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Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation

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ABSTRACT

Atlantic salmon, *Salmo salar*, in the North Atlantic are managed as a set of population complexes distributed in North America and Europe. In recent years, these complexes have experienced reduced marine survival and many populations within the complexes are at risk, especially those at the southern ends of the species amphi-Atlantic range. Atlantic salmon is an anadromous fish dividing its life history between residence in freshwater and the marine environment. The freshwater portion of the life history includes spawning and the rearing of juveniles where in-river production has tended to be relatively stable, whereas the first year at sea, termed the post-smolt year, is characterized by more variable rates of mortality. Although their habitats are widely separated geographically along the North Atlantic seaboards, strong recruitment coherence exists between North American and European stock complexes. This recruitment coherence is correlated with ocean temperature variation associated with the Atlantic Multidecadal Oscillation (AMO). The North Atlantic Oscillation (NAO) appears to be relatively unimportant as a driver of salmon abundance. The mechanism determining the link between AMO-related thermal variation and abundance appears to differ fundamentally for the two continental stock groupings. Whereas ocean climate variability during the first springtime months of juvenile salmon migration to sea appears to be important to the survival of North American stocks, summer climate variation appears to be central to adult recruitment variation for European stocks. This contrast in seasonal effects appears to be related to the varying roles of predation pressure and size-related mortality on the continental stock complexes. The anticipated warming due to global climate change will impose thermal conditions on salmon populations outside historical context and challenge the ability of many populations to persist.

1. Introduction

Atlantic salmon, *Salmo salar*, is an anadromous fish native to rivers in North America and Europe. The present construct used in population assessment of salmon has been to combine river-specific populations into regional stock complexes sharing common demographic trends and climate-forced responses (ICES, 2011). Collectively, North American river populations, ranging from the Northeastern United States to Labrador, Canada, have been categorized as a single stock complex, whereas for European rivers the populations which range from Spain to Russia (and including Iceland) have been distinguished into Southern and Northern European stock complexes. The latter complex includes rivers throughout Norway, north and east Iceland, the northern coasts of Finland and Russia, and Atlantic Sweden. Rivers south of Sweden and including south and west Iceland, United Kingdom, Ireland, France and Spain comprise the Southern European stock complex. As an anadromous species, Atlantic salmon divides its life history between freshwater and marine habitats (Aas et al., 2011). Adults spawn in freshwater and juveniles are reared in headwater stream nursery areas, often for multiple years, until they reach sufficient size to smoltify, or transform into seawater-tolerant juveniles that can sustain the physiological transition from freshwater to marine life (McCormick et al., 1998). Smolts generally leave the rivers in springtime and embark on their first year at sea — the so-called post-smolt year. Mortality during the post-smolt year has proven to be the most variable source of mortality in Atlantic salmon populations, and thus is associated with patterns of adult recruitment and abundance (Hansen and Quinn, 1998).

The first analyses testing the effect of ocean climate variability on the abundance of Atlantic salmon stocks utilized the concept of thermal habitat (TH) or the area of the ocean surface within a thermal

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range. These analyses were applied first to changes in salmon abundance among index rivers in North America; the indications were that the first winter at sea was the main recruitment bottleneck for successfully returning adult salmon (Ritter, 1989). Those results were extended by using stock abundance indicators representing the entire stock complex and by expanding the geographic range of the TH analysis to encompass much of the northwest Atlantic (Condron et al., 2005; Friedland et al., 1993; Reddin and Friedland, 1993). These studies highlighted the distribution of sea surface temperature (SST) in the Labrador Sea during the first winter at sea as being critical for post-smolt salmon, and that constricted TH led to poor over-wintering survival. Further support for this hypothesis was derived from targeted research fishing which showed that the part of the Labrador Sea region associated with the variation in TH was also part of the distributional range of post-smolts during the months prior to winter (Reddin and Short, 1991).

The proposed environmental correlates between salmon abundance and winter TH have not, however, held because the survival of North American salmon has continued to decline over recent decades (Friedland et al., 2009b) whilst TH increased, thus prompting a re-examination of climate variability and the need for new explanations of these stock declines. In the early analyses, the region used to calculate the area of TH was a large region comprising most of the northwest Atlantic Ocean. Inshore areas, such as the Gulf of St. Lawrence, were not included. Furthermore, by using such a large area to calculate TH, any variability associated with thermal conditions in coastal ocean habitats would have been masked. Hence, the early correlative analyses did not effectively test for the impact of environmental variability on post-smolts in inshore coastal habitats associated specifically with their very first months at sea. Using improved data sources, including satellite data, it was found that the abundance of Atlantic salmon stocks in North America could indeed be associated with climate variability in the inshore areas of the Gulf of Maine and Gulf of St. Lawrence (Friedland et al., 2003a, 2003b, 2012a). These latter studies indicate that post-smolts in their first months at sea are subject to differing mortality risks associated with variation in SST conditions in these particular inshore coastal habitats.

In contrast to North American stocks, analyses of climate effects on the survival of the European stock complexes followed a rather different direction because of the limitations of observational SST datasets at high latitudes and a basic lack of knowledge of where post-smolts were distributed. Friedland et al. (1993) found that TH variation during springtime early in the post-smolt year was associated with the abundance of European salmon, but did not test for the effect later into the year. Analyses were restricted to springtime because of the paucity of the available datasets to reliably calculate TH in other seasons at higher latitudes. Moreover, at that time there was a lack of detailed knowledge of post-smolt distribution throughout the post-smolt year, so only inferences about spring distributions could be made with any confidence. This analysis was retested by Friedland et al. (1998) with a higher resolution environmental dataset, but again, the analysis was limited to springtime only. Two subsequent studies expanded our understanding of recruitment control for European stocks. First, Holm et al. (2000) reported on the results of research fishing for post-smolt salmon in the northeast Atlantic and defined the post-smolt summer nursery in the Norwegian Sea. Second, Friedland et al. (2005) found that summer post-smolt growth was highly correlated with corresponding SST for the post-smolt nursery region of the Norwegian Sea. These findings provided the basis for evaluating SST correlates over the northeast Atlantic area and through the balance of the post-smolt year (Beaugrand and Reid, 2003; Friedland et al., 2009a). Specifically, Friedland et al. (2009a) showed that European post-smolts are impacted by ecosystem-level changes in the summer nursery habitat associated with SST variation, in contrast to the North American stock complex where impacts of spring habitat appear to be critical to survival.

In the previous studies described above, stock abundance trends of salmon in North America and Europe have been examined in a complementary manner, but not comparatively. Here, we compare aspects of the aforementioned working hypotheses of seasonally differing recruitment control for the stock complexes — growth mediated survival in European stocks versus predator driven mortality in North American stocks. Specifically, we examine the extent of coherence between continental stock complex abundances, and evaluate the relative role(s) of climate drivers, with particular emphasis on SST variation.

2. Methods

2.1. Coherence of stock complex abundance trends

The recruitment of Atlantic salmon returning to freshwater can be assessed by examining trends in abundance of adult salmon, which represents the cumulative effects of marine mortality following juvenile emigration from their natal rivers. The stock complexes of Atlantic salmon have been assessed with a modified virtual population analysis – or run reconstruction analysis – that estimates the size of the stock at a point in time preceding the commencement of one sea-winter (1SW) fisheries; hence this abundance quantity often is referred to as pre-fishery abundance, PFA (Chaput et al., 2005; Potter et al., 2004). These PFA estimates are disaggregated by sea-age of return – 1SW (=early-maturing) and 2SW (non-maturing) – which themselves represent the two predominant maturation schedules displayed by these fish. The abundances are further disaggregated geographically into the aforementioned single stock complex for North American rivers and the distinct Northern and Southern European stock complexes. The set of estimates used in the present study were derived from the 2011 stock assessment (ICES, 2011), which are based on data collected up to and including 2010, noting that the Northern European stock complex time series is shorter than either of that for North America or Southern Europe because the assessment working group deemed the stock estimates for Norway to be unreliable for the smolt years 1970–1981 (ICES, 2001).

Recruitment coherence between the continental stock complexes was tested by Pearson product-moment correlation. The significance test requires that the data be distributed as a bivariate normal distribution (Sokal and Rohlf, 1981). The distributions of stock abundances were tested for normality (Shapiro–Wilk *W* statistic) and by inspection of frequency distributions and normal probability plots. Non-normal variables were log-transformed. The time series compared here 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, in notation 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. The probability associated with a correlation coefficient using the corrected degrees of freedom is designated p*. Trends in the proportion of a given stock complex following an early-maturing (1SW) or non-maturing (2SW) life history pattern were evaluated for each stock complex by computing the fractional abundance of the stock total.

2.2. Climate indicators and stock response

The patterns of recruitment for Atlantic salmon were compared to a set of broad scale indices of climate forcing known to affect the physical environment and biological populations across the North