

# Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations

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## Abstract

North American Atlantic salmon (*Salmo salar*) populations experienced substantial declines in the early 1990s, and many populations have persisted at low abundances in recent years. Abundance and productivity declined in a coherent manner across major regions of North America, and this coherence points toward a potential shift in marine survivorship, rather than local, river-specific factors. The major declines in Atlantic salmon populations occurred against a backdrop of physical and biological shifts in Northwest Atlantic ecosystems. Analyses of changes in climate, physical, and lower trophic level biological factors provide substantial evidence that climate conditions directly and indirectly influence the abundance and productivity of North American Atlantic salmon populations. A major decline in salmon abundance after 1990 was preceded by a series of changes across multiple levels of the ecosystem, and a subsequent population change in 1997, primarily related to salmon productivity, followed an unusually low NAO event. Pairwise correlations further demonstrate that climate and physical conditions are associated with changes in plankton communities and prey availability, which are ultimately linked to Atlantic salmon populations. Results suggest that poor trophic conditions, likely due to climate-driven environmental factors, and warmer ocean temperatures throughout their marine habitat area are constraining the productivity and recovery of North American Atlantic salmon populations.

**Keywords:** capelin, chronological cluster analysis, climate change, dynamic factor analysis, Northwest Atlantic, phytoplankton, regime shift, sea surface temperature, zooplankton

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## Introduction

A large and continually growing body of evidence shows that marine ecosystems are affected by changing climate conditions (e.g. Hoegh-Guldberg & Bruno, 2010; Doney *et al.*, 2012), and that climate-related ecosystem changes can directly and indirectly impact marine fish species and communities (e.g. Rose, 2005; Nye *et al.*, 2009; Lucey & Nye, 2010). Many past studies of fish-climate interactions have focused on species that complete their entire life cycle in the ocean with relatively limited migrations. Less attention has been devoted to understanding how climate conditions may affect anadromous fish that move between freshwater and marine environments or species that undertake extensive migrations. Pacific salmon represent an exception, and for these species, clear linkages between climate indices, physical conditions, and population parameters have been documented (Mantua *et al.*, 1997; Beamish *et al.*, 1999; Hare *et al.*, 1999; Hilborn *et al.*,

2003). In addition, Beaugrand & Reid (2003, 2012) have described how climate-related ecosystem changes have affected European populations of Atlantic salmon. However, the relationship between ecosystem conditions and North American Atlantic salmon populations has not been characterized, despite widespread declines in return rates (Chaput *et al.*, 2005) concurrent with an ecosystem reorganization that has been attributed to climate-driven, basin-scale oceanographic changes (e.g. MERCINA Working Group, 2012) and possibly top-down changes due to overfishing (e.g. Frank *et al.*, 2005).

Atlantic salmon have a broad geographic range throughout northern portions of the Atlantic Ocean and a complex life history that includes a freshwater juvenile phase, an extensive oceanic migration, and a return migration to freshwater for spawning (Thorstad *et al.*, 2011). While freshwater life stages are influenced by local conditions, large-scale changes in the marine environment can affect Atlantic salmon while they are at sea. North American Atlantic salmon are known to feed off west Greenland in the summer and overwinter in the Labrador Sea (Reddin, 1988; Thorstad *et al.*, 2011),

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and considerable mixing of stocks occurs in these areas (Reddin, 1988; Reddin & Friedland, 1999; Gauthier-Ouellet *et al.*, 2009; Sheehan *et al.*, 2012), which suggests that salmon from widely distributed rivers are subject to the same marine ecosystem influences.

Declines in Atlantic salmon populations have been observed throughout North America and Europe in recent decades, reaching critically low levels at the southern extent of their range (Parrish *et al.*, 1998). In North America, native populations in the southernmost areas have been extirpated since the 1800s, and many extant populations, including those in the Gulf of Maine, Bay of Fundy, and Scotian Shelf, are considered endangered (Kocik & Sheehan, 2006; COSEWIC, 2010). Declines have been more severe among fish that spend two winters at sea (termed two sea-winter fish, or 2SW) than those at sea for one winter (1SW) (Potter *et al.*, 2004; ICES, 2012). For North American populations, the 1SW cohort has shown strong oscillations and a decline since the late 1980s, but abundance of the 2SW cohort dropped precipitously (Fig. 1; ICES, 2012).

These widespread declines of Atlantic salmon have been attributed to a reduction in growth, production, and survival during the marine life stages (Jonsson & Jonsson, 2004). Chaput *et al.* (2005) demonstrated that a phase shift in productivity of North American Atlantic salmon occurred in the 1990s, likely the result of reduced marine survival. Despite substantial efforts to

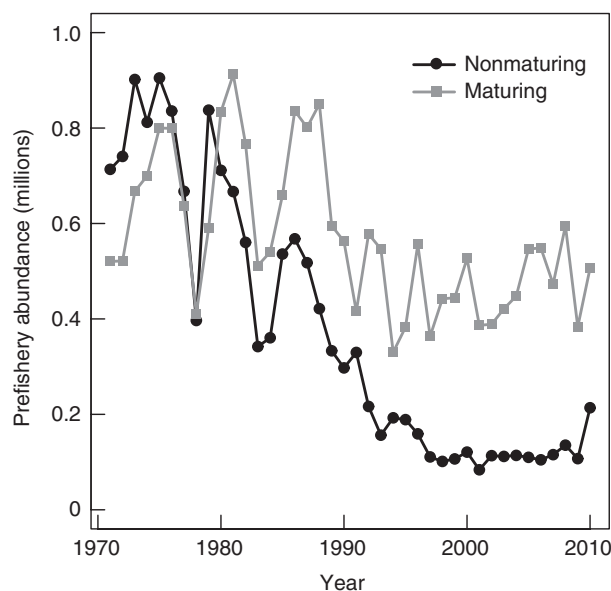
reduce fishing pressure and protect freshwater habitats, population abundance and productivity have remained at low levels. Many previous studies have focused on the importance of temperature in shaping North American Atlantic salmon population characteristics (e.g. Scarnecchia, 1983; Martin & Mitchell, 1985; Friedland *et al.*, 1993, 2003; Friedland, 1998; Reddin *et al.*, 2000; Miller *et al.*, 2012), but the implications of changes across multiple levels of the ecosystem have not been evaluated. An integrated understanding of how climate patterns and marine ecosystem conditions may have contributed to past Atlantic salmon population declines is critical for anticipating future population changes and for identifying conditions under which recovery of endangered populations may be feasible.

In this article, we adopt a broad geographic scope and multilevel ecosystem perspective to describe how North American Atlantic salmon populations have changed over time and to characterize associations with ecosystem conditions. We approach this effort by first assessing whether changes in salmon abundance and productivity occur coherently among regions spanning the North American range. We assume that populations behaving in a coherent manner are likely responding to common factors and, therefore, that consistent patterns across geographically disparate regions suggest a marine influence. To better understand how marine conditions may affect Atlantic salmon populations, we investigate associations between population trends and a suite of climate, physical, and biological factors in the Northwest Atlantic ecosystem. Results elucidate how climate shifts can directly affect Atlantic salmon, as well as how these effects propagate through the marine ecosystem. The findings provide insights into how Atlantic salmon and the marine ecosystems with which they interact may be affected by climate change in future decades.

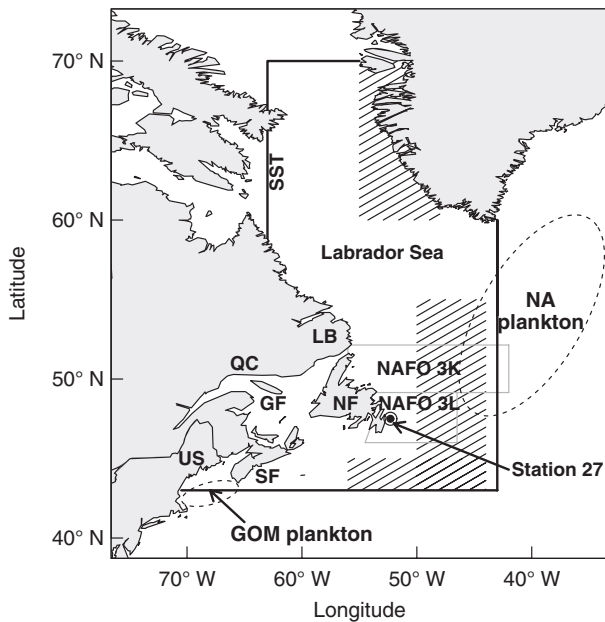
## Materials and methods

### *Atlantic salmon population data*

The North American range of Atlantic salmon historically extended from Ungava Bay, Canada, to Long Island Sound, United States. This geographic span is divided into six regions for assessment purposes – Labrador, Newfoundland, Quebec, Gulf of St. Lawrence, Scotia-Fundy, and United States (Fig. 2; ICES, 2012). Atlantic salmon stock complexes in these regions vary in abundance levels and life history characteristics (Chaput *et al.*, 2006). Historically, salmon abundance has been highest in Newfoundland, Quebec, and the Gulf of St. Lawrence, while abundance in the United States has been at least an order of magnitude lower. The United States and Quebec population complexes are predominantly composed of 2SW salmon (long-term 1SW : 2SW ratio of 1 : 5 and 1 : 2,



**Fig. 1** Time series of prefishery abundance of North American Atlantic salmon for 1SW maturing and 1SW nonmaturing population cohorts. The maturing portion of the complex will return to spawn as 1SW adults while the nonmaturing fish will spawn as 2SW adults.



**Fig. 2** Map of North American range of Atlantic salmon showing the location of six regions represented by salmon abundance and productivity estimates (US, United States; SF, Scotia-Fundy; NF, Newfoundland; GF, Gulf of St. Lawrence; QC, Quebec; LB, Labrador); salmon overwintering (shaded diagonals off of Newfoundland) and summer feeding (shaded diagonals off of Greenland) grounds; boundaries of areas from which sea surface temperature (SST), Gulf of Maine (GOM) and North Atlantic (NA) plankton, and capelin (NAFO areas 3K and 3L) data were retrieved; and the location at which surface salinity data were obtained (Station 27).

respectively) (ICES, 2012). In contrast, complexes in Newfoundland (11 : 1), Labrador (6 : 1), Gulf of St. Lawrence (1.7 : 1) and Scotia-Fundy (2.5 : 1) are dominated by 1SW returnees (ICES, 2012).

The abundance and productivity of Atlantic salmon stocks are estimated by ICES each year using a modified virtual population analysis that reconstructs salmon populations based on observed catches and returns to natal rivers (Rago *et al.*, 1993; Potter *et al.*, 2004; Chaput *et al.*, 2005; ICES, 2012). Populations in the six regions are considered in generating an overall assessment of the entire North American stock. Abundance values represent the estimated median number of *nonmaturing* 1SW fish before they encounter the fishery off West Greenland (termed the prefishery abundance (PFA); ICES, 2012). These fish are destined to become 2SW or multi-SW spawners in their natal rivers in subsequent years. Productivity is tracked by scaling the PFA in each year by the number of contributing 2SW spawners (e.g. productivity index =  $\ln(\text{PFA}/\text{lagged spawners})$ ). Lagged spawners are computed by lagging forward the number of 2SW spawners based on region-specific smolt age distributions (Rago, 2001; ICES, 2007) to index the parental stock contributing to each subsequent PFA cohort (Chaput *et al.*, 2005). The productivity index represents

survival from freshwater life stages to PFA. In this analysis, we use regional estimates of Atlantic salmon abundance and productivity from the 2012 assessment model (ICES, 2012); abundance values span 1978–2010, while the productivity time series extends through 2008 so that the model results are grounded in observations, instead of relying on forward projections.

### Ecosystem variables

Three types of variables were used to represent ecosystem conditions that may affect Atlantic salmon populations: (i) large-scale climate indices characterized by the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO); (ii) physical conditions (i.e. temperature and salinity); and (iii) biological conditions (i.e. phytoplankton, zooplankton, and prey fish).

**Climate indices.** Two climate indices that represent large-scale forcing over the Northwest Atlantic and Labrador Sea were considered in our analyses. The Atlantic Multidecadal Oscillation (AMO) characterizes variability in sea surface temperature (SST) in the North Atlantic, which is thought to be driven by variation in the strength of global thermohaline circulation (Delworth & Mann, 2000). The AMO influences weather patterns across the entire Atlantic basin, with particularly strong SST anomalies near Newfoundland and Greenland (Sutton & Hodson, 2005). The AMO data series was constructed using the Kaplan SST dataset ( $5^\circ \times 5^\circ$  latitude  $\times$  longitude grid) from  $0^\circ$  to  $70^\circ\text{N}$  after detrending to remove the influence of anthropogenic climate change (National Oceanic and Atmospheric Administration, 2012).

The North Atlantic Oscillation (NAO) is the dominant mode of interannual variability in atmospheric circulation over the North Atlantic (Hurrell, 1995), and the mouth of the Labrador Sea is one action center where the NAO index is highly correlated with SST (Visbeck *et al.*, 2003). The NAO affects physical conditions such as air and ocean temperatures, ocean currents and sea ice extent, and it has been linked to changes at higher levels of the North Atlantic marine ecosystem (Drinkwater *et al.*, 2003; Hurrell *et al.*, 2003). The NAO is most strongly associated with atmospheric and oceanic conditions during the winter, so the mean winter NAO index – the difference in normalized sea level pressure between the subtropical high (Azores) and the subpolar low (Reykjavik, Iceland) from December to March – was used for analyses (National Center for Atmospheric Research, 2012).

**Physical conditions.** Physical conditions were represented by time series of SST and sea surface salinity anomalies. Variations in temperature and salinity can directly impact salmon; however, they are also important indicators of oceanographic conditions, such as the volume transport in the Labrador Current and the strength of vertical stratification. Time series of SST were derived from the Extended Reconstructed SST (ERSST), version 3b (National Climatic Data Center, 2012). Data are resolved to a  $2^\circ$  latitude  $\times$   $2^\circ$  longitude grid, and spatial interpolation procedures are applied to reconstruct SST in

regions with sparse observations (Smith *et al.*, 2008). We used data for grids that spanned the North American range of Atlantic salmon (Fig. 2) and computed mean annual SST anomalies with respect to a 1971–2000 monthly climatology (Xue *et al.*, 2003).

Surface salinity anomalies were constructed from observations at Station 27, a hydrographic monitoring station located 8 km off St. John's, Newfoundland. Anomalies were computed as deviations from a harmonic regression model of the long-term seasonal salinity cycle, using 1946–1993 as the baseline (Akenhead, 1987; Myers *et al.*, 1990).

**Biological conditions.** Biological conditions in the Northwest Atlantic were represented across multiple trophic levels using indices of phytoplankton abundance, zooplankton community composition, and capelin spawning size. Plankton data were collected by continuous plankton recorder (CPR) surveys that have been conducted in the Northwest Atlantic by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS; Reid *et al.*, 2003) and across the Gulf of Maine by the US National Marine Fisheries Service (Jossi *et al.*, 2003) (Fig. 2). Plankton patterns in the Gulf of Maine are strongly correlated with those along the Scotian Shelf (Pershing *et al.*, 2010), so the Gulf of Maine provides a proxy for the broader southern region.

Phytoplankton and zooplankton on the CPR filtering silk are identified and enumerated using microscopic subsampling procedures (Warner & Hays, 1994). We constructed abundance anomalies for each taxon by fitting periodic splines to the log-transformed data to compute seasonal climatological cycles and then subtracting the expected abundance value from the measured value for each day to create seasonal anomalies; these were averaged to produce an annual anomaly (Pershing *et al.*, 2005). Diatoms and dinoflagellates were combined into a mean phytoplankton abundance anomaly. For zooplankton, we focused on five taxa in the Gulf of Maine (i.e. *Calanus finmarchicus* C5-6, *Calanus* spp. C1-4, *Metridia lucens* C5-6, *Oithona* spp. C4-6, *Pseudocalanus* species C6) and eight taxa in the North Atlantic (i.e. *Calanus* spp. C1-4, *Paracalanus* and *Pseudocalanus* spp. C6, *Oithona* spp. C4-6, *Calanus glacialis* C5-6, *Calanus finmarchicus* C5-6, *Calanus hyperboreus* C3-6, and *Metridia lucens* C6, and euphausiids). To represent changes in the zooplankton community, we applied a principal components analysis (PCA) to species abundance time series spanning 1978–2009 in the Gulf of Maine and 1978–2010 in the North Atlantic.

Capelin (*Mallotus villosus*) are found across the North Atlantic subpolar gyre, where they are important prey for fish, birds, and whales. However, their abundance, mean spawning size, and mean spawning age declined precipitously after 1990 (Department of Fisheries and Oceans Canada, 2011). We represent these capelin population changes with the length of spawning fish captured in Newfoundland's commercial inshore fisheries, the longest consistently sampled capelin indicator from this region. The mean spawning size, pooled over males and females, was computed as an annual index from 1980 to 2009 based on observations in NAFO Divisions 3K and 3L (B. Nakashima, personal communication).

## Data analysis

**Atlantic salmon population trends.** We conducted a dynamic factor analysis (DFA) to identify common trends among the six regional time series of Atlantic salmon abundance and productivity. As a dimension reduction technique, DFA is similar to traditional factor analysis or principal components analysis, but the axes are restricted by the temporal structure of the data, and DFA can be applied to nonstationary and relatively short time series. Time series are modeled as linear combinations of common trends, a level parameter, and noise, with models formulated as:

$$y_{it} = z_{i1}\alpha_{1t} + z_{i2}\alpha_{2t} + \dots + z_{im}\alpha_{mt} + \mu + e_{it}$$

where  $y_{it}$  is the value of the  $i$ th time series at time  $t$ ,  $\alpha_{mt}$  is the  $m$ th common trend at time  $t$ ,  $z_{im}$  is the factor loading for the  $i$ th time series and the  $m$ th common trend,  $\mu$  is a constant level parameter, and  $e_{it}$  is noise. The noise component,  $e_{it}$ , is typically represented as normally distributed with mean 0 and covariance matrix,  $\mathbf{R}$  (Zuur *et al.*, 2003). Explanatory variables can be included in dynamic factor models, but our analysis structure did not incorporate them.

The DFA was implemented using the MARSS package for Multivariate Autoregressive State Space Modeling (Holmes *et al.*, 2011) in R (R Development Core Team, 2013). Time series were first standardized by removing the mean and scaling by the standard deviation. We evaluated DFA models for Atlantic salmon abundance and productivity by varying the number of common trends from one to five and considering two structures for the error covariance matrix,  $\mathbf{R}$ : (i) diagonal and equal; and (ii) diagonal and unequal (i.e. 10 models for each population parameter). The former covariance structure implies that the same process variance is affecting all of the time series, while the latter incorporates unique variance values for each time series. Both of these structures assume there is no covariance among the series. Akaike's information criteria corrected for small sample sizes, AICc, was used to guide model selection (Hurvich & Tsai, 1989).

The fit and representativeness of the DFA model were assessed in two ways. First, the ability of the model to fit each time series was evaluated based on the variance values of the error covariance matrix,  $\mathbf{R}$ . These values indicate the amount of variance that cannot be explained by the model, with low values signifying a good fit. Secondly, canonical correlations were computed to evaluate how well each regional time series was represented by each common trend.

**Salmon-ecosystem relationships.** Relationships between Atlantic salmon population characteristics and marine ecosystem conditions were explored first by using chronological clustering to detect distinct temporal periods in the multivariate salmon and ecosystem data sets. Like all clustering approaches, this analysis partitions multivariate data into groups, but chronological clustering is constrained to preserve the sequence of years as groups are determined (Legendre *et al.*, 1985). The chronological clustering procedure was implemented using the CONISS method (Grimm, 1987) within the 'chclust' function in the R package 'rioja' (Juggins, 2012).

The number of clusters that were interpreted was defined from a broken stick model, wherein the proportion of variance accounted for by a given number of clusters should exceed the proportion expected based on a random distribution (Bennett, 1996). Three symmetric Euclidean distance matrices were used as inputs. These matrices represented the following: (i) common Atlantic salmon population trends identified from the DFA models; (ii) ecosystem conditions that exhibited low frequency variability (i.e. AMO, temperature, phytoplankton, zooplankton, and capelin); and (iii) ecosystem conditions that exhibited high frequency variability (i.e. NAO, salinity).

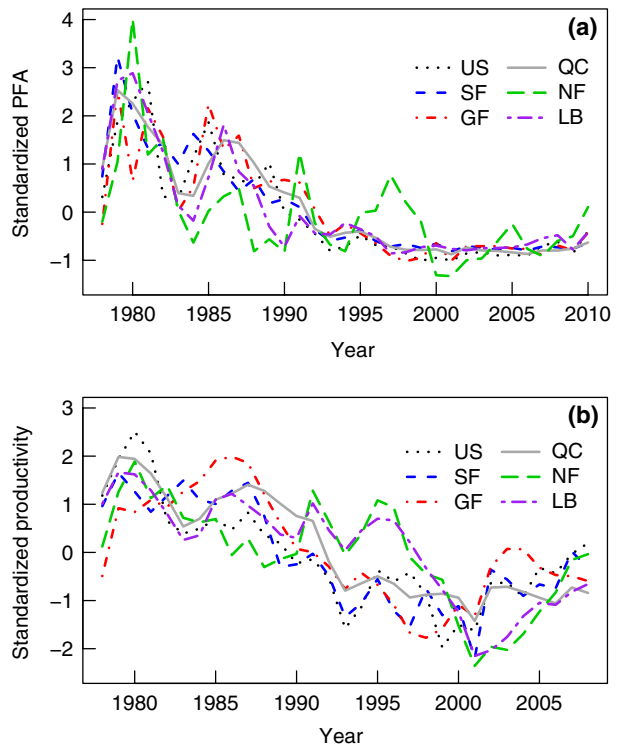
Furthermore, univariate correlations between variables representing different levels of the ecosystem were investigated. Specifically, we assessed correlations between low frequency and high frequency climate-physical conditions and biological indices, as well as between lower trophic level variables and Atlantic salmon population trends. Most correlations were conducted on the standardized time series, but biological variables were differenced before computing correlations to high frequency climate-physical variables. A cross-correlation analysis was first used to identify lags that maximized the correlation between two variables, allowing for lags of up to 2 years between changes in lower level variables and responses in higher level factors. The Pearson product moment correlation was computed, and its significance was evaluated after adjusting the effective degrees of freedom to account for autocorrelation (Pyper & Peterman, 1998).

## Results

### *Trends in Atlantic salmon populations*

Standardized time series of Atlantic salmon abundance and productivity show similar patterns of decline across six widespread regions of North America (Fig. 3). Abundance in most regions declined between the late 1980s and early 1990s, after which it remained stable at low levels (Fig. 3a). An exception to this pattern is seen in the Newfoundland population, in which abundance was more variable throughout the observation period. Productivity declined steadily from 1980 through 2000 in most regions except in Newfoundland and Labrador, where declines did not begin until the mid-1990s (Fig. 3b).

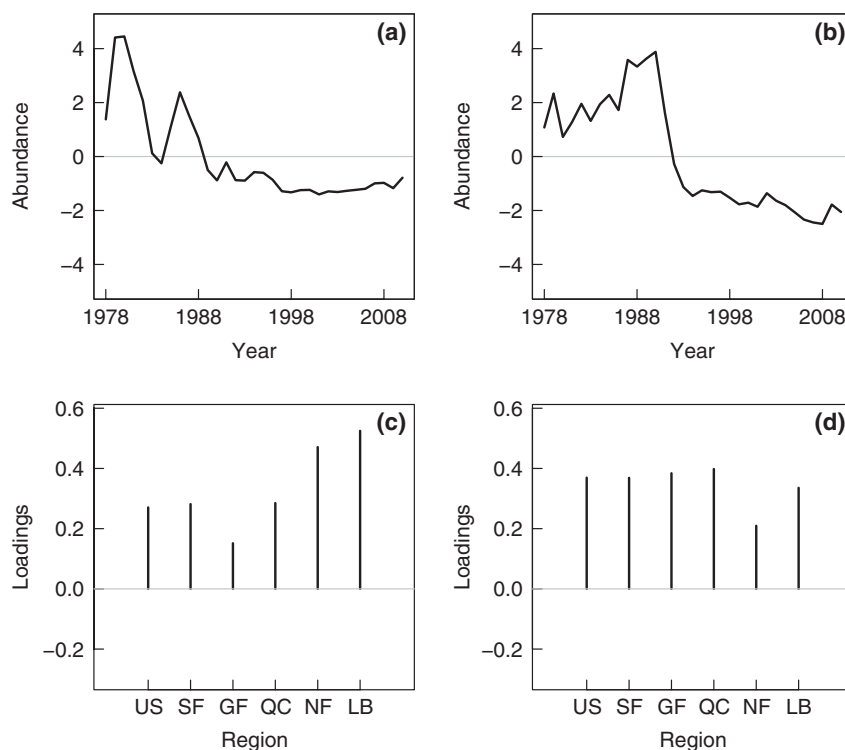
This pattern of population coherence was confirmed by dynamic factor analyses, which revealed common trends in abundance and productivity across North American population complexes. Of the dynamic factor models we tested, the most parsimonious model of abundance patterns included two trends and an unequal diagonal error covariance matrix ( $AIC_c = 276.79$ ). The first common trend (Fig. 4a) exhibited variable but declining abundance between 1978 and 1990, after which it stabilized at low values. The second common trend (Fig. 4b) revealed high abundance values until 1990, after which it abruptly declined to much



**Fig. 3** Standardized abundance (a) and productivity (b) of Atlantic salmon population complexes in six regions of North America: United States (US), Scotia-Fundy (SF), Gulf of St. Lawrence (GF), Quebec (QC), Newfoundland (NF), and Labrador (LB).

lower levels (Fig. 4b). All regions loaded in the same (positive) direction on these two trends, indicating that the abundance changes were geographically coherent (Fig. 4c and d). However, the strength of the loadings varied by region. Labrador and Newfoundland loaded strongly on the first common trend; the United States, Scotia-Fundy, and Quebec loaded moderately, and the Gulf of St. Lawrence loaded weakly on this trend (Fig. 4c). In contrast, Quebec, Gulf of St. Lawrence, Scotia-Fundy, and the United States loaded most strongly and at similar magnitudes on the second common trend, whereas Labrador and Newfoundland both loaded weakly (Fig. 4d).

The model fit the variability in each time series well for most regions, as represented by the variance in the error covariance matrix,  $\mathbf{R}$  (Table 1). Abundance patterns in Labrador and Quebec were extremely well fit, and the DFA model captured over 80% of the variability in the Gulf of St. Lawrence, Scotia-Fundy, and United States complexes. However, the model fit was relatively poor for Newfoundland, with nearly half of the variance in salmon abundance not explained by the model (Table 1; Fig. 5). All of the regional Atlantic salmon abundance time series were strongly correlated



**Fig. 4** Common trends (a and b) for the Atlantic salmon abundance time series obtained by the dynamic factor model containing two common trends and an unequal diagonal error covariance matrix. Factor loadings (c and d) for each of the six North American regions on the common abundance trends: United States (US), Scotia-Fundy (SF), Gulf of St. Lawrence (GF), Quebec (QC), Newfoundland (NF), and Labrador (LB). The common trends and factor loadings are unitless.

**Table 1** Regional fits ( $R$ ) to the dynamic factor models and canonical correlations (CC) between regional time series and each common trend

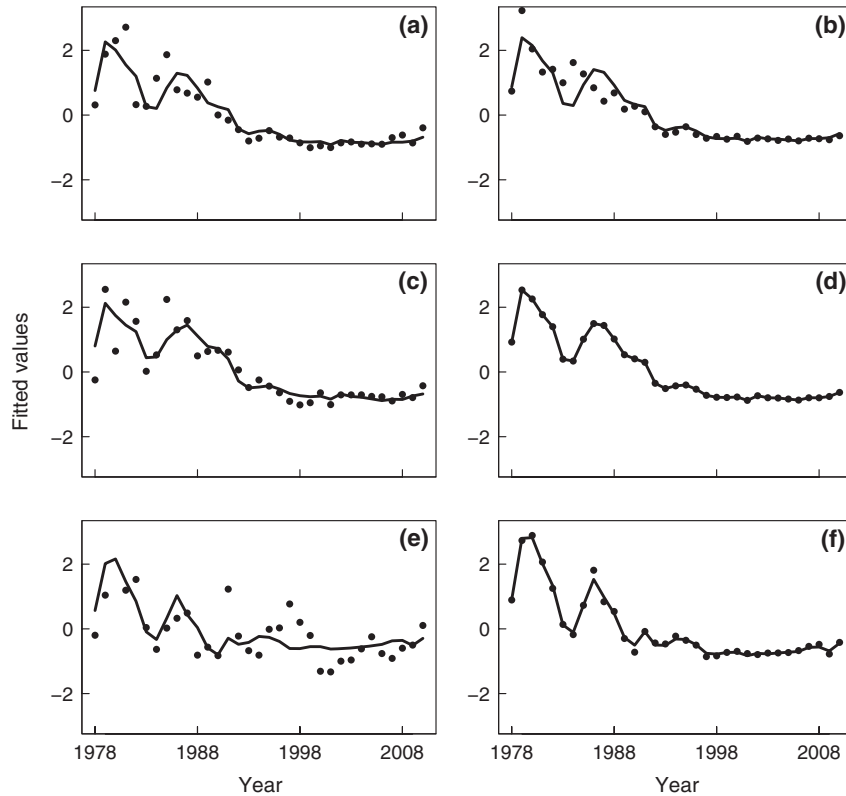
Region	Abundance model			Productivity model		
	$R$	CC1	CC2	$R$	CC1	CC2
US	0.18	<b>0.87</b>	<b>0.73</b>	0.24	<b>0.70</b>	<b>0.77</b>
SF	0.14	<b>0.90</b>	<b>0.74</b>	0.14	<b>0.66</b>	<b>0.87</b>
GF	0.18	<b>0.82</b>	<b>0.81</b>	0.24	<b>0.54</b>	<b>0.87</b>
QC	0	<b>0.96</b>	<b>0.81</b>	0.05	<b>0.82</b>	<b>0.80</b>
NF	0.46	<b>0.74</b>	0.31	0.20	<b>0.90</b>	0.22
LB	0.02	<b>0.99</b>	<b>0.57</b>	0	<b>1.00</b>	0.36

Values of  $R$  indicate the portion of variance in the regional time series that is unexplained by the dynamic factor model, such that low values indicate a good model fit. Canonical correlation values indicate the strength of the association between the regional series and common trends, with high absolute values representing strong correlations. Correlation coefficients in bold type are statistically significant after adjusting for temporal autocorrelation.

with the first common trend; each region except Newfoundland was also significantly correlated with the second common trend, although these relationships were weaker than observed for the first trend (Table 1).

An appropriate dynamic factor model for Atlantic salmon productivity was more difficult to identify. The two models ranked as most parsimonious included four ( $AICc = 249.2$ ) and five ( $AICc = 256.3$ ) common trends. However, at least one trend in each of these models represented only very weak loadings for all regions, indicating that too many trends were being used (Zuur *et al.*, 2007). Of the remaining models, a two trend model with an unequal diagonal variance structure offered the most parsimonious option ( $AICc = 284.2$ ), and we report and use its results.

The first common trend showed cyclical but gradually declining productivity until 1996, after which a precipitous decline occurred through 2001, followed by a moderate recovery (Fig. 6a). The second common trend was stable until 1987, after which it declined steadily through 1997; more recently, productivity values increased to approximately half of their pre-1987 levels (Fig. 6b). All regions loaded positively on the two common productivity trends, suggesting a coherent directional response across North American populations (Fig. 6c and d). However, the loadings indicate regional alignment with individual trends. Labrador and Newfoundland loaded strongly on the first productivity trend, with relatively weak loadings from the other four



**Fig. 5** Fitted values obtained by the dynamic factor model of abundance trends of Atlantic salmon in six North American regions: (a) United States, (b) Scotia-Fundy, (c) Gulf of St. Lawrence, (d) Quebec, (e) Newfoundland, and (f) Labrador. The lines represent the fitted values, and solid circles represent the observed values in each region. Fitted values are unitless.

regions (Fig. 6c). The opposite loading pattern was observed for the second trend, on which Quebec, Gulf of St. Lawrence, Scotia-Fundy, and the United States loaded more strongly (Fig. 6d).

The two-trend model fit productivity patterns well across the six individual North American regions (Fig. 7), as indicated by the values of the diagonal of the **R** matrix (Table 1). The United States, Gulf of St. Lawrence, and Newfoundland had poorer fits than the other regions, but <25% of the variance in productivity for these regions remained unaccounted for by the model. Productivity patterns for all regions were significantly correlated with the first common trend, whereas Labrador and Newfoundland were not significantly correlated with the second trend (Table 1).

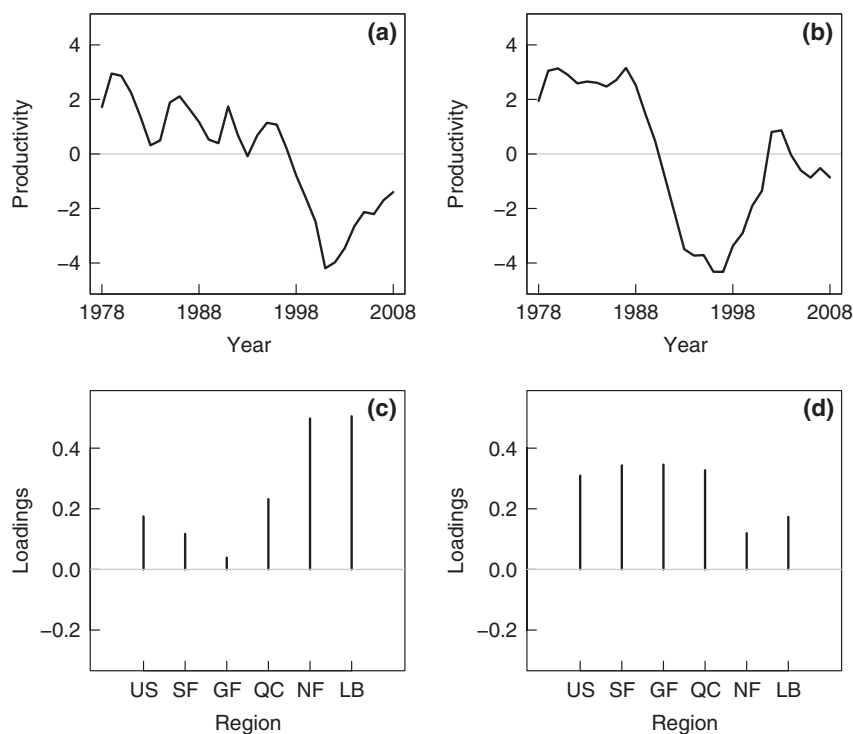
#### *Changes in ecosystem conditions*

To identify ecosystem conditions that may have affected Atlantic salmon populations, we evaluated long-term changes in climate, physical, and biological factors in the Northwest Atlantic between 1978 and the present. Due to its multidecadal periodicity, the AMO trended upwards over the entire time period (Fig. 8a).

The NAO showed considerable interannual variability; its values were generally lower during most of the 1980s than during the 1990s, but extremely low anomalies occurred in 1996 and 2010 (Fig. 8a).

Sea surface temperature varied without a distinct trend from 1978 to 1992, but a strong increasing trend occurred after 1992, with 2010 being an exceptionally warm year (Fig. 8b). Surface salinity showed high interannual variability, although the average salinity was generally lower in the 1990s than during the 1980s; in the 2000s, salinity returned to levels similar to those observed in the 1980s (Fig. 8b).

Phytoplankton in the Gulf of Maine showed strong interdecadal variability, with the abundance of diatoms and dinoflagellates at low levels during the 1980s, high levels during the 1990s, and declining again to low levels in the early 2000s (Fig. 8c). An interdecadal pattern was not as apparent in the North Atlantic. Phytoplankton abundance appeared to be relatively high during the early 1980s, but it declined by the middle of that decade. A gap in the sampling record precludes our understanding of phytoplankton in this region during the late 1980s and early 1990s, but abundance trended upwards after sampling resumed in the 1990s through



**Fig. 6** Common trends (a and b) for the Atlantic salmon productivity time series obtained by the dynamic factor model containing two common trends and an unequal diagonal error covariance matrix. Factor loadings (c and d) for each of the six North American regions on the common productivity trends: United States (US), Scotia-Fundy (SF), Gulf of St. Lawrence (GF), Quebec (QC), Newfoundland (NF), and Labrador (LB). The common trends and factor loadings are unitless.

2010, exceeding levels observed in the early 1980s (Fig. 8c).

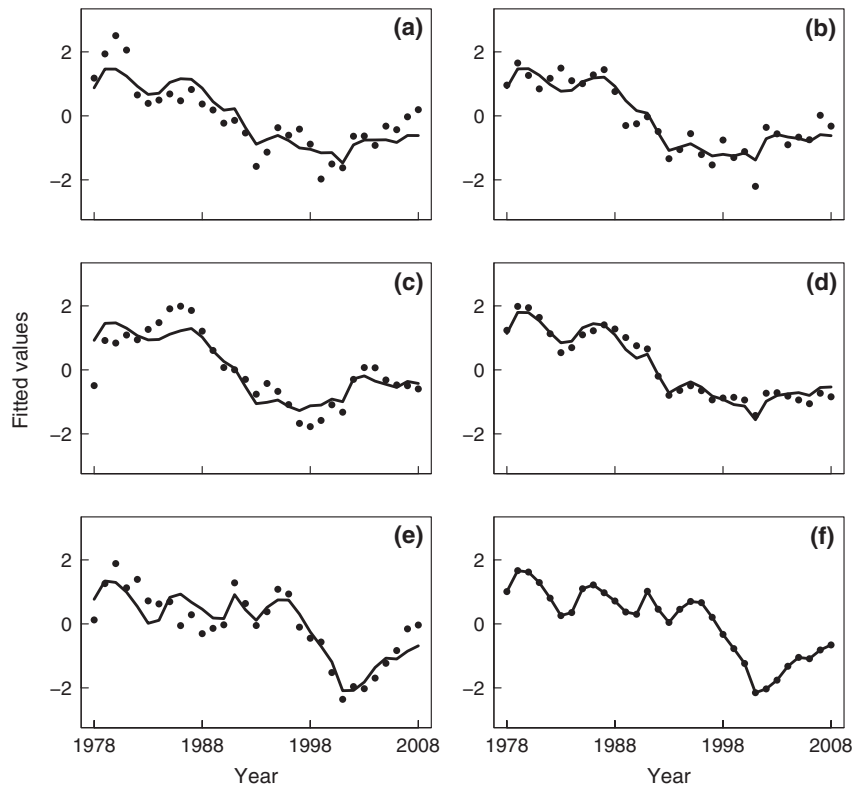
Changes in the Gulf of Maine zooplankton community over the last 30 years were strongly size-based. The first PC, which accounted for 61% of the variance in community structure, contrasted the late juvenile and adult stages of the large copepod *Calanus finmarchicus* with smaller copepod species and early *Calanus* life stages (Fig. 9a). *C. finmarchicus* is the dominant mesozooplankton species in the North Atlantic (Marshall & Orr, 1955) and an important food source for many small pelagic fish, including capelin (Gerasimova, 1994). Since the first PC captured most of the community variance, we focus on it for further analyses (Fig. 8d), but the second PC (23% of variance) separated all life stages of *Calanus* from other zooplankton species (Fig. 9a). Values on the first PC, which track the abundance of *C. finmarchicus*, were high during the 1980s, low throughout the 1990s, and subsequently increased and remained steady for the 2000s (Fig. 8d); this interdecadal pattern is inverse to phytoplankton abundance in the region (Fig. 8c).

In the North Atlantic, the first two principal components were similar in the amount of variance they explained. On the first PC, which captured 31% of the variance, the smaller species (e.g. *Oithona*, *Metridia*

*lucens*, and *Paracalanus* and *Pseudocalanus* spp.) loaded strongly, although *Calanus glacialis* was also represented (Fig. 9b). Most of the larger species, including other *Calanus* spp. and euphausiids, loaded negatively on the second PC (24% of variance) (Fig. 9b). Scores on the first PC indicate that abundance of the small-bodied species trended upwards since the early 1990s, while the second PC shows that many large-bodied species declined (Fig. 8e). The relationship between phytoplankton and zooplankton abundance in the North Atlantic is consistent with that observed in the Gulf of Maine: as phytoplankton increased, small-bodied species became dominant in the zooplankton community (Fig. 8c and e).

The size of capelin spawning in coastal areas of Newfoundland declined sharply between 1990 and 1992 (Fig. 8f). The average spawning capelin prior to 1990 was 17.7 mm longer than the average fish after 1992. This decline in size reflects a shift toward spawning at younger ages; spawners were predominantly 3–4 years old prior to 1992, but subsequently, 2–3 year olds have dominated the spawning population (Department of Fisheries and Oceans Canada, 2011). The loss of older spawning fish is not thought to be attributable to changes in fishing practices, but it instead reflects a





**Fig. 7** Fitted values obtained by the dynamic factor model of Atlantic salmon productivity trends in six North American regions: (a) United States, (b) Scotia-Fundy, (c) Gulf of St. Lawrence, (d) Quebec, (e) Newfoundland, and (f) Labrador. The lines represent the fitted values, and solid circles represent the observed values in each region. Fitted values are unitless.

broader ecosystem regime shift and coincides with movement of the capelin population from coastal Newfoundland to more southerly and offshore areas (Frank *et al.*, 1996; Carscadden *et al.*, 2001).

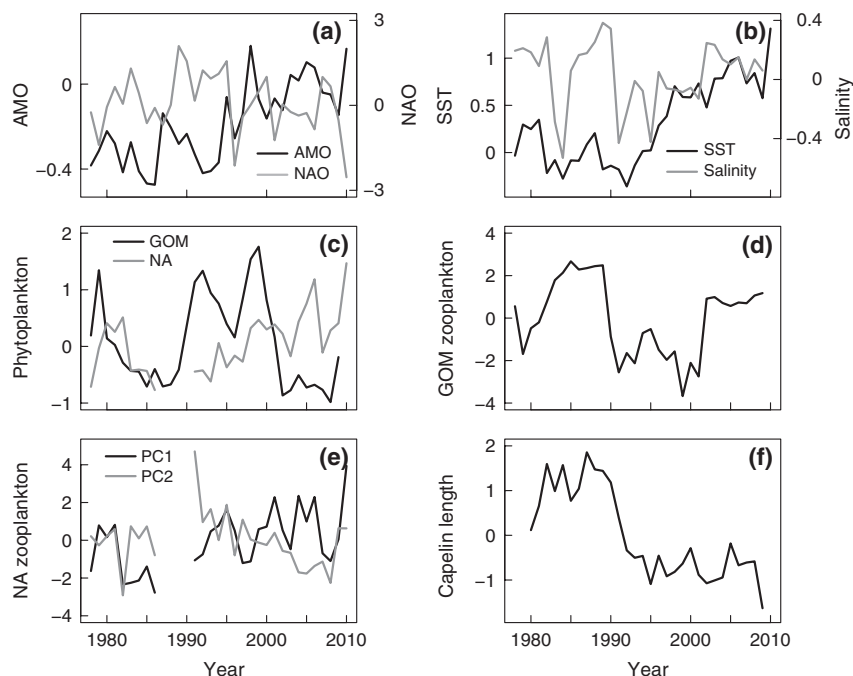
#### *Relationships between Atlantic salmon and ecosystem conditions*

Chronological cluster analyses revealed three distinct periods of Atlantic salmon abundance and productivity. A primary change in salmon population characteristics occurred between 1990 and 1991, and a secondary shift occurred between 1997 and 1998 (Fig. 10a). The temporal breaks that define changes in salmon populations appear to be influenced by a combination of changes in ecosystem conditions that vary at both low and high frequencies. Among the ecosystem conditions that varied at low frequencies (i.e. AMO, phytoplankton, zooplankton, capelin), four distinct periods were characterized by breaks that occurred after 1981, 1989, and 2001 (Fig. 10b). Higher frequency ecosystem variables (i.e. NAO, salinity) aligned with five distinct periods, with major breaks after 1988, 1995, 1996, and 2009 (Fig. 10c). The primary shift in salmon population characteristics between 1990 and 1991 sequentially followed

shifts in high and low frequency ecosystem variables in 1988 and 1989, respectively. The secondary shift in salmon populations after 1997 follows major changes in high frequency ecosystem variables that distinguished 1996 as an exceptional year.

These aggregate patterns indicate that salmon abundance and productivity are influenced by a suite of ecosystem conditions, but further insights can be gained by investigating associations between individual factors. The first set of analyses evaluated correlations between low frequency climate and physical conditions (i.e. AMO, SST) and biological responses (Table 2). The AMO was directly associated with North Atlantic phytoplankton and zooplankton, while it was inversely associated with capelin length, both Atlantic salmon abundance trends, and the first salmon productivity trend. Correlations between SST and the biological variables produced similar results, except that SST was not correlated with the first salmon abundance trend. Correlations between SST and the two salmon population trends were among the strongest detected from the pairwise analyses (Table 2).

A second set of correlations paired climate and physical factors that varied at high frequencies (i.e. NAO and salinity) with differenced biological time series



**Fig. 8** Time series of ecosystem variables used for analyses: (a) standardized Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) indices; (b) sea surface temperature (SST) and salinity anomalies; (c) Gulf of Maine (GOM) and North Atlantic (NA) phytoplankton abundance anomalies; (d) first principal component of zooplankton community composition in GOM; (e) first (PC1) and inverted second (PC2) principal components of zooplankton community composition in the NA; and (f) standardized average length of spawning capelin off of Newfoundland.

(Table 2). The NAO index was significantly correlated with changes in zooplankton communities, capelin length, the second salmon abundance trend, and the second salmon productivity trend. Salinity was negatively correlated with changes in both Atlantic salmon abundance trends and the second salmon productivity trend, but not with changes in phytoplankton, zooplankton, or capelin.

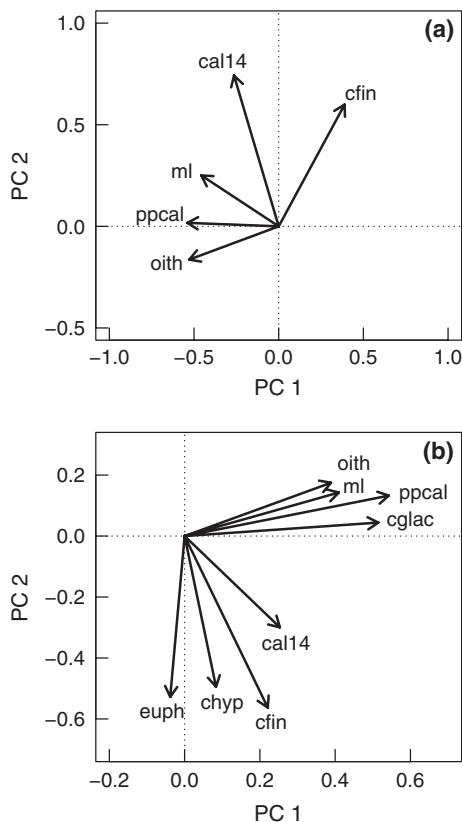
A final set of correlations investigated direct associations between lower trophic level biological variables and Atlantic salmon population trends. These results showed significant correlations between phytoplankton and zooplankton and the salmon population trends (Table 2). However, capelin size was most strongly and consistently associated with Atlantic salmon abundance and productivity; capelin length was significantly correlated with all salmon population trends, and for most trends, the correlation strength was the highest observed (Table 2).

## Discussion

Changes in the abundance and productivity of 2SW Atlantic salmon appear to have been largely coherent across the species' North American geographic range. Over this broad area, two common trends in salmon abundance declined to low levels after 1990, and pro-

ductivity trends showed declines between 1987 and 1996. While the coherence of these declines is strong, regional distinctions do appear. Loadings on each of the common trends for Newfoundland and Labrador contrasted those for Quebec, the Gulf of St. Lawrence, Scotia-Fundy, and United States. Salmon populations within the distinct regional groups differ in their age structure, with 1SW fish representing a large portion of returning salmon in Newfoundland and Labrador, while the remaining regions are either dominated by 2SW salmon or have a closer balance between 1SW and 2SW fish. In addition, Newfoundland and Labrador are both considerably closer to the overwintering and summer feeding areas in the Labrador Sea and Greenland, respectively; therefore, salmon from these regions have shorter migration distances that require less energy.

The general coherence of declines in abundance and productivity that have occurred across the North American range points toward marine conditions as critically influencing survival and population dynamics. Shifts in the marine environment affect large areas of the Northwest Atlantic and may impact Atlantic salmon from across North America when they are concentrated on overwintering and feeding grounds in the Labrador Sea. In contrast, river-specific changes in habitat quality are unlikely to be a major factor in salmon declines;



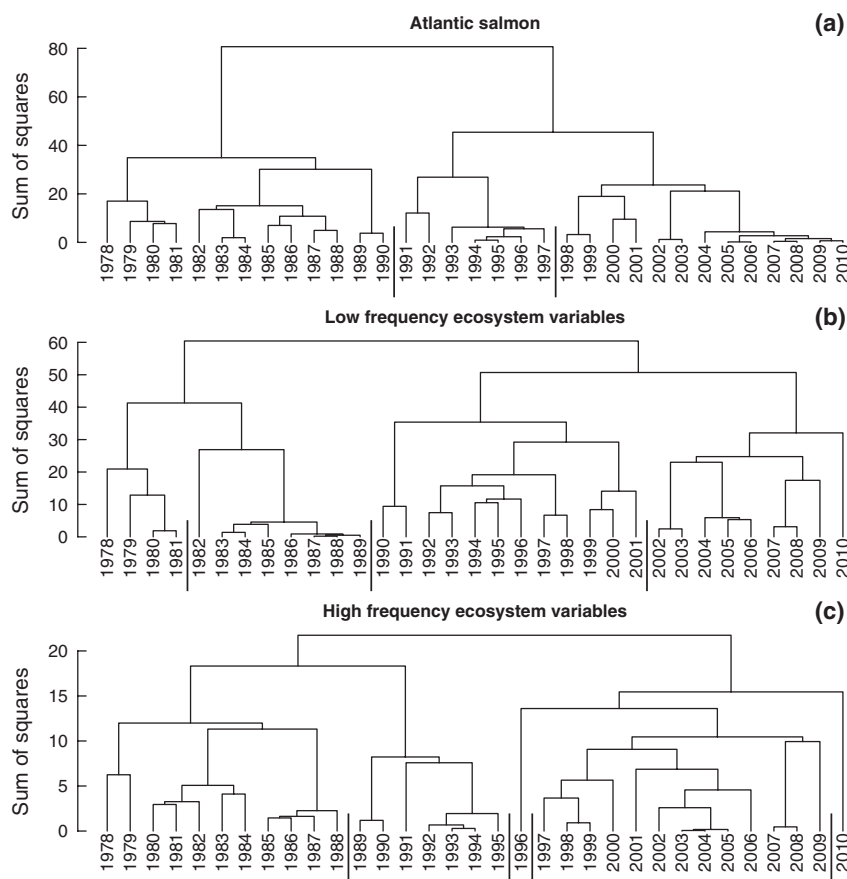
**Fig. 9** Loadings on first two principal components of variability in zooplankton community composition in the Gulf of Maine (a) and North Atlantic (b). Species and groups are abbreviated as follows: *Calanus finmarchicus*, cfin; *Calanus glacialis*, cglac; *Calanus hyperboreus*, chyp; *Calanus* spp. (C1-4), cal14; euphausiids, euph; *Metridia lucens*, ml; *Oithona* spp., oith; *Paracalanus* and *Pseudocalanus* spp., ppcal.

however, large-scale, atmospherically forced changes in river conditions over broad regions may merit further attention. The fact that declines in 2SW cohorts of Atlantic salmon populations have been much more severe than in 1SW cohorts suggests that climate and ecosystem conditions may either (i) negatively affect Atlantic salmon during their entire marine stage, with greater cumulative effects on 2SW fish as their marine residence time is twice as long or (ii) exert the strongest influence following the first winter at sea.

Climate patterns shape the marine ecosystem that Atlantic salmon encounter, and we find both direct and indirect associations between climate and Atlantic salmon population declines. The AMO is inversely correlated with Atlantic salmon abundance throughout North America and with productivity in the Newfoundland and Labrador regions. The strong relationship between the AMO and salmon populations has been recognized in other studies (Condrón *et al.*, 2005; Beau-

grand & Reid, 2012; Friedland *et al.*, 2013), which hypothesized that its influence operates through thermal stress and ecosystem changes that affect trophic interactions, consistent with our results. The NAO is inversely correlated with interannual variability in abundance and productivity in Quebec, the Gulf of St. Lawrence, Scotia-Fundy, and the United States. However, the correlation between salmon populations and the NAO was weaker than for many other variables, as has also been documented in other studies (Beaugrand & Reid, 2003, 2012). In addition to these direct linkages, the AMO and NAO influence SST and salinity, which are strongly associated with Atlantic salmon population trends. The Labrador Sea is warming faster than any other area of the North Atlantic (Taboada & Anadón, 2012). Elevated temperatures could directly impact salmon, and recent warming has restricted the area of preferred thermal habitat to record low levels (Friedland *et al.*, 2013). However, our study suggests that ecosystem responses to warming, including changes to phytoplankton, zooplankton and forage fish, reinforce and may be more important than the direct influence of temperature.

Capelin size is consistently highly correlated with salmon abundance and productivity trends. The strength of this relationship is not surprising as capelin are key prey for Atlantic salmon (Jacobsen & Hansen, 2000; Rikardsen & Dempson, 2011). Although we use a size-based index to track capelin status, a number of other changes align with the decline in body size that generally make capelin less available and less valuable as prey for salmon (Carscadden *et al.*, 2001). Around 1990, capelin shifted their distribution from Newfoundland to the Scotian Shelf and Flemish Cap (Frank *et al.*, 1996; Carscadden *et al.*, 2001) and stopped undertaking diurnal migrations that would bring them into the surface waters occupied by Atlantic salmon (Mowbray, 2002; Department of Fisheries and Oceans Canada, 2011). The onset of these changes aligned with an extremely cold period, but they did not return to pre-1990s conditions when water temperatures returned to normal; other factors, such as prey availability, may be playing a role in maintaining these patterns (Mowbray, 2002). As capelin size declined, so did the condition and energy content of each fish (Nakashima, 1996; Carscadden & Frank, 2002), which reduced their nutritional value as prey (Davoren & Montevecchi, 2003). Much of what we know about capelin in the Labrador Sea is derived from the Newfoundland population, but similar changes may be occurring in the West Greenland population. Some evidence suggests that the size distribution of capelin off West Greenland has declined compared to historical periods (Hedeholm *et al.*, 2010). Capelin growth is correlated with zooplankton abundance (Gjøsæter *et al.*, 2002; Hedeholm *et al.*, 2010), and



**Fig. 10** Chronological clustering of (a) Atlantic salmon population trends, (b) low frequency ecosystem variables, and (c) high frequency ecosystem variables. Key change-points are identified by bold vertical lines, with the number of periods determined by a broken stick model.

we show a decline in large zooplankton in the Labrador Sea, which may restrict capelin growth.

Characteristics of the marine ecosystem that Atlantic salmon experience are markedly different now than they were prior to recent salmon population declines. Investigating the timing of changes affords further insights into how Atlantic salmon populations may have been affected by this ecosystem regime shift and how it may constrain their productivity. We delineate three distinct periods in North American Atlantic salmon population trends: 1978–1990 (start of abundance and productivity declines), 1991–1997 (low abundance and continued productivity declines), and 1998–2010 (continued low abundance but increasing productivity). The 1990/1991 shift in Atlantic salmon populations appears to have been triggered by sequential changes through the ecosystem, beginning with a shift in the NAO and salinity after 1988 that subsequently affected lower trophic level biological characteristics. Our results parallel the MERCINA Working Group's (2012) description of an Arctic-origin atmospheric shift that increased freshwater export from the Arctic Ocean and

induced a regime shift across multiple trophic levels in the Northwest Atlantic. We can trace these same relationships through our analyses; specifically, the increased freshwater export following a high NAO index in 1989 reduced upper-layer salinities in the coastal current system. The lower salinities enhanced stratification and increased phytoplankton production, which favored faster growing, smaller bodied zooplankton from the Labrador Sea to the Gulf of Maine (Pershing *et al.*, 2010). We also show that these changes can be linked to shifts at even higher trophic levels, including capelin and, ultimately, Atlantic salmon.

The results of our analyses for North American Atlantic salmon populations reinforce findings of recent studies focused on European populations. Beaugrand & Reid (2003) associated major declines in European Atlantic salmon abundance with rising Northern hemisphere temperature and Northeast Atlantic SST. Following pronounced temperature increases in the late 1970s, sequential shifts occurred in biological components of the ecosystem, from phytoplankton through zooplankton to Atlantic salmon

**Table 2** Pairwise correlations between climate indices, physical conditions, lower trophic levels, and Atlantic salmon populations

	AMO		NAO		SST		Salinity		GOM_phyto		NA_phyto		GOM_zp		NA_zp1		NA_zp2		Capelin		
	lag	r	lag	r	lag	r	lag	r	lag	r	lag	r	lag	r	lag	r	lag	r	lag	r	
SST	0	<b>0.880</b>	0	<b>-0.484</b>																	
Salinity	2	0.170	2	<b>-0.409</b>	2																
GOM_phyto	0	-0.134	1	-0.078	2	-0.363	0	0.306													
NA_phyto	0	<b>0.692</b>	2	-0.131	0	<b>0.776</b>	1	0.216													
GOM_zp	2	-0.169	0	<b>-0.354</b>	0	-0.128	0	-0.277													
NA_zp1	0	<b>0.574</b>	0	<b>0.374</b>	0	<b>0.633</b>	1	0.110													
NA_zp2	1	<b>0.409</b>	0	0.115	1	<b>0.531</b>	0	-0.364													
Capelin	0	-0.554	1	-0.515	0	-0.631	2	-0.277													
AS_abund1	0	<b>-0.484</b>	1	0.015	0	-0.356	1	<b>-0.400</b>	2	-0.022	2	-0.385	2	0.283	2	<b>-0.405</b>	2	-0.070	0	<b>0.538</b>	
AS_abund2	0	<b>-0.608</b>	1	<b>-0.375</b>	0	<b>-0.700</b>	2	<b>-0.365</b>	2	-0.262	0	<b>-0.498</b>	2	<b>0.586</b>	1	<b>-0.601</b>	0	-0.250	0	<b>0.895</b>	
AS_prod1	0	<b>-0.670</b>	1	0.149	0	<b>-0.705</b>	0	0.077	0	0.213	2	<b>-0.579</b>	2	<b>0.463</b>	2	<b>-0.489</b>	0	-0.340	2	<b>0.644</b>	
AS_prod2	0	-0.326	0	<b>-0.421</b>	0	-0.247	2	<b>-0.526</b>	0	-0.515	0	-0.066	0	<b>0.667</b>	0	<b>-0.371</b>	2	0.355	0	<b>0.724</b>	

Values indicate the Pearson product moment coefficient, and values in bold are statistically significant after adjusting for temporal autocorrelation. The shaded cells indicate that the biological variables were differenced before the correlation analysis.

AMO, Atlantic Multidecadal Oscillation; NAO, North Atlantic Oscillation; SST, sea surface temperature; GOM\_phyto, Gulf of Maine phytoplankton; GOM\_zp, Gulf of Maine zooplankton; NA\_phyto, North Atlantic phytoplankton; NA\_zp1 and NA\_zp2, North Atlantic zooplankton principal components; AS\_abund1 and AS\_abund2, common trends in Atlantic salmon abundance; and AS\_prod1 and AS\_prod2, common trends in Atlantic salmon productivity.

(Beaugrand & Reid, 2003). These changes jointly contributed to a shift in aggregate ecosystem conditions between 1986 and 1987 and again between 1996 and 1997 (Beaugrand & Reid, 2003, 2012). Our findings parallel those of Beaugrand & Reid (2003, 2012) in demonstrating the effects of climate-driven changes on Atlantic salmon populations in the Northwest Atlantic. On both sides of the Atlantic basin, rising SST is strongly associated with salmon declines, both directly and through ecosystem changes that affect productivity and trophic interactions. In addition, the timing of shifts in ecosystem characteristics is generally aligned, with major shifts occurring in the late 1980s/early 1990s and in the mid-1990s. These results demonstrate that climate change is directly and indirectly structuring pelagic ecosystems throughout the northern Atlantic basin.

While declines in North American Atlantic salmon populations can be related to a series of climate-driven ecosystem changes throughout the Northwest Atlantic, their productivity and recovery may be constrained by persistent physical and ecological trends, particularly in the Labrador Sea. Many factors that showed major shifts between the 1980s and 1990s reverted back to 1980s-like conditions in the 2000s, including the NAO, salinity, and phytoplankton and zooplankton in the Gulf of Maine. However, SST has continued to rise through the end of the period we examined. In the Labrador Sea, higher phytoplankton abundance has persisted over time, but this productivity supports a small-bodied zooplankton community in which lipid-rich species, such as *Calanus* spp. and euphausiids, have continued to decline. In addition, capelin populations have not rebounded, and capelin that are present remain small (Department of Fisheries and Oceans Canada, 2011). Not only do capelin population trends indicate reduced availability for Atlantic salmon but their smaller size would require salmon to catch a larger number of capelin, and thus expend more energy, to acquire the same number of calories.

The factors that appear to be constraining North American Atlantic salmon populations can be linked to global climate change. Rising ocean temperatures are consistent with projections from climate change scenarios (Meehl *et al.*, 2007). In addition, climate change is expected to enhance stratification, which may increase primary production in high latitudes (Sarmiento *et al.*, 2004; Behrenfeld *et al.*, 2006), and we observe corresponding upward trends in phytoplankton abundance in the Labrador Sea. At higher trophic levels though, the influence of climate change is more complex. It is anticipated that zooplankton will increase in conjunction with phytoplankton, but it is unclear which zooplankton may benefit; geographic ranges, thermal

niches, and species interactions must all be considered in evaluating how zooplankton communities may respond to climate change (Pershing *et al.*, 2005; Reygondeau & Beaugrand, 2011; Record *et al.*, 2013). Similarly, the effects on both capelin and Atlantic salmon are likely to be characterized by interactions between direct climate effects, climate-driven ecosystem changes, and species-specific physiological tolerances.

Given that recent conditions in the Labrador Sea appear to be unfavorable for Atlantic salmon, and these conditions are expected to become more pronounced with climate change, the forecast for recovery of North American Atlantic salmon populations is not optimistic. However, the 1990s regime shift that led to the decline of Atlantic salmon populations occurred rapidly, and natural variability may again shift conditions toward more favorable states. While climate and marine ecosystem dynamics cannot be directly controlled, the adaptability of Atlantic salmon populations can be enhanced at other life stages through efforts such as protecting genetic diversity and reducing freshwater and estuarine mortality. Managing Atlantic salmon populations for resilience is critical for buffering future effects of climate change. A better understanding of how climate and marine ecosystem factors influence Atlantic salmon can help anticipate population trajectories, identify recovery opportunities, and support evaluation of management actions.

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