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Environmentally driven changes in Baltic salmon oxidative status during marine migration

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Abstract

The fitness and recruitment of fish stocks can be markedly affected by environmental disturbances including global warming, eutrophication and contamination. Understanding the effects of environmental stressors on salmon physiology during marine residence is of a global concern as marine survival has decreased. We present a unique combination of physiological responses - antioxidant defence and oxidative damage biomarkers, stable isotopes and contaminant exposure biomarkers - measured from adult Atlantic salmon (*Salmo salar*) collected at the Baltic Sea and studied in relation to environmental variables and fitness estimates. The results demonstrate that feeding populations of salmon display marked temporal and spatial variation in oxidative status. Better oxidative status of salmon was characterized by a higher amount of reduced glutathione (GSH) and decreased lipid peroxidation (LPX), when the weight-at-age of 3-4-year old sprats was higher and contaminant exposure biomarker (EROD) was lower. Summer season conditions, which included cooler sea surface temperature (SST), higher bottom O2 and less cyanobacteria also indicated conditions for better oxidative status. Summer SST was additionally shown to affected glutathione metabolism enzyme activities. Oxidative status was associated with stable isotopes $\delta^{13}C$ and $\delta^{15}N$ indicating indirect effect of abiotic conditions and lower levels of the food web. Differences in condition factor and growth were associated with oxidative status in one and two sea winter salmon, respectively. Wild salmon survival was higher in years when they had higher GSH and catalase activity and lower LPX. Enhanced glutathione metabolism and increased protein carbonyls were associated with higher occurrence of yolk-sac fry mortality (M74). Our results show that oxidative status can provide information on exposure to complex combinations of environmental conditions and stressors in the wild and provide a link of physiological function to individual and population level fitness effects.

KEYWORDS: oxidative status, salmon, marine migration, Baltic Sea, environmental stress, ecophysiology

1 Introduction[3]

The fitness and recruitment of fish stocks can be markedly affected by present and future environmental disturbances. Climate change is predicted to be the dominant factor shaping aquatic food webs in the future as temperature has a fundamental influence on all levels of biological organization (Hochachka and Somero, 2002). The cumulative impacts of climate and other stressors in the aquatic ecosystems, including hazardous substances (Nikinmaa, 2013; Nikinmaa, 2014; Sánchez-Bayo et al., 2011) and eutrophication (Friedrich et al., 2014; Gasiunaite et al., 2005; Gooday et al., 2009) are projected to increase as well. Various environmental stressors may exert their impacts through direct effects on individual physiology and life history, and/or indirectly through changes in food webs and ecosystem structure. Therefore, better understanding of the integration of physiological and ecological processes requires linking experimental and observational results and ecosystem-level changes (Koenigstein et al., 2016; Portner and Peck, 2010; Rijnsdorp et al., 2009) and also studying individuals and populations in the wild. The co-occurrence of environmental

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[3] Abbreviations: B: Biomass, BB: the Bornholm Basin, BS: the Bothnian Sea, Carbonyls: protein carbonyls, CAT: catalase, GB: the Gotland Basin, GoF: the Gulf of Finland, GP: glutathione peroxidase, GSH: total glutathione, GSH/GSSG: reduced/oxidised glutathione ratio, GST: glutathione-S-transferase, GR: glutathione reductase, G6PDH: glucose 6-phosphate dehydrogenase, HER: herring, Hsurv: hatchery-reared Baltic salmon survival, LPX: lipid peroxidation, M74: Baltic salmon yolk-sac fry mortality syndrome, NAO: North Atlantic Oscillation, PCA: principal component analysis, SB: spawning stock biomass, SOD: superoxide dismutase, SPR: sprat, SW: age of salmon in sea years, TK: transketolase, WC: weight-at-age at 1-8 years, Wsurv: wild Baltic salmon survival

disturbances in aquatic ecosystems highlights the need for considering multiple stressors in physiological research for improving predictions of organismal responses to global change (Todgham and Stillman, 2013).

The anadromous life cycle exposes salmon to a variety of stressors in freshwater and marine environments. Populations worldwide are threatened by climate change, migration barriers, overexploitation, hazardous substances, and ecosystem changes. Examples include geographical range shifts, population declines, phenology changes, mortality during spawning migration and interactive effects of stressors such as temperature and disease, contaminants, or hypoxia (Crozier, 2015; Crozier, 2016; Crozier, 2017).

Understanding the effects of environmental stressors on salmon physiology during marine residence requires attention and is of global concern. Increased mortality in the North Atlantic has been associated with increased sea surface temperature, the Atlantic Multidecadal Oscillation, and altered zooplankton composition (Beaugrand and Reid, 2003; Beaugrand and Reid, 2012; Friedland et al., 2005; Friedland et al., 2009; Friedland et al., 2014; Peyronnet et al., 2008). Stachura et al. (2014) found complex patterns between indicators of oceanographic variability and the temporal abundance of 34 different salmon stocks. Thayer et al. (2014) reported that recent population crashes of California fall chinook may be linked to changes in diet. Malick et al. (2015) found associations between an early phytoplankton spring bloom and productivity of northern pink salmon (*Oncorhynchus gorbuscha*) populations. Studies attempting to link the effects of environmental drivers on physiological variables of adult salmon individuals during marine migration phase in the wild or the effects of individual physiological variables on survival or reproduction success are, however, lacking.

One of the indicators of limits to tolerance under environmental and life stresses is the increased demand for antioxidant defences for maintenance and repair, and oxidative stress (Costantini 2014; Portner et al., 2017; Portner and Peck, 2010). While the redox state and reactive oxygen species (ROS) play an important role in normal cellular signalling and ROS are produced in normal metabolism (Halliwell and Gutteridge, 2007), redox balance can easily be disturbed. Excess ROS damage cellular lipids, protein or DNA, and disrupt normal physiological functions (Halliwell and Gutteridge, 2007). Biochemically, oxidative stress is an imbalance between oxidants and antioxidants in favour of the oxidants, leading to a disruption of redox signalling and control and/or molecular damage (Sies and Jones, 2007), whereas biologically it can be defined to be any change in one of the molecular components of the redox system that has an effect on any metric of Darwinian fitness (Costantini, 2019). Oxidative stresses in marine environments may be caused by various abiotic and biotic changes including increased temperature (eg. Heise et al., 2006; Portner et al., 2017), hazardous substances (Regoli and Giuliani, 2014) and changes in the composition and transfer of non-enzymatic antioxidants in the food web (Häubner, 2010). Oxidative damage and increased or altered antioxidant defence may therefore be used as a general estimate for exposure to environmental stressors.

In the Baltic Sea region, warming is exceeding the global average, particularly in winter and in the northern areas. The projected atmospheric changes are accompanied by an increase in water temperature, reduced ice cover, and reduced salinity due to increased precipitation and river runoff (Meier et al., 2012; Räisänen, 2017; Vuorinen et al., 2015). The warming will likely enhance the negative effects of other environmental stressors, such as eutrophication and contamination, on Baltic Sea organisms (Räisänen, 2017). The feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea lasts one to four years, thus the conditions in the sea affect individual survival, health, and reproduction (Ikonen 2006; Vuori & Nikinmaa 2007; Vuori et al. 2008). Despite the positive outcomes of conservation efforts, Baltic salmon populations are still negatively affected by decreased post-smolt survival in the sea (ICES, 2018b) and yolk-sac fry mortality M74 (Keinänen et al., 2012; Majaneva et al., 2020; Mikkonen et al., 2011). Notably, Baltic salmon M74-related mortality increased in 2016–2017 (19-34%) after having remained at a much lower level (1–6%) in the five preceding years. Health issues (disease outbreaks of unknown cause) with large numbers of dead spawners and collapsed parr densities in some rivers were observed as well (ICES, 2018b). The first attempts to investigate physiological indicators of exposure to environmental stressors during feeding migration of the salmon in the Baltic Sea point out marked spatial environmental stressor-induced variation in biochemical and molecular indicators during salmon feeding migration (Kanerva et al., 2014; Vuori et al., 2008).

The main objective of this study was to relate the physiological condition and oxidative status of field-collected salmon to abiotic and biotic conditions that are expected to vary with regime shifts and climate change in the Baltic Sea. We hypothesize that environmental stressors including temperature increase, contamination, eutrophication and quality of prey affect Baltic salmon physiology leading to negative effects on the fitness of the individuals, and that selected antioxidant defence and oxidative damage biomarkers analysed from salmon from the wild can provide information on the exposure to these environmental stressors. We collected over 500 samples from four different Baltic Sea areas over the course of seven years and analysed them for eleven antioxidant defence and oxidative damage biomarkers. To our knowledge, this is the first study to report and compare temporal and spatial variation in physiological variables and their relation to environmental variables and fitness in salmon during the marine phase in the wild.

2. Materials and methods

2.1 Sample collection, characteristics

The salmon were caught during their marine migration in November-January from the International Council for the Exploration of the Sea (ICES) subdivisions 25 (the Bornholm Basin, BB), 28 (the Gotland Basin, GB), 30 (the Bothnian Sea, BS), and 32 (the Gulf of Finland, GoF) during the years 2006-2011, with the help of Finnish fishermen. Samples collected in 1999 from GB were obtained from the Environmental Specimen Bank, Swedish Museum of Natural History. The fish were killed with a blow to the head and the livers were excised, frozen immediately in liquid nitrogen (LN_2) and stored at -80 °C until analysis. The scales were collected from each fish for stable-isotope analyses, and for age and yearly growth determination. Fulton's condition factors (CF) were calculated with the formula: weight (g) / total length (cm) $^{3\wedge}$100.

2.2 Tissue homogenates

Pieces of liver about 0.5 x 0.5 cm in size were homogenized in 1.5 ml of 0.1M K_2HPO_4+ 0.15M KCl buffer (pH of 7.4) using a TissueLyser II Bead mill (Qiagen, Austin, USA). Aliquots of homogenate were pipetted into centrifugation tubes for reduced and oxidized glutathione (GSH and GSSG, respectively) measurements. The GSSG aliquot tubes contained a GSH scavenger; 3µM 1-methyl-2-vinylpyridinium trifluoromethanesulphonate (Sigma-Aldrich, St Louis, USA). Both tubes were frozen in LN_2 and stored at -80 °C. The rest of the homogenate was centrifuged for 15 min at 10 000 g in +4 °C and the supernatant was aliquoted to several centrifugation tubes, frozen in LN_2 and stored at -80 °C until further analyses. For lipid hydroperoxide determination a 15-20 mg piece of liver was homogenized in 300 µl methanol, centrifuged for 10 min at 5000 g at room temperature, and the supernatant was aliquoted and stored at −80 °C.

2.3 Determination of oxidative status

We used a multibiomarker approach for the determination of oxidative status including eleven measurements for enzymes and molecules preventing oxidative changes and markers of oxidative damage (Table 1). All measurements were done in triplicate using 96- or 384-well microplates. The inhibition rate of superoxide dismutase (SOD) was measured using a kit (Sigma-Aldrich). The measurement for catalase (CAT) activity was modified to microplate, by reducing the volumes, from the assay kit (Sigma-Aldrich). The glutathione peroxidase (GP) activity was measured with a kit (Sigma-Aldrich) using 2 mM H_2O_2 as a substrate. The glutathione reductase (GR) activity was measured according to (Smith et al., 1988). The glutathione S-transferase (GST) activity was measured according to (Habig et al., 1974), except that 2 mM GSH was used instead of 1 mM. Reduced:oxidized glutathione ratio (GSH/GSSG) and the concentrations of GSSG (treated with 1-methyl-2-vinylpyridium trifluoromethanesulphonate) and total GSH were determined using a reaction mix containing 1 mM dithiobisnitrobenzoic acid, 1 mM nicotinamide adenine dinucleotide phosphate and 2 U ml−1 GR in 100 mM sodium phosphate buffer + 5 mM EDTA (Tietze, 1969). Glucose-6-phosphate dehydrogenase (G6PDH) activity was measured as described by Noltmann et al. (1961). Transketolase (TK) activity was measured according to Hammes et al. (2003). The protein contents of the samples were determined with the Bradford method using Bio-Rad Protein Assay (Hercules, California, USA) with bovine serum albumin (Sigma-Aldrich) as the standard. The lipid hydroperoxides (LPX) were measured using the FOXII assay modified from the protocols described by Eymard and Genot (2003) and Bou et al. (2008) as described in Vuori et al. (2012). The LPX results were normalized with the masses of the liver pieces used in the sample preparation. The protein carbonylation was measured following protocol presented in Karjalainen (2013) and Rainio et al. (2015). The measurements were conducted with an EnVision Xcite microplate reader (Perkin-Elmer, Waltham, Massachusetts, USA). The average intra-assay and inter-assay coefficient of variations were 3.9% and 8.7% respectively. The GR, GP, GST, CAT, SOD, GSH and GSSG and G6PDH activity data of 2006 samples are from Vuori et al. (2008).

2.4 Sea years and back calculated growth

The scales were collected from the dorsal posterior surface from each fish for age determination (Hiilivirta et al., 1998; Shearer, 1992). Only the number of sea years (SW) was determined. The age was determined without prior knowledge of the size of the fish and problematic scales were evaluated by two separate persons. The growth of salmon in previous SW before capture can be evaluated from scales and the length at the capture time. For this, the most intact and symmetrical scales were selected and soaked in deionized water for 2–3 min, manually cleaned and impressed on polycarbonate slides. The scale radius and distance between focus and each annulus to the nearest millimetre was measured using a microfiche reader (Northwest Microfilm, Minneapolis, Minnesota, USA) with 25 times magnification. A measurement line according to Heidarsson et al. (2006) from scale focus towards the front edge of the scale was used. The Monastyrsky (Monastyrsky, 1926; 1930) regression model was used in the back-calculation of length after 1 and 2SW as cited in (Raitaniemi et al., 2000), using the following formula: Li=(Si/S)bL, where Li is the back-calculated fish length at the time of the annulus formation at age i, Si is the scale radius at the time of the annulus formation, S is the scale radius at the capture, b is a constant from power regression model (0.712, SE= ±0.288) and L is fish body length at capture. In the power regression model, the scale-length relationship from all scales was used, to obtain the constant b. The >2SW salmon were return spawners and weren't included in the growth analyses because of the possible measurement errors caused by spawning marks.

2.5 Environmental variables

Environmental variables, fitness/survival estimates, salmon stable isotope ratios and contaminant exposure biomarkers included in the study as explanatory factors were obtained from various databases and previously published work or measured in this study. The variables, justification for selection, and references for the data are listed in Table 2.

2.6 Statistics

R software, version 3.5.1 (www.r-project.org) was used for statistical analyses. Area-year interactions on biomarkers, stable isotopes, growth and condition factor were studied with two-way ANOVA and TukeyHSD post-hoc tests. A three-table ordination method, RLQ analysis (Dolédec et al., 1996) in ‘ade4’ package (Dray et al., 2007), was used for visualizing the associations between sample biomarkers and environmental data, and combined with false discovery rate corrected fourth-corner analysis (Dray et al., 2014) for final variable selection and statistical significances on biomarker axis - fitness estimate (H/Wsurv, M74) associations. First, principal component analyses (PCA) were done for both the biomarker and the environmental/fitness variables and a correspondence analysis was performed on the sample groups (presence-absence values for samples in different years). These three analyses were then passed to the RLQ function. The RLQs were first run with all environmental/fitness variables followed by a final analysis using five variables with highest and lowest scores on both axes and/or fdr-corrected significance $p \leq 0.05$ with biomarker axes. The effects of environmental conditions on biomarkers and their PCA scores general to all sea areas were studied with generalized linear mixed models, with Gaussian distribution and log link, using the function glmer in the package "lme4” (Bates et al., 2015). Environmental variables were used as fixed effects and sampling year and area as random factors. When selected environmental variables correlated, a sum/mean was used, or the reported model was selected based on AIC. Multiple regressions in Minitab 18 software (Minitab, LLC) were used for GSH-LPX, SW1cm - $\delta^{13}C$ and PCA score-$\delta^{13}C/\delta^{15}N$ associations with area as a cofactor. The distributions were checked before analyses and variables were transformed accordingly.

3 RESULTS

3.1 Sample characteristics

The number of samples included in the data analyses and the characteristics of the sample groups are shown in Table 3. The percentages of wild salmon were 60% and 67% for the BB and GB, respectively. The percentage of wild salmon was lower in the BS and especially in the GoF. The majority of the samples were 1SW fish. The 2SW fish were more abundant in the samples from the BB and GB than from other areas. Most of the >2SW fish were return spawners. Overview of the samples' stock composition is given in the supplementary material (Figure S1.) The ratios of wild vs hatchery-reared fish, the annual percentages of 1SW and ≥2SW salmon and the feeding area-specific stock composition (defined as river of origin based on genetic analysis) in our data are in line with the ICES Baltic Salmon and Trout Assessment Working Group reports (ICES, 2014, 2018b).

3.2 Abiotic and biotic conditions at the sea

The abiotic and biotic conditions varied between the study years (Figure 1). The cold season NAO was highest in 2008 and lowest in 2010. The winter and spring SSTs were 1.4-4 °C higher in 2008, the warmest year of our sampling period, compared to the coldest year of our sampling period, 2010, in the main feeding area, Baltic Main Basin (the BB and GB). The winter and spring SSTs were also high in 2007 in the BB and GB. The coldest year of the sampling period in the GoF and BS was 2006, and the warmest were 2008 and 2007.

The warmest summers of this study's time period were 2006 and 1999, and intensive cyanobacterial blooms were observed in both summers in the BB, in 1999 in the GB, and in 2006 in the GoF. The summer of 2008 was warm in the BB, GB and BS regions as well, and led to high biomasses of cyanobacteria in the GB and BS. The primary production (CHLP) was in general high in the summers 2007-2008 and low in 2006 and 2010.

The highest abundances of most of the zooplankton taxa in the BB in May were in 2007-2009 when the winter/spring temperatures and annual sea surface salinities were highest. Years of the highest levels of SummerCopepods in the BB were 2010-2011, and the highest levels of SummerCladocerans were in 2006 and 2011. The levels of SummerCopepods were highest in 2006 and lowest in 1999 in the GB, and SummerCladocerans were highest in 2008 and lowest in 2006.

SPRB and SPRSB were highest in 1999 and lowest in 2011. SPRWC1 and SPRWC2 were highest in 2008 whereas SPRWC3 and SPRWC4 were highest in 2009 and lowest in 2006. HERB and HERSB increased towards the end of the study period being highest in 2009-2010. Herring stock descriptors had their lowest values in 1999. (Figure 1)

The levels of contaminant exposure biomarkers in salmon liver varied temporally and spatially and the interaction of year and area on both variables is highly significant ($P<0.001$). EROD activity was highest in 2006 in the GoF. In general, higher values were measured in 2006 and 2008 and lower values in 2007 and 2009 in fish from all sea areas. DRE was highest in 2006-2007 in the GoF and in 1999 in the GB. (Figure 1).

The levels of stable isotopes in salmon scale samples varied temporally and spatially and the interaction of year and area on both variables is highly significant ($P<0.001$). $\delta^{13}C$ values were lowest in 2007 in all sea areas. $\delta^{13}C$ values were in general highest in 2008 and 2009 in the BB, BS and GB. In the GoF, $\delta^{13}C$ values had a different temporal pattern. Salmon from the GoF had significantly higher $\delta^{15}N$ values and salmon from the BS had significantly lower $\delta^{15}N$ values compared to those from the BB/GB. $\delta^{15}N$ values were highest in 2008 in the BB and BS, and in 2007 in the GB. $\delta^{15}N$ were in general lowest in 2006-2007 and 2010 in BB, BS and GB. The annual variation in $\delta^{15}N$ had a different temporal pattern in the GoF. (Figure 1).

3.3 Temporal variation in fitness estimates

Wsurv and Hsurv were highest in 1999 and lowest in 2006. W/Hsurv were higher in the coldest year (2010) compared to the warmest year (2008). M74 was highest in offspring of females which fed in the sea in 1999 and lowest (nearly absent) in females which fed in 2010. M74 mortality was also higher in females which fed in 2007 and 2008 compared to the females which fed in 2010. (Figure 1)

The interaction of year and area is highly significant ($P<0.001$) for 1SW growth (Table 4 A) which was lowest in northern sea-areas (BS, GoF) and the GB in 2008. While in the BB, 1SW growth increased from 2006 to 2009, was lowest in 2010 and returned to the same level as 2009 in 2011. Because of the smaller number of individuals, data for Baltic Main Basin sampling locations (the BB and GB) were combined for statistical analyses of annual differences in 2SW growth, which was significant ($P<0.05$). 2SW growth was lowest in fish caught in 2008 and highest in fish from 2007 and 2010 (Table 4 B). Likely due to the high variation, only the difference between 2007 and 2008 is significant in the post hoc analysis ($P<0.05$).

Lowest CFs were in the BB and GB in 2007 and 2008, and in the BS 2008 (Table 4 C-D). The mean CF of salmon from the BB and GB was significantly lower compared to salmon from the GoF. In the BS salmon, CF was at the same level as in the GoF in 2006-2007 and at the same level with the BB and GB in 2008-2009.

3.4 Temporal and spatial variation in biomarkers

The results indicate marked temporal and spatial variation in the antioxidant defence and oxidative damage biomarkers of salmon feeding in the Baltic Sea (Figure 2). The interaction of year and area is highly significant ($P<0.001$) for all biomarkers except for G6PDH, where it was significant ($P<0.05$) and for TK, where it was not significant. The TK activity is significantly higher in the BB samples compared to other areas ($P<0.001$). GST and GR activities were especially high in all sea areas in 2008, but also in 2007 and 2011 compared to years 2006 and 2010. GP activity was high especially in 2008. Higher LPX levels were detected in 2006, 2007 and 2011 whereas GSH levels were low in 2006 and 2007 and increased towards year 2010. The PCA of associations of biomarkers in all sea areas and years are shown in the supplementary material Figure S2 and Table S1. The sample scores of the biomarker PCA (first and second axes) were used in further analyses and are denoted as OS1 (glutathione metabolism variables and Carbonyls) and OS2 (GSH, CAT, LPX, G6PDH).

3.5 Associations of biomarkers with environmental variables and fitness

Antioxidant defence and oxidative damage biomarkers associated with environmental data and fitness estimates were visualized with RLQ in the important feeding area, the BB. RLQ was done separately for 1SW and 2SW fish (Figure 3 A-B, supplementary material Table S2, significances model2 $P=0.13$, model4 $P<0.001$, and model2 $P<0.05$, model4 $P<0.001$ for 1SW and 2SW fish). High glutathione metabolism enzyme activities (GST, GR and GP) were associated with low GSH/GSSG on the RLQ x-axis in both 1SW and 2SW fish. An inverse relationship between LPX and GSH, and an association of CAT and Carbonyls with PC2 on the y-axis, were also apparent in both RLQs. Variables with the highest PC2 loadings included CF in 1SW and growth in 2SW salmon. In 1SW salmon CF was in inverse relation with growth (CF was not included in other final RLQs as it had low scores on both axes and thus did not provide additional information). The common, most influential environmental variables based on the highest/lowest loadings on the RLQ x-axis in both 1SW and 2SW fish were SPRWC3, SPRWC4, HERWC4 and bO2 in inverse relationship with summerSST and autumnSST, cyanobacteria and SPRSB. The environmental and fitness variables with highest loadings found on both the 1SW and 2SW RLQ y-axes were high Wsurv and Hsurv and HERB in inverse relationship with high M74 estimates and high SPRWC7. The associations of survival and M74 estimates (Wsurv, Hsurv, M74_31, M74_30) with the biomarker y-axis, including LPX and Carbonyls, GSH and CAT as the most important determinants based on variable loadings, were highly significant (*P*<0.001 in fourth-corner tests between the RLQ biomarker y-axis and the estimates).

Variations in biomarkers associated with environmental data and fitness estimates were also visualized with RLQ in the GoF, where previous studies suggest increased environmental stress (Kanerva et al., 2014; Vuori et al., 2008) (Figure 3 C and supplementary material Table S2, significances model2 *P*=0.059, model4 *P*=0.001). High GSH, GSH/GSSG and GR activity were associated with high HERB, HERSB, SPRWC3, SPRWC4, HERWC4 and high survival in an inverse relationship with growth, increased oxidative stress (LPX, Carbonyls), high cyanobacteria, high autumnSST and high M74_30 on the x-axis. The associations of survival and M74 estimates (Wsurv, Hsurv, M74_30) with the biomarker x-axis were highly significant (*P*<0.001 in fourth-corner tests between the RLQ biomarker x-axis and the estimates). The environmental variables with highest loadings on y-axis were summerSST and SPRSB in inverse relationship with NAO, springSST and bottom/surface oxygen variables, which associated with EROD, SOD and CAT in an inverse relationship with GST and G6PDH.

We next studied the generalizations of the most evident associations between biomarker and environmental/fitness variables in all sea areas and samples. The selection was made based on the results of RLQ analyses (with a focus on variables with highest component loadings), literature about Baltic Sea ecosystem, and data availability. The amount of GSH was significantly associated with mean SPRWC3 and SPRWC 4 (Figure 4 A) (*P*<0.001, *t* = 7.150) but not with SPRSB. The value of LPX was significantly inversely related to the amount of GSH (*P*<0.001 *f*(4,568) = 19.88). GST and GR activities appeared to decrease significantly as a result of higher summer temperature (*P*<0.001 *t*= -4.555, *P*<0.001 t= -4.088) (Figure 4 B and C). We could not test associations between cyanobacteria and biomarkers due to different data units, but the associations between cyanobacteria and the biomarker axis was significant (*P*<0.001) in RLQs of 1SW salmon from the BB and GoF.

Back-calculated growth was available for salmon from years 2006-2011. Second sea year growth of 2SW salmon was significantly affected by winter, spring, summer and autumn SSTs (*P*=0.0017 *t* = 3.229 for the annual sum of SSTs). We didn’t find statistical significance between 1SW salmon growth and SST. CF was significantly inversely related to the winter, spring, summer SSTs (*P*<0.001 *t*= -4.263 for sum of January-August SSTs). OS2 was significantly (*f*(4) =2.69, *P*=0.031) associated with the growth of 1SW fish and OS1 was significantly (*f*(3) =25.04, *P*=0.002) associated with the CF of 1SW fish (areas the BB, GB and BS included) (Figure 4 D and E). We did not find statistically significant associations between 2SW salmon growth and OS1/2. The δ^{15}N value was significantly (*f*(4) = 14. 39, p<0.001) inversely related to the OS1 in the BB, GB and BS (Figure 4 F). The δ^{13}C value was significantly (*f*(4) = 10.91, *P*<0.001) inversely related to the OS2 (Figure 4 G) and growth (*f*(4,320) = 4.12, *P*=0.003 and *f*(4,85) = 3,16, *P*=0.018 for 1SW and 2SW fish respectively). OS2 was significantly (*P*=0.00315 *t*=-2.953) associated with the survival of wild salmon (Figure 4 H). OS1 was significantly (*P*=0.0137 *t*=-2.465) associated with M74_31 in 1SW salmon originating from 31 rivers (Figure 4 I), and the trend was the same in 2SW fish, but not significant likely due to the lower number of individuals. Associations between M74_30 and OS2 scores in salmon originating from 30 rivers were not tested due to a low number of eligible samples.

4 DISCUSSION

4.1. Spatial and temporal variation in Baltic salmon oxidative status is related to Baltic Sea ecosystem state

The Baltic Sea is a large body of brackish water with special hydrographical and climatic conditions (Feistel et al., 2008). Climate change has already influenced its ecosystem (ICES, 2019; Räisänen, 2017). A warming trend in SSTs and changes towards milder ice winters have been demonstrated. These, together with changes in salinity and the extent of hypoxic or anoxic deep water, will have an increasing influence on the ecosystem structure. Phytoplankton species composition and the timing of spring bloom have shifted, and summer phytoplankton blooms dominated by cyanobacteria have become more frequent and extensive (Hjerne et al., 2019; Suikkanen et al., 2013). Baltic zooplankton community composition and abundance are affected by hydroclimatic factors. Climate change associated shifts in species composition, from a shift in the dominance of large marine copepods to small neritic copepods and brackish cladocera, have been observed in the open sea, but with variation and differences between sub basins (Möllmann et al., 2000; Vuorinen et al., 2003). Although our dataset had an overall span of seven years, this period demonstrated exceptionally warm winters, springs, and higher chlorophyll versus cooler/normal winter and spring, and warm summers with intense blooms.

We found indications of better oxidative status characterized by a higher amount of reduced glutathione (GSH) and decreased lipid peroxidation (LPX), when the weight-at-age of 3-4-year old sprats was higher and the sprat spawning stock biomass was lower. Summer season conditions, which included cooler SST, higher bottom O_2, less cyanobacteria and higher amounts of copepods also characterized better oxidative status. Sprats' proportion in the food available for Baltic salmon has increased, except in the BS where herring is the main prey (Mikkonen et al., 2011) as the recent hydroclimatic regime has not supported a higher abundance of the large copepods which are selected by herring (e.g. Viitasalo et al., 2001). The density-dependence and availability of zooplankton are responsible for the temporal changes in the weight-at-age of the Baltic sprats and herring (Cardinale and Arrhenius, 2000; Cardinale et al., 2002; Rönkkönen et al., 2004). The known relationships between copepod abundance, sprat and herring stocks and weight-at-age strengthen the idea of better-quality salmon prey in the conditions favouring higher weight-at-age of 3-4 year sprats. The effect of changes in quality of prey species on the oxidative status of Baltic salmon was supported by the significant association between weight-at-age of 3-4 year sprats and the amount of GSH general to all sea areas where sprat is significant as salmon prey (the BB, GB, GoF). Moreover, there was an inverse connection between GSH and LPX. We also found an effect of summerSST on glutathione metabolism enzyme activity (GST and GR) later in the year in all sea areas, with a clear decrease of activity observed above approximately 18.5°C.

GSH/GSSG, which is lower for organisms experiencing oxidative stress, was in general low when the glutathione enzyme activities were high in our results (years 2007-2008 and 2011). Higher GSH/GSSG in 2006 despite the unfavourable conditions in the summer could be explained by colder preceding winter and spring, small sprat stock in preceding years, and lower contaminant exposure when compared to year 1999 (Vuori et al., 2008). In the GoF, higher GSH/GSSG was associated with higher GSH amount, higher GR and lower LPX.

GSH and glutathione metabolism enzymes are part of the first line defence against oxidative stress and one of the major cellular redox balance systems (Halliwell and Gutteridge, 2007). Glutathione metabolism responds to various oxidative stressors in fish, including temperature, contaminants and cyanobacterial toxins (Leggatt et al., 2007; Lushchak, 2011; Madeira et al., 2013; Złoch et al., 2018). Decreased GSH level have been found to be associated with increased LPX in fish with or without contaminant exposure (Ploch et al., 1999) and as a result of heat stress (Kaur et al., 2005; Parihar et al., 1996; Parihar et al., 1997).

We explored the influence of diet on the oxidative status by looking at the relationship between biomarkers and the stable isotope signature of the scales. $\delta^{13}C$ and $\delta^{15}N$ values differed between the sea areas as expected based on the previous studies (Kiljunen et al., 2008; Torniainen et al., 2014; Vuori et al., 2012). Notably, the indirect effect of abiotic conditions and lower levels of food web on salmon oxidative status is supported by the inverse association of δ^{13}C values with the OS2s in our data, including GSH and LPX as main variables, in all sea areas. The variation in δ^{13}C could result from changes at lower trophic levels, which are influenced by carbon sources for fixation and other abiotic and biotic parameters including water mass, SST, phytoplankton species composition, and differences in plankton biosynthesis and/or metabolism (Dempson et al., 2009; Torniainen et al., 2017). Interestingly, indications of differences between Baltic salmon stocks known to have partially different diets during marine phase were found for δ^{13}C, and CAT, a significant contributor to OS2, in a previous study (Vuori et al., 2012). CAT has an important role in redox balance, H_2O_2 removal, and its activity in fishes is affected by abiotic and biotic conditions, including temperature and diet, (Madeira et al., 2013; Martínez-Álvarez et al., 2005; Solé et al., 2010). δ^{15}N, in turn, was associated with OS1, indicative of glutathione metabolism, in all sea areas except the GoF. Apart from Vuori et al. (2012), there are no publications on the associations between stable isotopes and oxidative status in salmon. CAT and GST have been linked to fish species' trophic level (Solé et al., 2009), GST linked to δ^{15}N in barnacles (Laitano et al., 2018) and lower δ^{15}N connected to higher antioxidant capacity in gulls (García-Tarrasón et al., 2014).

4.2. Environmental stressors' effects on fitness through changes in oxidative status

In the wild, potentially stressful environmental factors exist as complex and variable regimes. They exert their effects on individuals directly or indirectly through changes in food webs or ecosystem structure. Such combinations of factors must be considered stressful when the performance, survival and fitness, of organisms are decreased. Organisms may respond to environmental stressors by using existing phenotypic plasticity for compensation, but this might nevertheless come at the expense of health, growth, or reproduction (Freedman, 2015; Portner et al., 2017; Portner and Peck, 2010; Schulte, 2014). Changes in oxidative balance have thus potential as indicator of life-history trade-offs and associations with reproduction and survival (Birnie-Gauvin et al., 2017; Costantini et al., 2010; Nikinmaa et al., 2013). The recent review by Birnie-Gauvin et al. (2017) suggests a significant role for oxidative stress and antioxidant defence in the life histories and fitness of fish but highlights a lack of linking studies. To our knowledge, the present results are the first reporting associations between oxidative status, individual-level fitness and population-level fitness estimates in salmon during marine migration.

We found significant links between biomarkers and salmon survival (H/Wsurv) and M74 estimates in RLQs of salmon feeding in the BB and GoF. In 2SW RLQ, 2nd sea year growth was related to higher survival and lower M74. Furthermore, we found a connection between oxidative status and Wsurv. In years when Wsurv was higher, the wild salmon from all sea areas had lower levels of LPX and higher levels of GSH and CAT activity, combined as OS2, compared to the years when Wsurv was lower. The years with highest survival are the ones with highest herring biomass as well as colder winter and spring temperatures. Conversely, when the survival was lower and M74 higher, the winter and spring temperatures were high.

Increased temperature and altered zooplankton composition have been reported to be associated with increased mortality of salmon feeding in the North Atlantic (Beaugrand and

Reid, 2003; Friedland et al., 2009; Peyronnet et al., 2008). In the Baltic Sea, Friedland et al., (2016) found Baltic salmon marine survival to be strongly negatively correlated with SST and positively with dissolved oxygen levels, with regional effects of salinity. Physiological mechanisms leading to adult marine mortality have not been established before, as studies linking environmental stressors to a disturbance in function are lacking.

In 1SW salmon originating from Bothnian Bay rivers, OS1, indicative of enhanced glutathione metabolism and increased protein carbonyls referring to increased oxidative damage, was associated with the occurrence of M74. It should be noted, that a substantial portion of ascending salmon especially in years 1999, 2007-2008 when the occurrence of M74 was higher, were 2SW based on the available data from the Tornio river (ICES, 2018b) corresponding to the 1SW fish in our study. It has been suggested that the unbalanced diet of eating mainly sprats and especially smaller sprats and to a lesser extent smaller herring increases the polyunsaturated lipid supply in the salmon diet and induces M74 through increased susceptibility to lipid peroxidation (Keinänen et al., 2017; Keinänen et al., 2012; Mikkonen et al., 2011). The changes in the amount of LPX in relation to the amount of GSH associated with weight-at-age of middle-sized sprats and herring biomass, and the connection of OS1 with M74 in our data are in line with these previous publications, although the analyses and timelines are different. OS1 was also related to CF in the BB, GB and BS. The increased sprat biomass in the Baltic Main Basin has been shown to have a connection to a high CF (> 1.05) of pre-spawning salmon, predicting high M74 (Mikkonen et al., 2011). More recent statistics, however, indicate that ascending females affected by M74 have a lower weight and CF suggesting a change in aetiology in recent years compared to the 1990’s, or origin-specific differences (ICES, 2018b). The mean CFs of salmon from the BB and GB in this study were lowest in 2007 and 2008, the same years when M74 was highest within the study period 2006-2011. Interestingly, Majaneva et al. (2020) recently demonstrated that M74 was associated with large-scale ecosystem changes in the southern Baltic Sea in 27-year time series and concluded that Baltic salmon reproductive success is affected by the abiotic conditions and food web composition preceding migration from the southern Baltic Sea to northern spawning rivers.

Growth is a profound part of fish fitness as it affects both mortality risk and reproduction. The adult marine growth in the wild might rather be optimized than maximized, because fast growth can have physiological costs/trade-offs. Atlantic salmon marine growth is sensitive to large-scale oceanic properties, including SST (Friedland et al., 2014), but the combined effects of different abiotic and biotic factors are largely unresolved (Forseth et al., 2010). Baltic salmon have been larger in size but lower in abundance during maritime, temperate climate regimes compared to continental, cold climate regimes (Huusko and Hyvärinen, 2012). Finally, as also our results suggest, oxidative stress is both a constraint and a cost of growth (Smith et al., 2016).

We found a direct temperature effect on the growth of 2SW fish, which grew less when the annual SST was highest (in 2008). This may be an indication of multi-sea winter Baltic salmon surpassing pejus temperature during marine residence on exceptionally warm years. We also found a possible indirect temperature effect on 1SW fish which grew more in the BB when the winter and spring SSTs were higher, but had lower CF. On the other hand, 1SW salmon grew less in the Northern Sea areas in 2008. The growth of 1SW salmon in particular was related to the value of $\delta^{13}C$, evidencing the importance of ecosystem effects on salmon growth in the natural environment, and indicating possibly different influences (ecosystem vs temperature) on 1SW and 2SW salmon. 1SW salmon growth and CF were associated with oxidative status.

The concentrations of contaminants have been declining in the Baltic Sea for several decades, but the amounts of several compounds still exceed the legal levels developed within OSPAR and the European Commission. For salmon, separate studies on fish collected from various parts of the Baltic Sea have been conducted, but no standardised long-term monitoring has been done. Polychlorinated biphenyls (PCBs), dibenzo-p-dioxins, dibenzofurans, and polybrominated diphenylethers (PBDEs) are the most commonly measured compounds in salmon (e.g. Airaksinen et al., 2015; Szlinder-Richert et al., 2009a; Szlinder-Richert et al., 2010; Szlinder-Richert et al., 2009b; Vuorinen et al., 2014; Vuorinen et al., 2017). Based on previous studies, it can be assumed that PCBs are higher in salmon from the GoF than in the fish from the BS, BB and GB (Hallikainen et al., 2011; Hallikainen et al., 2004; Vuorinen et al., 2012) and that PBDE levels are more similar throughout the Baltic Sea (Vuorinen et al., 2012). Contaminants are known to cause oxidative stress and weaken the antioxidant defence (e.g. Birnie-Gauvin et al., 2017; Lushchak, 2016) and therefore it can be assumed that fish from the GoF are especially affected. Our previous results support contaminant-associated increased environmental stress in the GoF salmon in 2006 (Kanerva et al., 2014; Vuori et al., 2008).

In this study, EROD activity had a negative connection with the same environmental variables which are associated with higher GSH and lower LPX level, including herring biomass and weight-at-age of 3-4-year old sprats and herring. Bignert et al. (1993) have found a strong negative correlation between herring fat content and organochlorine contaminant concentrations in the Baltic Main Basin. This fits with our RLQ analyses indicating higher EROD activity as biomarker of stronger exposure to contaminants, when HERWC3 and HERWC4 are lower.

Salmon feeding in the GoF, the most stressful ecosystem of the studied areas, may thus be mostly influenced by and susceptible to oxidative stress. It should be noted that the survival estimates and oxidative stress indicators were on the x-axis instead of the y-axis in RLQ for the GoF salmon, supporting the importance of the association in especially this area. Salmon from the other sea areas are known to feed in the GoF transiently (Kiljunen et al., 2008; Torniainen et al., 2014).

Oxidative stress may cause thiamine deficiency as thiamine can reduce oxidative damage by scavenging ROS and the thiamine requirement for pentose phosphate pathway enzyme cofactors may be increased (Gibson and Zhang, 2002; Lukienko et al., 2000). This may have importance for Baltic salmon as M74 is associated with thiamine deficiency (Keinänen et al., 2012; Mikkonen et al., 2011). We found no evidence of marked oxidative status-associated variation in TK activity. On the other hand, G6PDH, rate-limiting enzyme in the pentose phosphate pathway and a provider of NADPH for glutathione regeneration, was increased especially in the GoF in 2006-2007 and in the BB and GB in 2007 when more oxidative stress was present.

According to the concept of oxygen- and capacity-dependent thermal tolerance (Pörtner, 2010, 2012), all organisms specialize on a limited range of temperatures and functional disturbances occur beyond these ranges. Biochemical and physiological processes are involved in characterizing the various phases of thermal limitation. By combining biomarker, growth, and diet measurements with ecosystem data, we found direct temperature effects on the oxidative status and growth as GR and GST activities were affected by summer temperatures and 2SW growth by annual SST. However, our results strongly support the importance of indirect effects through the food web. We also found indications of additional modulation by hazardous substances (Nikinmaa, 2013; Pörtner, 2012). Jørgensen et al. (2014) found cardiac impairment in adult Atlantic salmon after extended exposure to 19°C in laboratory conditions. In our data, the temperatures exceeded 19°C in the BB and GB in July and August in 1999 and 2006 and in the BB, GB and GoF in July 2010. We found a drop of two key glutathione metabolism enzyme activities in the natural environment at temperatures below described for cardiac dysfunction.

5 CONCLUSIONS

In this study, we suggest links between oxidative status of adult Atlantic salmon in the sea and ecosystem-related phenomena. We demonstrate the importance of ecosystem state effect on oxidative status via quality of food in addition to direct temperature and contaminant effects. The oxidative status of salmon during their marine residency is thus an outcome of complex interactions including abiotic factors, lower food web composition, quality of prey, and additional stressors such as contamination, and may have a profound effect on fitness. The combination of antioxidant defence and oxidative damage biomarkers, stable isotopes, and growth measured from salmon at the sea bring together the effects of ecosystem state on salmon individuals. Oxidative status can thus provide information on exposure to complex combinations of environmental conditions and stressors in the wild and provide a link in physiological function to individual and population level fitness effects (Figure 5).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure 1. Heatmap illustrating the variation in the environmental variables, including mean contaminant exposure biomarkers, mean stable isotope values, and fitness estimates for the study years. Abbreviations as in Table 2. The warmest year of this study's period was 2008 and the coldest year 2010. The yellow – green colour scale indicates the highest – lowest values of the variables. White cells = no data in this study. The numeric values are given for selected variables only. The temperature and primary production data are given for the whole study period for the Baltic salmon main feeding area, the Baltic main basin (the BB and GB), whereas only the years with collected salmon samples are shown for the BS and GoF.

Figure 2. Annual mean(ci) antioxidant defence and oxidative damage biomarkers from salmon samples collected from four areas in the Baltic Sea: the Southern Main Basin (BB), the Eastern Main Basin (GB), the Bothnian Sea (BS) and the Gulf of Finland (GoF). Abbreviations as in Table 1. Significant differences between years and areas are denoted with letters.

Figure 3. First two axes of RLQ analysis: Scores of A) 1SW and B) 2SW salmon samples from the BB and C) 1SW salmon samples from the GoF, loadings for environmental- and fitness variables and antioxidant defence/oxidative damage biomarkers (multiplied by six for fit in the same graph). Abbreviations as in Table 1 and 2. Biomarkers purple, abiotic environmental variables blue, biotic environmental variables turquoise, fitness variables yellowgreen.

Figure 4. Significant relationships of Baltic salmon oxidative status biomarkers with selected environmental and fitness variables. Abbreviations as in Table 1 and 2.

Figure 5. Conceptual model/summary of the effects of the abiotic and biotic environmental variables on salmon oxidative status and associations with fitness variables and estimates based on the study results. Abbreviations as in Table 1. and 2.

Table 1. A summary of antioxidant defence and oxidative stress biomarkers used in the study, their functions and interpretation. O_2^{-} = superoxide radical, H_2O_2 = hydrogen peroxide.

Biomarker	Function	Interpretation
GSH	Antioxidant, thiol buffer and major cellular redox balance system	↑ indicates increased anti-oxidative function
GSH/GSSG	Glutathione redox state	Low ratio or increase in GSSG indicates stress
GST	Conjugation and detoxification of harmful compounds	↑ indicates increased anti-oxidative function
GR	Reduces GSSG back to GSH	↑ indicates increased anti-oxidative function
GP	Reduces H_2O_2 and lipid peroxides to water and lipid alcohol	↑ indicates increased anti-oxidative function
SOD	Part of enzymatic defence to remove O_2^{-}	↑ indicates increased anti-oxidative function
CAT	Part of enzymatic defence to remove H_2O_2	↑ indicates increased anti-oxidative function
LPX	Oxidative degradation of cellular lipids, resulting in cell damage	↑ indicates increased oxidative stress
Carbonyls	Modification of amino acid side chains to carbonyl derivatives (aldehydes and ketones)	↑ indicates increased oxidative stress
G6PDH	Rate-limiting enzyme in pentose phosphate pathway. Provides NADPH for the regeneration of glutathione	↑ in oxidative stress
TK	Connects the pentose phosphate pathway to glycolysis, necessary for production of NADPH.	Activity is dependent on the level of cofactor thiamine

Table 2. A summary of environmental and fitness variables in the study, justification for use and data sources. Variables are shown in the same order as discussed in the Results Section 3.2 except for surface and bottom oxygen and salinity.

Variable	Justification	References	Available data
North Atlantic Oscillation index (NAO)	Long-term changes in Atlantic salmon marine survival associated with NAO.	Beaugrand & Reid, 2003, 2012; Friedland et al. 2005, 2009; Peyronnet et al., 2008	NOAA standardized seasonal mean NAO index during cold season (January-March). (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml).
Sea surface temperature, sum of selected months (SSTwinter Jan-Feb, SSTSpring Mar-May, SSTsummer Jun-Aug, SSTautumn Sep-Nov)	Long-term changes in Atlantic salmon marine survival associated with Sea surface temperature (SST). Decreased marine survival associated with high SST in Baltic salmon.	Beaugrand & Reid, 2003, 2012; Friedland et al., 2005, 2009, 2016; Peyronnet et al., 2008;	The Met Office Hadley Centre's sea ice and sea surface temperature (SST) data set (Rayner et al., 2003).
Bloom forming cyanobacteria (*Nodularia*, *Aphanizomenon* and *Dolichospermum* (previously *Anabaena*); Cyano)	Potential risks of cyanobacterial toxins for high-trophic-level consumers through bioaccumulation in the food web.	Lehtinen et al., 2016	Phytoplankton community data from Swedish Meteorological and Hydrological Institute (SMHI; www.smhi.se, biovolume concentrations (mm3/l)) and International Council for the Exploration of the Sea (ICES; www.ices.dk, biomass cell volumes (ug/l)) web databases.
Summer chlorophyll-A (CPHL)	Primary production estimate, increased nutrient load stimulates eutrophication in the Baltic Sea.	Lehtinen et al., 2016	Summer (Jun-Aug, except station C3 in the BS in 2007 where Sep 3rd value was used because of absence of Aug values) surface (0-10m) chlorophyll-A for offshore stations BY5 (the BB), BY15 (the GB) and C3 (BS) from Swedish Meteorological and Hydrological Institute (SHMI) data service (www.shmi.se). Summer chlorofyll-A in HELCOM area Gulf of Finland from ICES Datasets (www.ices.dk; The International Council for the Exploration of the Sea, Copenhagen. 2014).

Zooplankton community (SpringCopepods, SpringCladocerans, SummerCopepods, SummerCladocerans)	Long-term changes in Atlantic salmon marine survival associated with changes in the zooplankton community composition. Zooplankton species composition in Baltic Sea varies spatially and temporally in relation to salinity and temperature changes and may affect the Baltic salmon indirectly by altering the composition and/or chemical quality of the diet.	Beaugrand & Reid, 2003, 2012 Baltic: Flinkman et al., 1998; Hernroth & Ackefors, 1979; Möllmann et al. 2000; Ojaveer et al. 1998; Vuorinen et al., 1998, 2003	Bornholm Basin (BY5) zooplankton community data for spring (May) and summer (August) from Leibniz Institute for Baltic Sea Research (IOW, www.io-warnemuende.de) and SHMI (www.smhi.se). Gotland basin (BY15) zooplankton community data for summer (August) "Finnish Baltic Sea Monitoring: Zooplankton abundance data collected by the Finnish Institute of Marine Research (1979-2008) and the Finnish Environment Institute Marine Research Center (2009-onwards)" (http://www.st.nmfs.noaa.gov/plankton/data/fimr/index.html) and year 2009 from SHMI. Biomass/m^3. Zooplankton data were not available for the GoF for all study years and is therefore not included.
Sprat (*Sprattus sprattus*) stock biomass (SPRB, SPRSB) and weight-at-age (SPRWC1-8)	All age groups of sprat are Baltic salmon prey. Increase in sprat stock biomass and feeding especially young sprat associated with higher incidences of Baltic salmon M74 yolk-sac fry mortality.	Hansson et al., 2001; Mikkonen et al., 2011	Total biomass, spawning stock biomass, mean weight-at-age. (ICES, 2018a)
Herring (*Clupea harengus*) stock biomass (HERB, HERSB) and weight-at-age (HERWC1-5)	Herring age groups of <19 cm length (1-5 years) are Baltic salmon prey.	Hansson et al., 2001; Mikkonen et al., 2011	Total biomass, spawning stock biomass, mean weight-at-age. (ICES, 2018a)

Ethoxyresorufin-O-deethylase activity (EROD), DNA-binding of Aryl Hydrocarbon Receptor to the dioxin response element (DRE)	Biomarker of organochlorine contaminant exposure (CYP1A enzyme activity). DRE measures transcription factor complex binding to the dioxin response element in DNA. An increase in the concentrations of particular organochlorines in salmon muscle coincident with the outbreak of M74 at the start of the 1990s from enhanced feeding on sprat.	Vuori et al., 2008; Vuorinen et al., 2002	EROD activity was measured according to Burke & Mayer (1974) and Vuori et al. (2008) from all samples. DRE was evaluated from nuclear extracts using electro mobility shift assay (EMSA), following the method described in Vuori et al. (2004) from samples collected in 1999, 2006-2010.
Stable isotopes δ^{13}C and δ^{15}N	Outcome of the recent year's ecosystem state and food web structure on salmon.	Kiljunen et al., 2020; Torniainen et al., 2014	δ13C and δ15N were analysed from scales of samples collected in 2006-2010 as described in Vuori et al. 2012.
Wild and hatchery-reared Baltic salmon marine survival (Wsurv, Hsurv)	Decline in Baltic salmon survival rates during the marine phase has been a key parameter affecting the dynamics and recruitment of Baltic salmon populations in recent decades.	Friedland et al., 2016	Survival at the sea (%) (ICES, 2018b)
Baltic salmon yolk-sac fry mortality (M74) in Swedish and Finnish salmon	Decreased offspring survival may result in decreased stock	Keinänen et al., 2012; Majaneva et al., 2020; Mikkonen et al.,	M74 yolk-sac fry mortality frequency (%) as a proportion of females with partial or total offspring M74 mortality in monitoring hatchery (ICES, 2018b). M74 estimates were averaged for the Bothnian Bay rivers (Simojoki, Torniojoki, Kemijoki, Luleälven, Skellefteälven, Umeälven) and

rivers in ICES areas 31 (Bothnian Bay) and 30 (Bothnian Sea) (M74_31, M74_30)	status. Reported associations with large-scale ecosystem changes, prey quality and abundance during feeding migration.	2011;	the Bothnian Sea rivers (Angermanälven, Indalsälven, Ljusnan, Dalälven). The yolk-sac mortalities of a specific year are given with a two-year time lag for the specific years compared to the original data.
Surface and bottom oxygen, surface and midwater salinity; May-June and July-October surface (1-10m) oxygen (sO2_56, sO2_710), Spring bottom oxygen (bO2), Spring surface (1-10m) and bottom (70-90m for Bornholm basin) salinity (SSS, S90)	Baltic salmon Survival was found to be positively correlated with dissolved oxygen levels and regionally related to shifts in salinity.	Friedland et al., 2016	HELCOM combine data for offshore stations in the study areas from International Council for the Exploration of the Sea (ICES; www.ices.dk) web database.

Table 3. The number and basic biological characteristics of salmon samples collected from four areas in the Baltic Sea: the Southern Main Basin (BB), the Gotland Basin (GB), the Bothnian Sea (BS) and the Gulf of Finland (GoF). Sex was not recognized in 50 fish. The origin of fish is based on DNA-analysis. NA = not available. RS = return spawners. Samples in 1999 were only from the GB.

Area		Variable	1999	2006	2007	2008	2009	2010	2011
BB		*n*		49	33	51	50	51	52
		*sex (**f**/m)*		31	33	47	43	38	48
		*Origin (**w**/h)*		23	21	25	35	32	NA
	Age compostion								
		0SW		0.00	0.00	0.00	0.00	0.06	0.04
		1SW		0.76	0.85	0.65	0.38	0.59	0.42
		2SW		0.20	0.12	0.29	0.50	0.28	0.39
		>2SW		0.04	0.03	0.04	0.12	0.08	0.15
		Unknown		0.00	0.00	0.02	0.00	0.00	0.00
		RS		0.04	0.03	0.02	0.14	0.10	0.12
GB		*N*	22	9	48	51	-	-	-
		*sex (**f**/m)*	NA	8	44	47	-	-	-
		*Origin (**w**/h)*	13	5	37	32	-	-	-
	Age compostion								
		0SW		0.00	0.04	0.02	-	-	-
		1SW		0.44	0.73	0.57	-	-	-
		2SW		0.56	0.13	0.31	-	-	-
		>2SW		0.00	0.10	0.10	-	-	-
		Unknown		0.00	0.00	0.00	-	-	-
		RS		0.11	0.10	0.12	-	-	-
BS		*N*		25	6	20	8	-	-

		*sex (**f**/m)*		20	5	18	7	-	-
		*Origin (**w**/h)*		8	3	13	6	-	-
	Age compostion								
		0SW		0.24	0.00	0.00	0.00	-	-
		1SW		0.56	0.83	0.85	0.50	-	-
		2SW		0.16	0.00	0.15	0.25	-	-
		>2SW		0.04	0.17	0.00	0.00	-	-
		Unknown		0.00	0.00	0.00	0.25	-	-
		RS		0.04	0.17	0.05	0.00	-	-
GoF		*N*		30	25	5	16	27	-
		*sex (**f**/m)*		18	21	5	12	22	-
		*Origin (**w**/h)*		5	10	0	7	5	-
	Age compostion								
		0SW		0.03	0.12	0.00	0.06	0.30	-
		1SW		0.97	0.88	1.00	0.69	0.56	-
		2SW		0.00	0.00	0.00	0.13	0.15	-
		>2SW		0.00	0.00	0.00	0.13	0.00	-
		RS		0.00	0.00	0.00	0.13	0.00	-

Table 4. A) 1SW growth, B) 2SW growth, C) 1SW condition factor and D) 2SW condition factor of salmon samples collected from four areas in the Baltic Sea: the Southern Main Basin (BB), the Gotland Basin (GB), the Bothnian Sea (BS) and the Gulf of Finland (GoF). Values are means (ci). Different lowercase letter indicates significant differences between either within areas or within years.

A)

Area	BB	GB	BS	GoF
Year				
2006 b	41.33(3.18)	42.13(3.55)	49.41(5.72)	47.13(2.12)
2007 ab	44.34(2.43)	44.17(2.77)	41.24(5.26)	42.09(3.02)
2008 ab	46.28(2.97)	40.15(2.62)	38.38(3.13)	40.23(6.97)
2009 b	48.44(5.28)	-	46.70(23.00)	43.65(3.58)
2010 a	40.61(3.44)	-	-	49.69(3.40)
2011 b	48.84(5.77)	-	-	-

B)

Area	BB	GB	BS	GoF
Year				
2006 ab	69.26(5.39)	74.22(24.30)	67.40(9.53)	-
2007 a	78.86(13.10)	78.07(11.61)	-	-
2008 b	66.33(6.17)	64.33(8.51)	49.37(96.96)	-
2009 ab	69.32(5.69)	-	58.11(158.98)	46.58(10.00)
2010 ab	75.66(11.15)	-	-	65.09(28.07)
2011 ab	71.02(3.08)	-	-	-

C)

Area	BB c	GB c	BS b	GoF a
Year				
2006 b	0.89(0.03)	0.93(0.16)	1.09(0.07)	1.15(0.04)
2007 c	0.77(0.03)	0.86(0.04)	1.14(0.12)	1.14(0.05)
2008 a	0.82(0.03)	0.73(0.03)	0.87(0.04)	1.09(0.21)
2009 bd	0.89(0.03)	-	0.95(0.10)	1.16(0.09)
2010 cd	0.84(0.03)	-	-	1.11(0.10)
2011 cd	0.85(0.03)	-	-	-

D)

Area	BB a	GB a	BS a	GoF a
Year				
2006 b	0.95(0.11)	1.11(0.18)	1.03(0.06)	-
2007 ab	0.80(0.14)	0.94(0.12)	-	-
2008 a	0.85(0.06)	0.80(0.06)	0.82(0.29)	-
2009 b	0.97(0.04)	-	1.03(0.34)	1.24(1.63)
2010 b	0.93(0.03)	-	-	1.05(0.43)
2011 b	1.03(0.09)	-	-	-

Credit author statement

Mirella Kanerva: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization

Mikko Kiljunen: Methodology, Formal analysis, Investigation, Writing - Original Draft

Jyrki Torniainen: Methodology, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing

Mikko Nikinmaa: Supervision, Resources, Writing - Original Draft, Writing - Review & Editing

Jörg Dutz: Data Curation, Investigation, Formal analysis, Writing - Original Draft

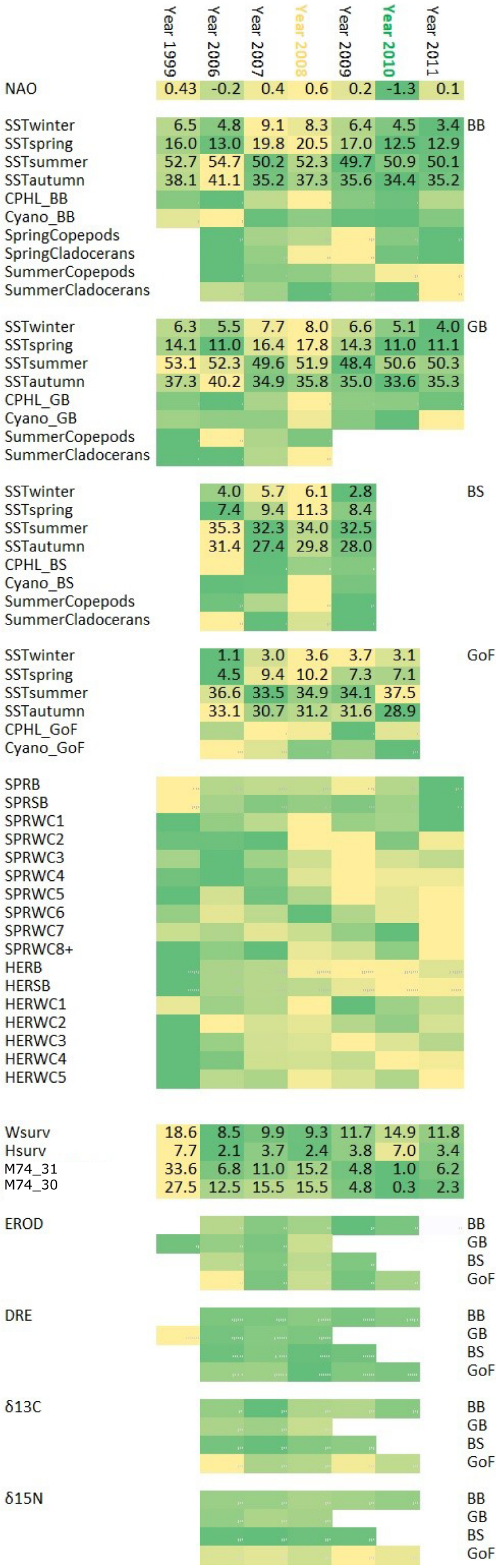
Kristiina Vuori: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Highlights

- We studied associations between oxidative status, environment and fitness in salmon.
- Salmon oxidative status varied temporally and spatially during marine migration.
- Abiotic and biotic conditions in the sea affected salmon oxidative status.
- Salmon condition, growth and survival were associated with oxidative status.



	Year 1999	Year 2006	Year 2007	Year 2008	Year 2009	Year 2010	Year 2011	
NAO	0.43	-0.2	0.4	0.6	0.2	-1.3	0.1	
SSTwinter	6.5	4.8	9.1	8.3	6.4	4.5	3.4	BB
SSTspring	16.0	13.0	19.8	20.5	17.0	12.5	12.9	
SSTsummer	52.7	54.7	50.2	52.3	49.7	50.9	50.1	
SSTautumn	38.1	41.1	35.2	37.3	35.6	34.4	35.2	
SSTwinter	6.3	5.5	7.7	8.0	6.6	5.1	4.0	GB
SSTspring	14.1	11.0	16.4	17.8	14.3	11.0	11.1	
SSTsummer	53.1	52.3	49.6	51.9	48.4	50.6	50.3	
SSTautumn	37.3	40.2	34.9	35.8	35.0	33.6	35.3	
SSTwinter		4.0	5.7	6.1	2.8			BS
SSTspring		7.4	9.4	11.3	8.4			
SSTsummer		35.3	32.3	34.0	32.5			
SSTautumn		31.4	27.4	29.8	28.0			
SSTwinter		1.1	3.0	3.6	3.7	3.1		GoF
SSTspring		4.5	9.4	10.2	7.3	7.1		
SSTsummer		36.6	33.5	34.9	34.1	37.5		
SSTautumn		33.1	30.7	31.2	31.6	28.9		
Wsurv	18.6	8.5	9.9	9.3	11.7	14.9	11.8	
Hsurv	7.7	2.1	3.7	2.4	3.8	7.0	3.4	
M74_31	33.6	6.8	11.0	15.2	4.8	1.0	6.2	
M74_30	27.5	12.5	15.5	15.5	4.8	0.3	2.3	

Figure 1

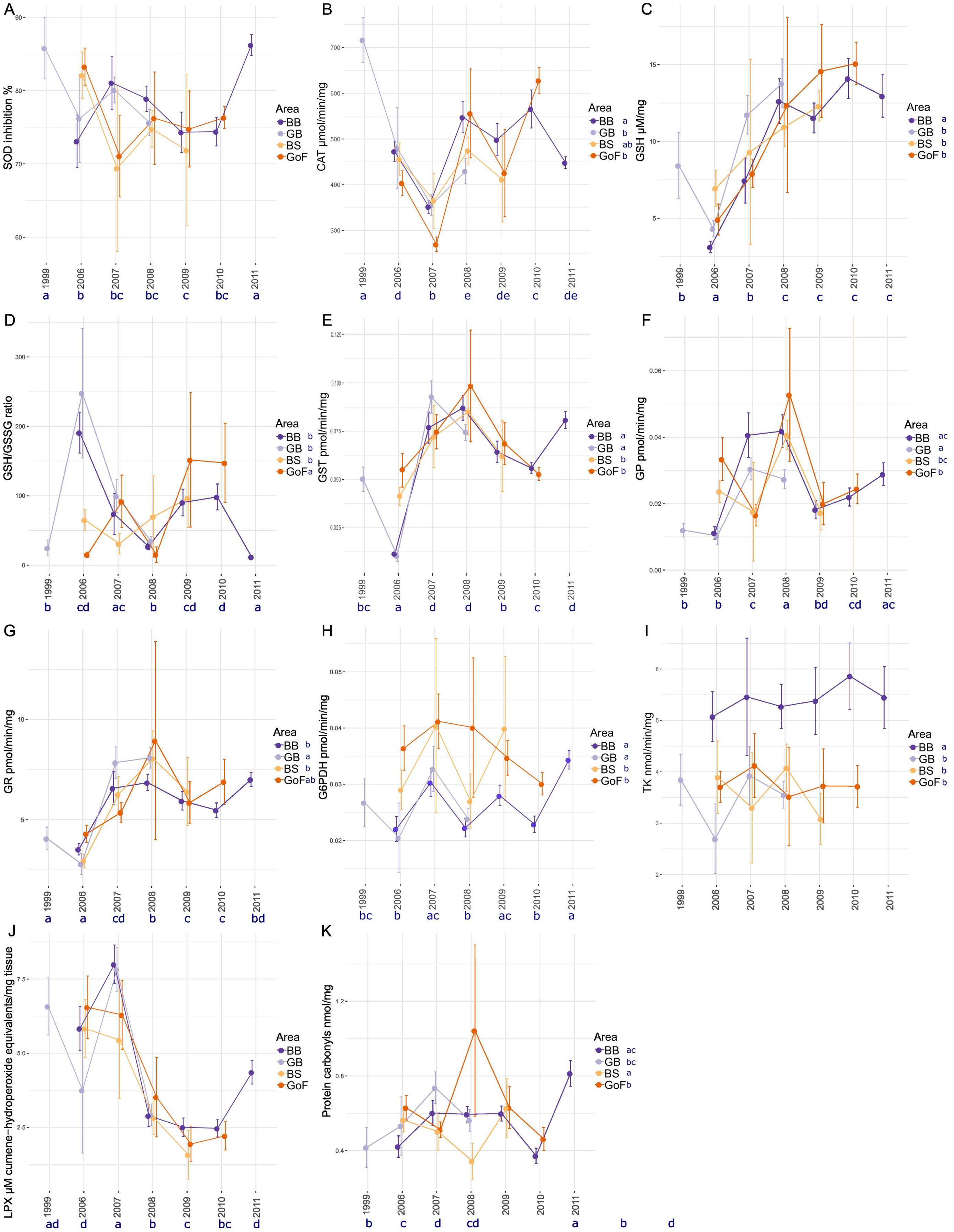

A
SOD inhibition %
Area
BB
GB
BS
GoF
1999 2006 2007 2008 2009 2010 2011
a b bc bc c bc a
B
CAT µmol/min/mg
Area
BB a
GB b
BS ab
GoF b
a d b e de c de
C
GSH µM/mg
Area
BB a
GB b
BS b
GoF b
b a b c c c c
D
GSH/GSSG ratio
Area
BB b
GB b
BS b
GoF a
b cd ac b cd d a
E
GST pmol/min/mg
Area
BB a
GB a
BS b
GoF b
bc a d d b c d
F
GP pmol/min/mg
Area
BB ac
GB a
BS bc
GoF b
b b c a bd cd ac
G
GR pmol/min/mg
Area
BB b
GB a
BS b
GoF ab
a a cd b c c bd
H
G6PDH pmol/min/mg
Area
BB a
GB a
BS b
GoF b
bc b ac b ac b a
I
TK nmol/min/mg
Area
BB a
GB b
BS b
GoF b
J
LPX µM cumene-hydroperoxide equivalents/mg tissue
Area
BB
GB
BS
GoF
ad d a b c bc d
K
Protein carbonyls nmol/mg
Area
BB ac
GB bc
BS a
GoF b
b c d cd a b d

Figure 2

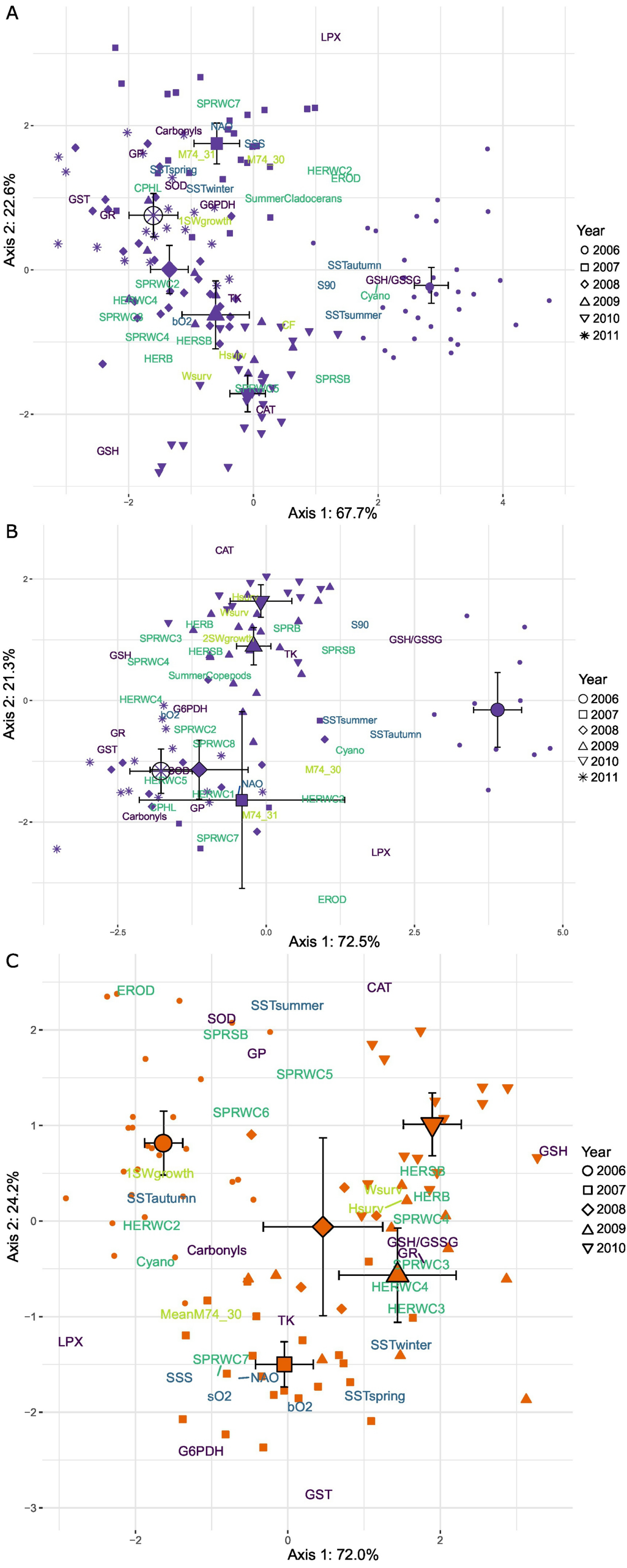

A
LPX
SPRWC7
Carbonyls
NAO
GP
M74_31
SSS
M74_30
SSTspring
HERWC2
EROD
CPHL
SOD
SSTwinter
GST
SummerCladocerans
G6PDH
GR
1SWgrowth
SSTautumn
S90
GSH/GSSG
Cyano
SPRWC2
TK
HERWC4
SSTsummer
SPRWC8
bO2
CF
SPRWC4
HERSB
Hsurv
HERB
Wsurv
SPRSB
SPRWC5
CAT
GSH
Axis 2: 22.6%
Axis 1: 67.7%
2
0
−2
−2
0
2
4
Year
○ 2006
□ 2007
◇ 2008
△ 2009
▽ 2010
✳ 2011
B
CAT
Hsurv
Wsurv
HERB
SPRB
S90
SPRWC3
2SWgrowth
GSH/GSSG
HERSB
TK
SPRSB
GSH
SPRWC4
SummerCopepods
HERWC4
G6PDH
bO2
SSTsummer
GR
SPRWC2
SSTautumn
GST
SPRWC8
Cyano
M74_30
SOD
HERWC5
NAO
HERWC1
HERWC2
CPHL
GP
M74_31
Carbonyls
SPRWC7
LPX
EROD
Axis 2: 21.3%
Axis 1: 72.5%
2
0
−2
−2.5
0.0
2.5
5.0
Year
○ 2006
□ 2007
◇ 2008
△ 2009
▽ 2010
✳ 2011
C
EROD
CAT
SSTsummer
SOD
SPRSB
GP
SPRWC5
SPRWC6
GSH
1SWgrowth
HERSB
Wsurv
SSTautumn
HERB
Hsurv
SPRWC4
HERWC2
GSH/GSSG
Carbonyls
GR
Cyano
SPRWC3
HERWC4
HERWC3
MeanM74_30
TK
LPX
SSTwinter
SPRWC7
SSS
NAO
sO2
SSTspring
bO2
G6PDH
GST
Axis 2: 24.2%
Axis 1: 72.0%
2
1
0
−1
−2
−3
−2
0
2
Year
○ 2006
□ 2007
◇ 2008
△ 2009
▽ 2010

Figure 3

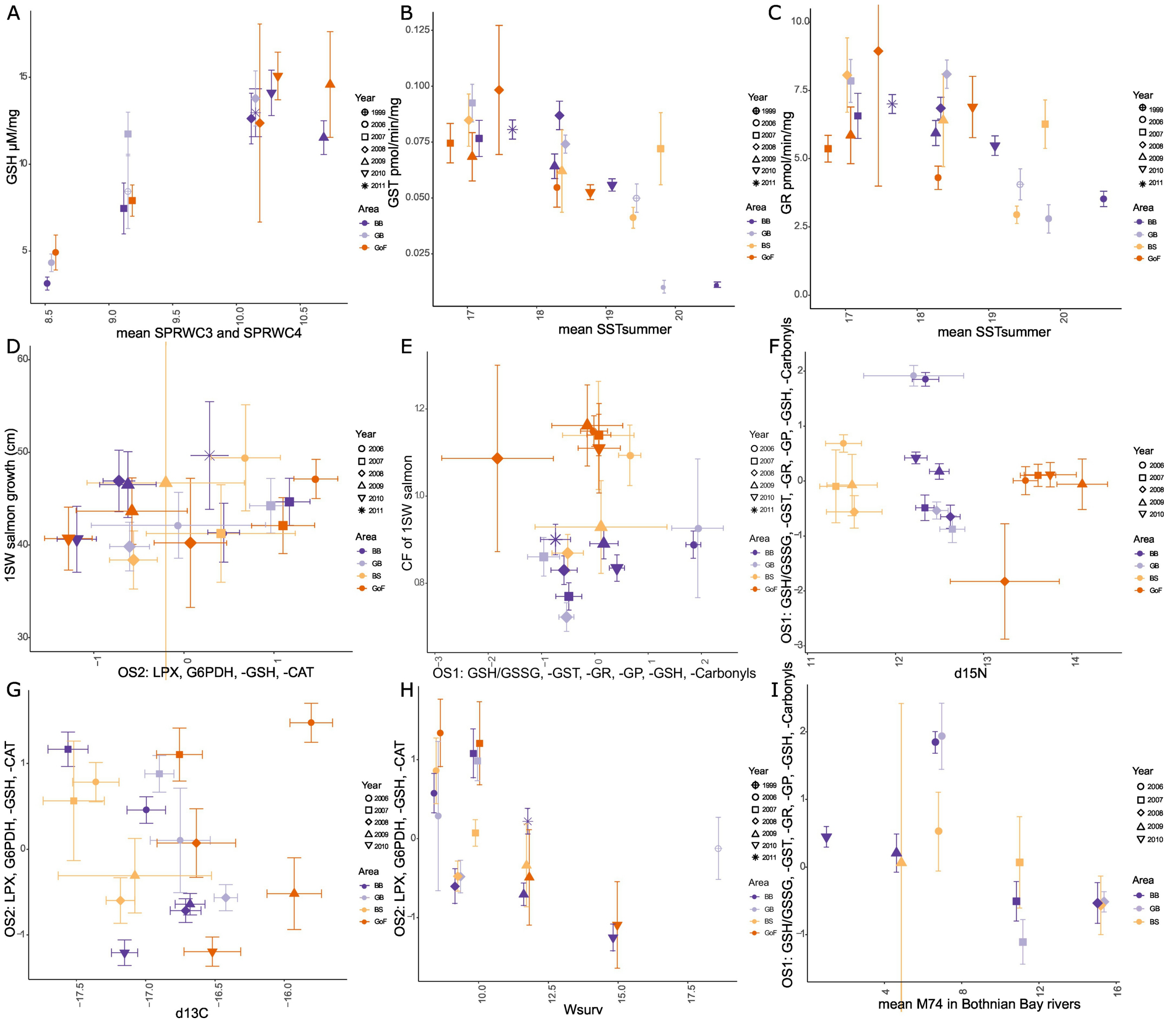

A
GSH µM/mg
mean SPRWC3 and SPRWC4
5
10
15
8.5
9.0
9.5
10.0
10.5
B
GST pmol/min/mg
mean SSTsummer
0.025
0.050
0.075
0.100
0.125
17
18
19
20
C
GR pmol/min/mg
mean SSTsummer
0.0
2.5
5.0
7.5
10.0
17
18
19
20
Year
1999
2006
2007
2008
2009
2010
2011
Area
BB
GB
BS
GoF
D
1SW salmon growth (cm)
OS2: LPX, G6PDH, -GSH, -CAT
30
40
50
60
-1
0
1
E
CF of 1SW salmon
OS1: GSH/GSSG, -GST, -GR, -GP, -GSH, -Carbonyls
08
10.0
12
-3
-2
-1
0
1
2
F
OS1: GSH/GSSG, -GST, -GR, -GP, -GSH, -Carbonyls
d15N
-3
-2
-1
0
1
2
11
12
13
14
G
OS2: LPX, G6PDH, -GSH, -CAT
d13C
-1
0
1
-17.5
-17.0
-16.5
-16.0
H
OS2: LPX, G6PDH, -GSH, -CAT
Wsurv
-1
0
1
10.0
12.5
15.0
17.5
I
OS1: GSH/GSSG, -GST, -GR, -GP, -GSH, -Carbonyls
mean M74 in Bothnian Bay rivers
-1
0
1
2
4
8
12
16

Figure 4

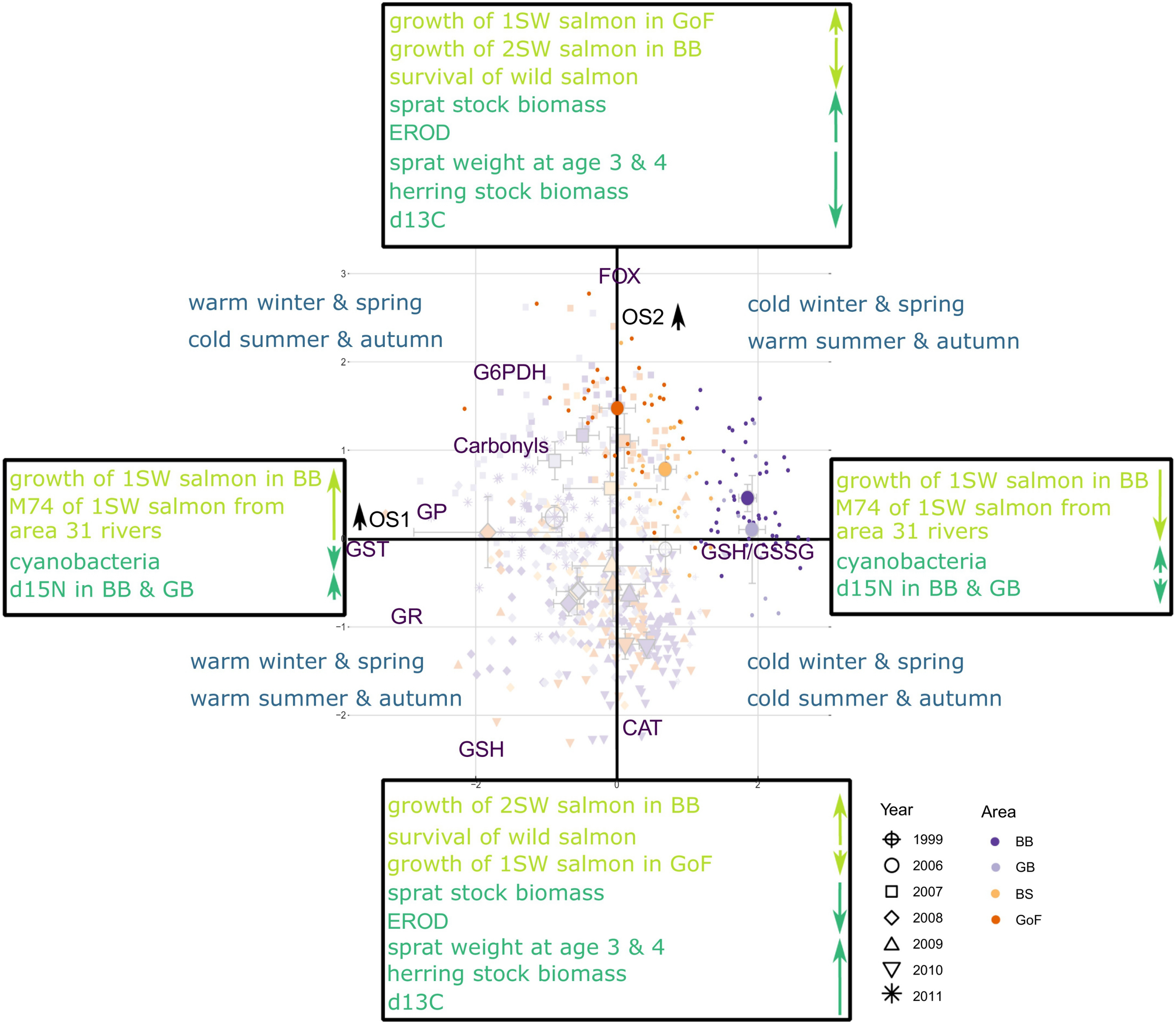

growth of 1SW salmon in GoF
growth of 2SW salmon in BB
survival of wild salmon
sprat stock biomass
EROD
sprat weight at age 3 & 4
herring stock biomass
d13C
FOX
OS2
warm winter & spring
cold summer & autumn
cold winter & spring
warm summer & autumn
G6PDH
Carbonyls
growth of 1SW salmon in BB
M74 of 1SW salmon from area 31 rivers
cyanobacteria
d15N in BB & GB
OS1
GP
GST
GSH/GSSG
growth of 1SW salmon in BB
M74 of 1SW salmon from area 31 rivers
cyanobacteria
d15N in BB & GB
GR
warm winter & spring
warm summer & autumn
cold winter & spring
cold summer & autumn
CAT
GSH
3
2
1
0
−1
−2
−2
0
2
growth of 2SW salmon in BB
survival of wild salmon
growth of 1SW salmon in GoF
sprat stock biomass
EROD
sprat weight at age 3 & 4
herring stock biomass
d13C
Year
1999
2006
2007
2008
2009
2010
2011
Area
BB
GB
BS
GoF

Figure 5