institute; in most cases the tag returns included biological data on the fish. The analysis was restricted to data from post-smolts ≤ 450 mm in length and fish ≤ 400 g in weight where length data were missing. The tag recovery data were post-stratified by 2-month periods and 0.5 degree latitude and longitude bins for plotting purposes. This provided 1117 post-smolt tag recoveries over the study time series of 1959–2014. During the May–June time period, 665 tags were recovered; in the following time periods, tag recoveries decayed exponentially to 268, 120, and 64 for the July–August, September–October, and November–December periods, respectively.

Survival of Baltic salmon post-smolts

The survival of salmon during the post-smolt phase was estimated in the Baltic salmon stock assessment conducted by ICES (2015) using a Bayesian full life-cycle framework (Michielsens *et al.*, 2008; ICES, 2015). This framework makes it possible to estimate survival rates based on a wide range of information gathered during the salmon life cycle. The main data sets used in the life-cycle model comprise juvenile and spawner abundance surveys, stocking statistics (for hatchery-reared fish), fisheries data (effort, catches) and tag recapture data. These data sets, in concert with various auxiliary data and background information, enable estimation of abundance and survival at various stages of salmon's life cycle (Michielsens *et al.*, 2008; ICES, 2015). No direct observations about post-smolt survival are available; observations of abundance of smolts initiating sea migration from rivers exist, but there are no observations from the sea about abundance immediately after the post-smolt phase. In the life-cycle model, natural survival rates at sea are assumed to be the same for salmon originating from different river populations. Because of this, data-rich stocks, for instance, that contain information on annual number of smolts and spawners have a stronger influence on the resulting survival estimates than stocks with incomplete data. In addition to observed strengths of smolt and spawner cohorts, post-smolt mortality estimates before 2010 are influenced by data from Carlin tag-recapture experiments.

The post-smolt mortality for wild salmon is defined as a lognormal prior distribution with mean 1.3 year^{-1} and SD 0.3 year^{-1} given for instantaneous mortality of the first 4 years in the time series (smolt cohorts 1987–1990). These distributions are restricted between 0.5 and 5 year^{-1} , i.e. between a survival probability of 0.7 and 61%. Onwards from 1991, the instantaneous mortality is considered to follow a lognormal distribution with expected value as a moving average of the corresponding mortalities during past 4 years. The coefficient of variation of the

instantaneous mortality is assumed to have the same distribution within the time series, prior for this being uninformative Beta (1,1).

Instantaneous mortality for reared salmon is assumed to depend on the instantaneous mortality of wild salmon, through an annual effect term indicating that the mortality of reared can be the same, or maximum 2.5 times as high as the mortality of wild. Prior mean of the multiplicative effect term is 1.5. This prior information is based on the results of old experiments carried out in the Baltic Sea and elsewhere, and it covers the whole plausible range of values in the light of available information. The annual effect terms for the mortality of reared salmon are considered to have a hierarchical structure, following the assumption that these terms can have common hyperpriors and that nothing is known (a priori) that would distinguish any of the terms from another in a particular way.

The full life-cycle model with the above specifications for post-smolt survival and the corresponding specifications for other life stages and fisheries effects is then fed with the data. The marginal posterior probability distributions of the model parameters, including annual post-smolt survival rates, are approximated by WinBUGS (Bayesian inference using Gibbs sampling) software, version 1.4 (<http://www.mrc-bsu.cam.ac.uk/bugs>).

Environmental parameters in the Baltic

The survival of Baltic salmon was correlated with a suite of environmental parameters salinity, dissolved oxygen, sea surface temperature, and chlorophyll concentration. It is assumed that these parameters may affect the interaction of salmon and predators or impact the growth of salmon, this affecting the size-mediated dynamics of their survival. Pearson-product moment correlations were done on monthly data, stratified on a 1° grid, or in the case of salinity and oxygen on a subset of the grid, for the survival time series of 1987–2014. The time series used in these correlations displayed varying degrees of autocorrelation. Autocorrelation was corrected by adjusting the effective degrees of freedoms of each test according to Pyper and Peterman (1998). The effective degrees of freedom (N^*) of a correlation between two time series x and y was estimated by:

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N} \sum_{j=1}^{N/5} \frac{(N-j)}{N} \rho_{xx}(j) \rho_{yy}(j)$$

where N is the number of time series values and $\rho_{xx}(j)$ and $\rho_{yy}(j)$ are the autocorrelations of x and y at lag j . Following Garrett and Petrie (1981), we took the autocorrelation at lag j of the cross-products of standardized time series of x and y . Salinity and oxygen data were extracted from the HELCOM COMBINE oceanographic database (<http://helcom.fi/>). The Baltic Sea monitoring program occupies a series of standard stations and collects water column profiles of a range of physical and biological data from designated depths. We worked with water column average salinity (practical salinity unit; PSU) and dissolved oxygen (ml l^{-1}) for each station; monthly averaged salinity and dissolved oxygen were then assigned to the study grid. Sea surface temperatures were extracted from the NOAA Optimum Interpolation $1/4$ Degree Daily Sea Surface Temperature Analysis (OISST) dataset, which provides high resolution SST with a spatial grid resolution of 0.25° and temporal resolution of 1 day (Reynolds *et al.*, 2007). Chlorophyll- a concentrations were based on remote-sensing

measurements made with the Sea-viewing Wide Field of View (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer, Medium Resolution Imaging Spectrometer, and Visible and Infrared Imager/Radiometer Suite sensors. We used the GSM (Garver, Siegel, Maritorena Model) merged data product at 100 km and 8-day spatial and temporal resolutions, respectively, obtained from the Hermes GlobColour website (hermes.acri.fr/index.php). These four sensors provide an overlapping time series of chlorophyll *a* concentrations during the period 1998–2014 and were combined based on a bio-optical model inversion algorithm (Maritorena *et al.*, 2010).

Post-smolt growth

We examined two proxy variables to test the hypothesis that post-smolt growth is the main factor influencing salmon survival in the Baltic. We used scale growth measurements from returns to the River Tornionjoki, which is the northernmost of the Baltic Sea catchment river basins and the largest producer of wild salmon in the Baltic Sea. The scale samples were collected from the catches of local river fishermen over the years 1992–2005. The scales of multi-seawinter fish were cleaned and impressed onto acetate; using a microfilm reader, the post-smolt growth increment was measured as the distance from the end of the freshwater zone to the first sea annulus. A total of 128 scale measurements were made during the time period, averaging ~ 10 scale samples per year. We also examined the size (total length to nearest cm) of returning grilse to the Tornionjoki during the period 1987–2014. We consider this length to be an index of the post-smolt growth occurring the year prior to return. A total of 1033 length measurements were made during the time period, averaging ~ 37 measurements per year.

Distribution of cod

Fish populations have been sampled in the Baltic by a series of national bottom trawl surveys starting in 1991. The focus of these surveys is marine groundfish species found in higher salinity portions of the Baltic, thus most of the survey effort is in stations south of 59°N. Since 2001, the Baltic International Trawl Surveys (BITS) instituted standard gear types used by all participating countries. Mean catch-per-unit-effort (CPUE, num h^{-1}) values of cod (*G. morhua callarias*) per length and haul in units of the large standard gear were estimated according to the BITS manual (ICES, 2014). Time series of arithmetic mean CPUE values were calculated for data aggregated into 100 mm length intervals (110–200 mm, 210–300 mm, ..., >500 mm) and latitudinal bands (truncated to latitude) over the period 1991–2014. We considered cod >210 mm; cod of these sizes would be able to consume or injure post-smolt salmon for much of the post-smolt year at sea (Scharf *et al.*, 2000). CPUE was transformed ($\log(\text{CPUE} + 1)$) before being correlated to the salmon survival rates and as with the environmental data, correlation probabilities were corrected for time series autocorrelation.

Results

Seasonal movement of salmon

Salmon originating from Gulf of Bothnia river systems migrate south to the main basin of the Baltic during the post-smolt year. These migration movements are imputed from the tag recoveries of both wild and reared origin salmon. The tag recoveries from wild fish were less numerous than recoveries from reared fish;

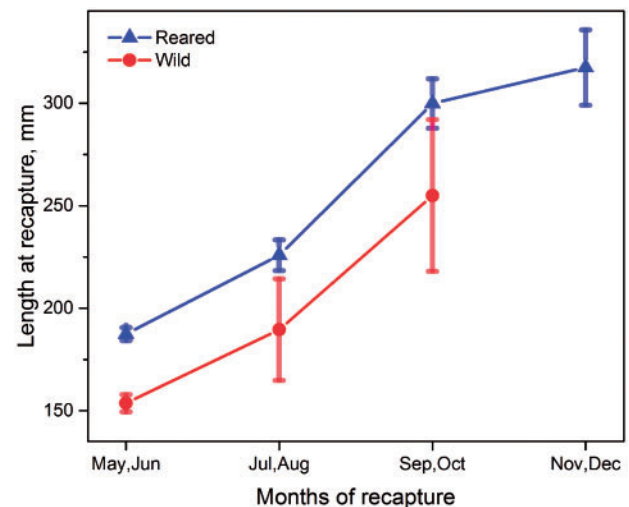


Figure 2. Size at recovery for tagged reared and wild post-smolt salmon during the post-smolt year. The analysis was restricted to salmon ≤ 450 mm. Error bars are 95% CI.

hence, the use of both data sources is needed to develop a comprehensive depiction of their distribution in time and space. We assume that the factors affecting the migration of wild and reared fish are equivalent, but there are some differences in the two groups that affect our interpretation of the ecology of post-smolts during their migration. Reared post-smolts were found to be larger at recapture than wild fish by an average of 38 mm during May through October (Figure 2). The importance of this observation is in the interpretation of the potential effect of predators on post-smolts; post-smolt samples that include reared fish represent a smolt size at the higher end of the likely size of wild fish.

Post-smolts were captured at high frequency close to their natal river early in the post-smolt year, and progressively move south during summer into fall, with some suggestion of an affinity for littoral habitats during the migration. Most tag recoveries of Gulf of Bothnia post-smolts were during the May through June time frame (Supplementary Figure S1a). By July/August, post-smolts were widely distributed over the northern half of Baltic, with most recoveries on the western coast (Supplementary Figure S1b). The September/October distribution was similar to the July/August one, with the exception that more fish appeared to be further south (Supplementary Figure S1c). By the late fall (November/December), many post-smolt were found in the southern end or main basin of the Baltic (Supplementary Figure S1d). The mode of tag recoveries was $\sim 65^\circ\text{N}$ during the May/June time frame (Figure 3a). During both July/August and September/October, high numbers of tag recoveries were from latitudes north of 60°N ; this distribution suggests a discontinuity of tag recoveries associated with 60°N (Figures 3b and c). By November/December, there were lower numbers of tag recoveries over the full latitudinal range of the Baltic (Figure 3d).

Survival rates of wild and reared salmon

The post-smolt survival of both wild and reared origin stocks declined during the study period (Figure 4). Wild fish survival was higher than the survival of reared fish; the wild and reared survival time series were highly correlated ($r = 0.98$, $p < 0.01$).

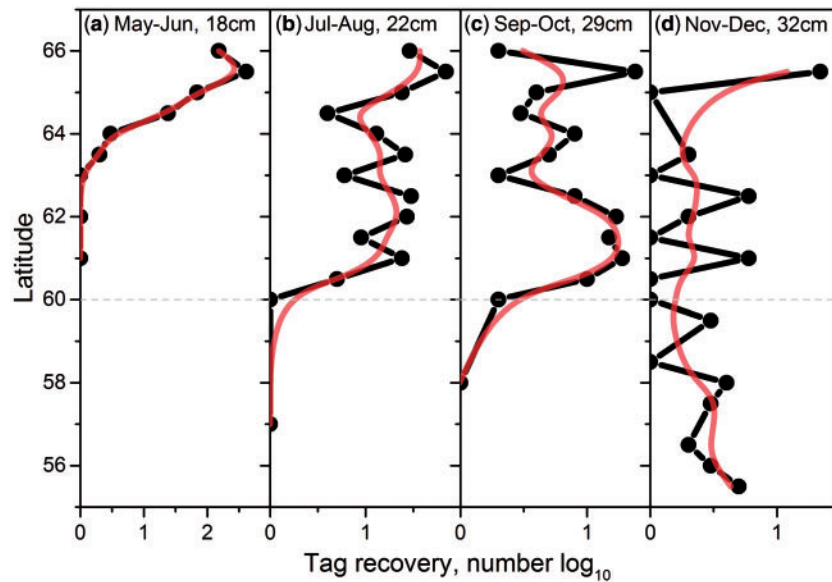


Figure 3. Tag recoveries for reared and wild post-smolt salmon by latitude (a–d, 2-month periods May/June, July/August, September/October, November/December, respectively). The analysis includes post-smolts ≤ 450 mm in length and for those fish with missing length data which were ≤ 400 g in weight. Red (gray) lines are LOESS smoothing.

Survival of wild fish was $\sim 35\%$ of the cohort at the beginning of the time series and declined to 10% by 2004. In recent years, survival has increased to $\sim 15\%$. Subsequent correlation analyses relating environmental conditions to survival were performed using the data for wild fish only, assuming they represent the performance of salmon in the environment without the confounding effects associated with hatchery rearing.

Survival and environmental parameters

The associations between the survival of wild fish and salinity, dissolved oxygen, sea surface temperature, and chlorophyll concentration were tested by correlations between survival and bi-monthly or monthly data fields. The Baltic has a salinity gradient ranging from ~ 4 to 10 PSU as based on water column averaged data, with some high salinity water episodically found at lower latitudes and deeper portions of the system (Supplementary Figure S2a). Salmon survival was negatively correlated with salinity trends in the lower latitude range ($56\text{--}59^\circ\text{N}$) of the Baltic and positively correlated with salinity at the extreme northern end of the system throughout the post-smolt year (Figure 5a–d).

Dissolved oxygen in the Baltic ranged from ~ 5 to 8 ml l^{-1} (Supplementary Figure S2b). Dissolved oxygen declined to critically low levels $< 5\text{ ml l}^{-1}$ during the early 2000s between the latitudinal range of $58\text{--}60^\circ\text{N}$. Salmon survival was positively correlated with dissolved oxygen trends over most of the Baltic throughout the post-smolt year (Figure 5e–h).

Annual average sea surface temperature ranged from $\sim 5\text{--}10^\circ\text{C}$ from north to south (Supplementary Figure S2c). There has been a trend of increasing temperature over time; average annual temperature associated with latitude has increased by about one degree over the study period. Salmon survival was negatively correlated with sea surface temperature in the gulfs of Finland and Bothnia during the early segment of the marine migration, i.e. during the months of May through August (Figures 6a–d). The negative correlation fields expanded to include most

of the Baltic during months September through December (Figures 6e–h).

Chlorophyll concentration varies over time and space in the Baltic; under low light availability conditions, minimum concentrations were $< 1\text{ mg m}^{-3}$ and during blooms levels exceeded 40 mg m^{-3} (Supplementary Figure S3). The highest chlorophyll concentrations were associated with spring blooms that occurred in April and May, and in particular in the middle latitude reaches of the Baltic (Supplementary Figures S3b and c). There appears to be some level of secondary bloom activity in July (Supplementary Figure S3e). There is also some evidence of increasing chlorophyll concentrations during the study period, in particular in the data for April and July. The only significant correlations between survival and chlorophyll concentration were found in a limited portion of the Baltic main basin during June (Figure 7d) and in one grid location in the Gulf of Finland during April (Figure 7b).

Growth of salmon post-smolts and grilse

Post-smolt growth indices and the size of returning grilse in the Baltic suggest that growth during the post-smolt year has remained relatively constant over time. Scale growth suggests somatic growth during the post-smolt period either remained constant or increased slightly over the period 1992–2005 (Figure 8a), noting that this period was marked by a decline in survival fraction from ~ 0.3 to 0.1. The size of returning grilse (one sea-winter fish) was also constant or suggestive of an increase in growth over the study period (Figure 8b).

Survival and the distribution of cod

The abundance of Baltic cod in the northern segments of the Baltic main basin has increased over time as salmon survival has declined. The CPUE of cod averaged $485\text{ fish hour}^{-1}$ in the southern latitude bands (Figure 9a–e). CPUE in the most northern band ($58\text{--}59^\circ\text{N}$) has a high proportion of missing values and is not used in the correlation analysis. The correlation between

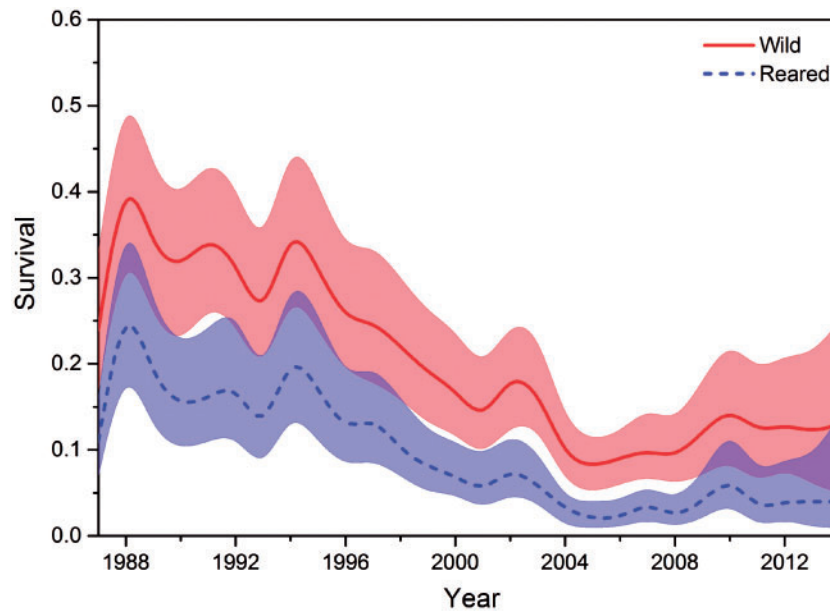


Figure 4. Time series of Baltic salmon post-smolt survival for wild and reared origin stocks. Bold line is the estimated median of the posterior distribution, whereas the shaded region illustrates 95% probability intervals of the estimates for the period 1987–2014 (B-splines).

salmon survival and cod abundance was negative in all latitude bands (Figure 10); the 57–58 band correlation was significant at $p = 0.010$ and the 56–57 band at $p = 0.052$.

Discussion

We found that Baltic salmon post-smolt survival is correlated with shifts in sea temperature, dissolved oxygen levels, and in a regional context, salinity as well. Our findings suggest that post-smolt survival has been impacted by environmental factors that may have changed the distribution and intensity of the predator fields along the migration routes used by post-smolts. Survival is strongly and negatively correlated with temperature, which may be related to the direct effects of increasing temperature on the physiology of post-smolts, but we suggest a more likely explanation is that temperature has changed the distribution of predators in the Baltic. In the analysis, we focused on the potential role of cod, a species which may be an effective predator on young salmon (Hvidsten and Lund, 1988; Hedger *et al.*, 2011). Despite lacking the demonstration of causalities related to predation, the strong correlation between temperature and post-smolt survival should have potential for improving short-term predictions of adult salmon abundance as a basis for management and conservation.

Baltic cod has increased almost 50-fold in abundance in higher latitude reaches of the Baltic main basin with increasing temperature over the study period, resulting in a potentially more aggressive predator field in areas used by migrating post-smolts during summer. Cod has the ability to consume prey items that are up to half their size (Scharf *et al.*, 2000), and though a demersal species, cod seek forage in the water column making them pelagic piscivores (Sparholt, 1994; Uzars, 1994). Their role as pelagic feeders is substantial as confirmed by feeding studies that show that Baltic cod >30 cm in length utilize fish prey at a level of 25% of their diet by weight (Sparholt, 1994). It is not without precedent that Baltic cod has the potential to exert top-down control over a lower trophic level species.

Bagge *et al.* (1994) showed that recruitment of herring and sprat stocks in the eastern Baltic Sea are influenced by the cod predation. The influence of cod predation on salmon was not reported in that study, probably because salmon are much less abundant than herring and sprat. Importantly, analyses suggest that cod predation on fish species with lengths smaller than ~25 cm (similar sizes to salmon post-smolts during summer; Figure 2) can be intense and significant at the population level (Bagge, 1989). In addition to cod now occupying habitats used by post-smolts, the interaction of the two species may have been intensified by changes in dissolved oxygen over time by further concentrating predators into coastal waters and shallow depths used by post-smolts. We feel our findings are compatible with previous reports suggesting that predation on post-smolts has increased and is responsible for the decline in post-smolt survival in recent years. Mäntyniemi *et al.* (2012) suggested that predation by seals may affect post-smolt survival. Gray seals, *Halichoerus grypus*, have increased in abundance in the Baltic and consume a range of fish prey, including salmon (Lundström *et al.*, 2010). They are highly abundant in the middle latitude reaches of the Baltic (Vanhatalo *et al.*, 2014), and stomach analyses of seals from the Gulf of Bothnia indicate that salmon and sea trout account for 8% of the consumed biomass (Lundström *et al.*, 2010). Their predation effects would overlap spatially with the impact of the increasing cod population. Other groundfish taxa such as haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, Norway pout *Trisopterus esmarkii*, European hake *Merluccius merluccius*, long rough dab *Hippoglossoides platessoides*, which comprise the complex of demersal species in the Baltic, co-occur with cod in the mid-latitude reaches of the Baltic. In perspective, the only other species of moderate abundance compared with cod has been whiting; however, we think it is balanced to consider predation pressure as being exerted mainly by cod, but that a suite of other species may also comprise the predator field, which cod may be an indicator of its time and space varying abundance.

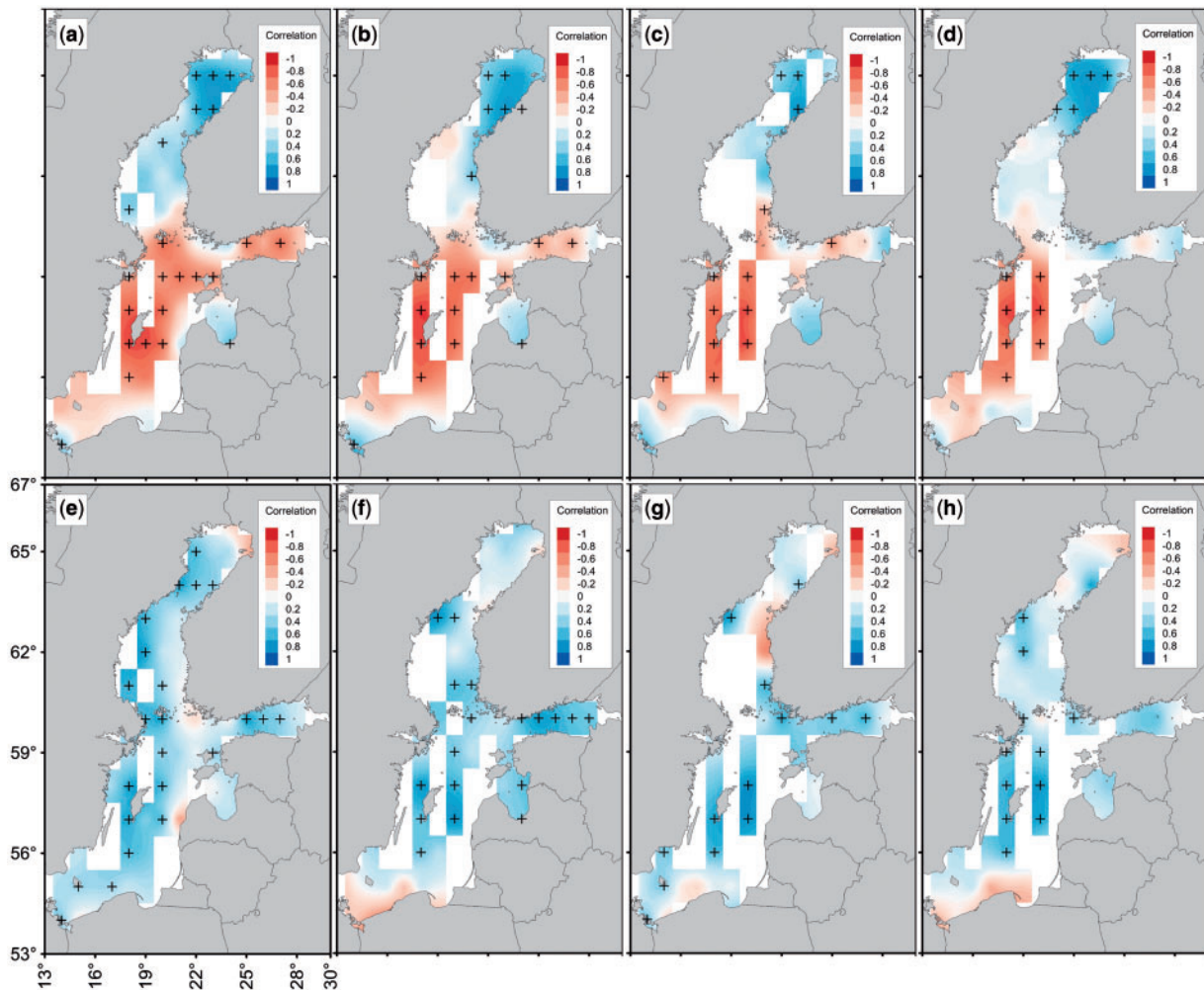


Figure 5. Maps of Pearson Product Moment Correlation between an index of Baltic salmon survival and salinity (a–d, 2-month periods May/June, July/August, September/October, November/December, respectively) and dissolved oxygen (e–h, same time periods as salinity maps). Contouring restricted to grid locations with data. “+” indicate grid location where the correlation was significant ($p < 0.05$).

The absence of tag returns from tagged post-smolts during summer, south of 60°N , may suggest a very specific time and area interaction between migrating post-smolts and the temporal and spatial distribution of predators. As post-smolts migrate south, they remain vulnerable to predation, as gauged by their size, through the summer into the fall. It is through this period that tag returns drop precipitously south of 60°N , which is related to the same latitude band where cod has increased in abundance in negative correlation to salmon survival rate. By fall, salmon post-smolts would likely be >30 cm in length, and only vulnerable to the largest cod, those fish >50 cm. Also by fall, tag returns of salmon are found uniformly throughout the Baltic, suggesting by this time the fish have outgrown their vulnerability to not only cod, but to the piscivorous predator field in general. An alternative (but not mutually exclusive) explanation for the observed recapture pattern is that the fishing season and type of fishing gears change rather markedly around 60°N ; in the Gulf of Bothnia young salmon are bycaught mainly in coastal gill net fisheries targeting other species, whereas in the Main Basin tagged salmon are mainly caught by salmon fisheries located offshore, which use longlines and drift nets (historically). Thus, the absence of tag

returns from post-smolts in summer south of 60°N may at least partly be explained by spatial differences in fishing patterns between north and south, i.e. differences in gears, size-selectivity and fishing season.

The distribution of dissolved oxygen may be playing a nuanced role in intensifying the effects of predators on salmon post-smolts during their feeding migration in the Baltic. The high temperatures associated with littoral waters in summer suggest that cod reside at deeper depths during summer and may be less likely to make feeding excursions that interact with salmon post-smolts. During their feeding migrations, cod is distributed over very large areas, which give the appearance of random movements inside the distribution area (Aro, 1989). If oxygen stress can actuate the movement of cod, it would tend to force the movement of fish from deeper depths where oxygen depletion is most intense, to shallower waters, thus having the effect of increasing interactions between cod and salmon. The period of highest oxygen stress, from ~ 2004 to 2008, matches the period of lowest salmon survival. However, it is important to note, the conservative trend of declining salmon survival over the time series is not matched by the trend in oxygen concentration. The conservative trends that

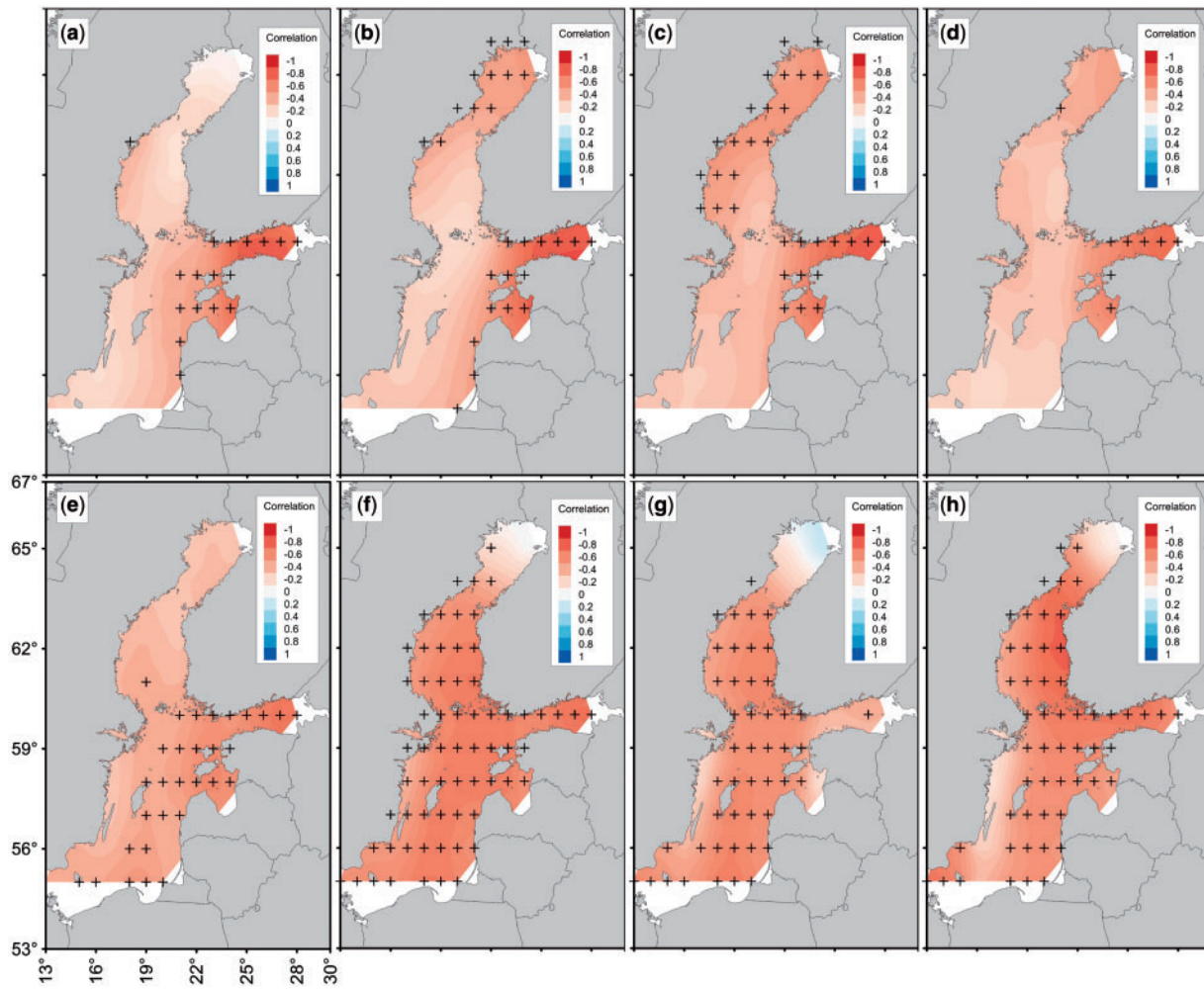


Figure 6. Maps of Pearson product moment correlation between an index of Baltic salmon survival and monthly sea surface temperature (a–h, May through December, respectively). “+” indicate grid location where the correlation was significant ($p < 0.05$).

do match salmon survival are present in the temperature and cod abundance data. Change in environmental conditions may be contributing to the expanded range of cod in the Baltic, but we are also mindful that cod abundance has increased and may be utilizing additional habitat as a consequence (Eero *et al.*, 2015).

First entry into the marine environment has been identified as an important period controlling recruitment for some salmon stocks; however, the data from our analysis does not offer any definitive conclusions on how changing factors during this period may be affecting Baltic salmon. The timing of smolt migrations and the size of smolts during migration (Jonsson and Jonsson, 2014) raises concerns over the effect of phenology mismatches during the smolt run (Friedland *et al.*, 2003; Otero *et al.*, 2014). We did not observe any correlation between SST in May and survival in the Gulf of Bothnia, the relative time frame to consider thermal phenology effects, but we do see a positive correlation between salinity and survival. The negative SST correlations observed in the Gulf during June are consistent with those observed by Jutila *et al.* (2005) in the sense that both studies report declining survival with higher SST. However, our data do not show the same thermal optimal range reported earlier, noting that the studies were based on different time series. This correlation is

opposite to the salinity correlation we see in the southern half of the Baltic, so in summary, the post-smolts appear to have migrated into fresher conditions in the Gulf of Bothnia and into increasing salinity conditions over time as they move south. Increasing temperature and salinity would be consistent with a shift in the marine predator field further north and thus caused increased predator interactions throughout summer that we associate with the 60°N parallel. The decline in salinity in the northern end of the Baltic may also increase the spatial range of freshwater predators that can interact with post-smolts (Jepsen *et al.*, 2006) and overall warming is likely increasing the abundance of freshwater coastal predators such as pike-perch *Sander lucioperca* (Pekcan-Hekim *et al.*, 2011). There are still multiple lines of evidence to support the contention that summer predation is also affecting the survival pattern, which leads us to suggest that the seasonal predation effects may be synergistic (Jutila *et al.*, 2005).

Though growth mediated survival has been identified as the underlying mechanism of recruitment control for a number of salmon stocks in the Atlantic Ocean (Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008; Friedland *et al.*, 2009a), we see no evidence to support a similar hypothesis for Baltic salmon. With salmon in

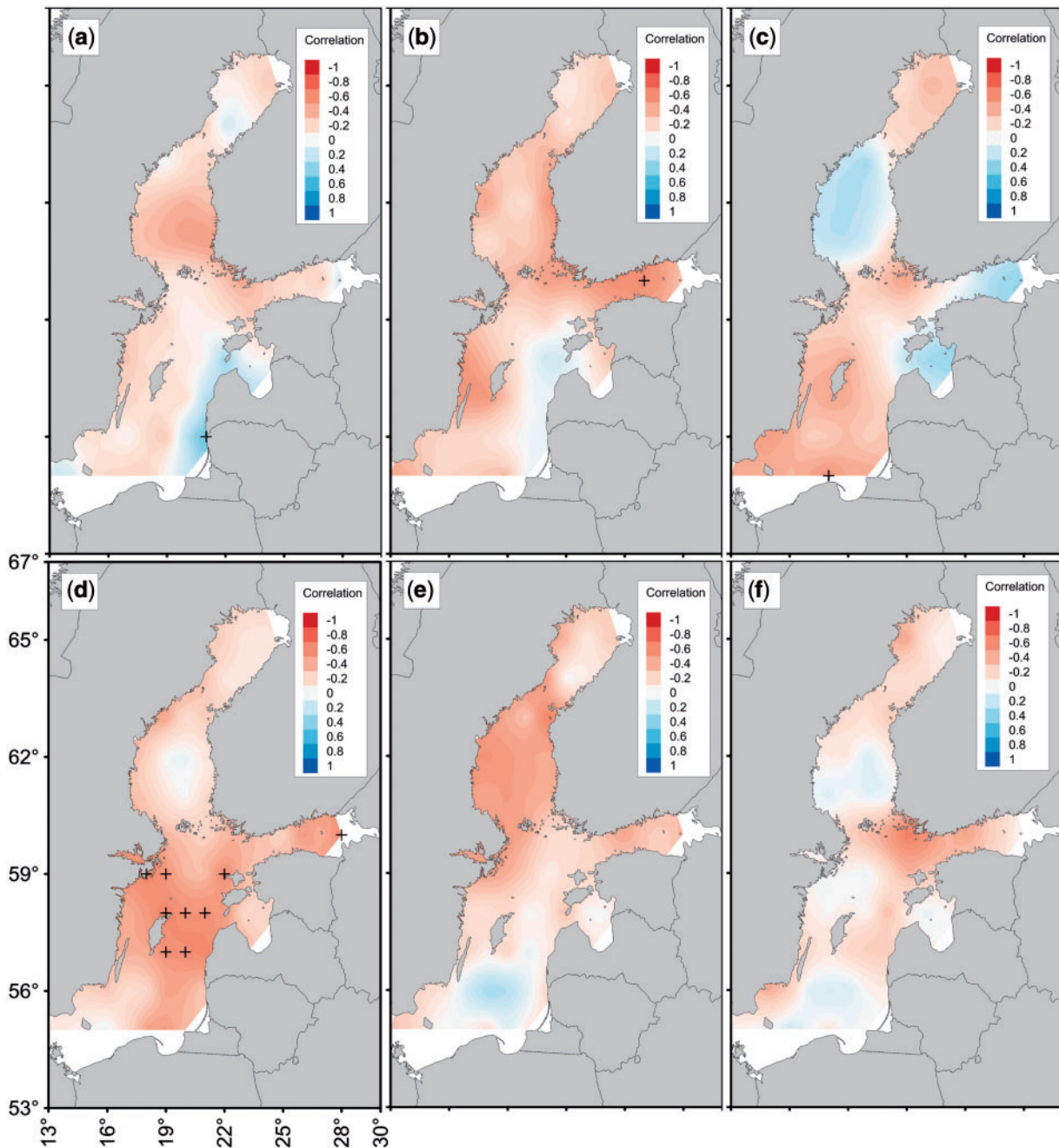


Figure 7. Maps of Pearson Product Moment Correlation between an index of Baltic salmon survival and monthly chlorophyll concentration (a–f, March through August, respectively). “+” indicate grid location where the correlation was significant ($p < 0.05$).

the North Atlantic, regional stocks complexes show varied dependency on post-smolt growth as a determinant of survival (Friedland *et al.*, 2014a). Where it occurs, it is associated with the climate patterns of the eastern boundary of the Atlantic basin, which also forms the basis for a similar mechanism in a species of Pacific salmon (Friedland *et al.*, 2014b). There is evidence that inter-annual variation in feeding opportunity may affect Baltic salmon survival, but the trends in forage species fail to explain the conservative downward trend in survival (Mäntyniemi *et al.*, 2012). The increased temperatures of the Baltic have the potential of increasing metabolic demand in post-smolts with a net effect

of decreasing growth if feeding opportunities remain the same (Portner and Peck, 2010). However, what is inescapable is that two growth indices that should reflect a change in post-smolt growth do not show any change over time. Finally, though a less direct form of evidence, remote sensing data on chlorophyll concentration shows a trend that is opposite to a proposed role of feeding and growth control of recruitment.

Climate forcing appears to affect Baltic salmon productivity on a number of levels related to both numerical recruitment and fishery yields in weight. Over century time scales, the abundance and weight of individual salmon show distinct regimes associated

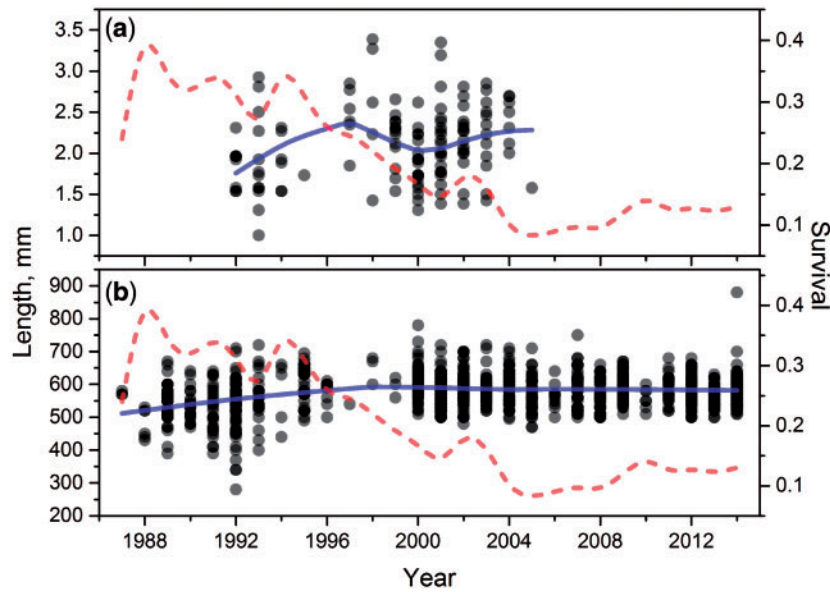


Figure 8. Scatterplots of length of the post-smolt growth zones (a) and grilse total lengths (b) vs. smolt year of Baltic salmon plotted with the survival rate of wild fish (dashed red lines, B-splines). Blue lines are LOESS smoothers.

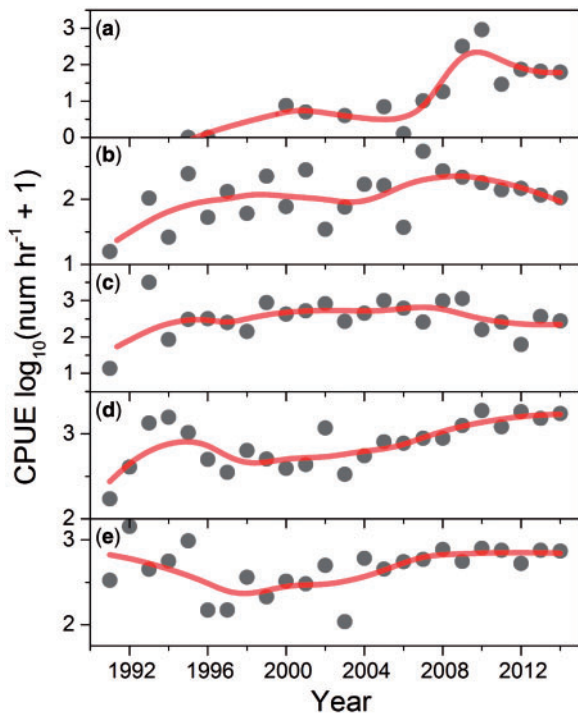


Figure 9. CPUE time series of cod *G. morhua callarias* >21cm TL by latitude bands 58–59, . . . ,54–55 (panels a–e, respectively) over the years 1991–2014. Red lines are LOESS smoothers.

with climate regimes, most notably, the North Atlantic Oscillation (Huusko and Hyvärinen, 2012). In their study, regimes producing low fishery yields were associated with high individual body weights, suggesting that growth was a density dependent response and that yield was controlled by the recruitment patterns. Here we provide evidence that climate exerts control over salmon recruitment, and further hypothesize how

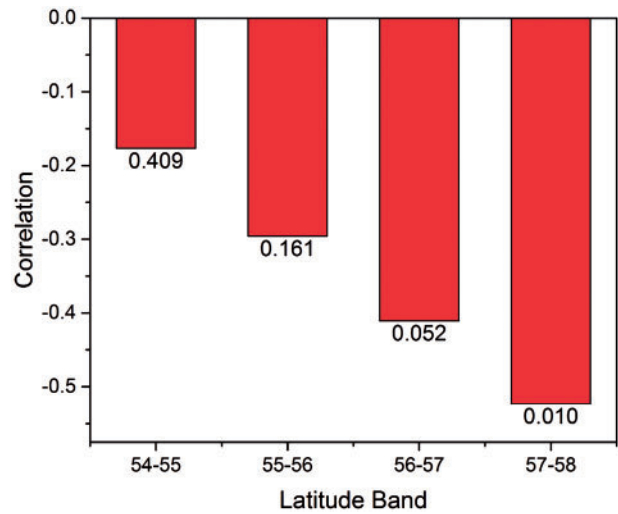


Figure 10. Pearson product moment correlation between Baltic salmon survival and CPUE time series for cod *G. morhua callarias* >210 mm TL by latitude bands, correlation probabilities below each band column.

environmental variation may be influencing predation pressure on juvenile fish; however, it would require subsequent analyses to confirm whether climate has an effect on individual size or if it is simply a density dependent response. Future work may also be directed towards more in-depth analyses of prey versus predator interactions, e.g. including long-term correlations between stock size fluctuations for Baltic salmon and cod, based on historic time series available for these species (Eero *et al.*, 2008; Huusko and Hyvärinen, 2012).

The recruitment control mechanism we suggest for Baltic salmon most closely resembles the hypothesis developed to explain the recruitment of Atlantic salmon in North America. Like the

evidence for these Baltic stocks, the time series pattern of post-smolt growth of North American salmon is uncorrelated with survival (Friedland *et al.*, 2009b; Hogan and Friedland, 2010). Furthermore, climate effects have caused a distributional shift of a cross-section of species to the north along the US Northeast coast (Nye *et al.*, 2009), most significantly, putative predators on salmon smolts now occupy habitats in the migration corridors of salmon post-smolts in that region (Friedland *et al.*, 2012). Similarly, we attribute post-smolt survival variation in the Baltic to a change in predator abundance rather than a change in post-smolt growth. We suggest a generalization for salmon populations with a juvenile marine phase: survival appears to depend on whether growth varies enough to influence the time spent by post-smolt juveniles at sizes vulnerable to predators. If that is the case, survival is growth mediated. Alternatively, growth may not vary sufficiently to influence survival; or stated differently, growth mediated mortality may be overwhelmed by variation in predator fields, making survival predator driven.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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