

Poissons sans frontières: Comparing contiguous surveys for major ecological and commercial species in the Northwest Atlantic, with a focus on trends, synchronies and coherences

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Abstract

Fish know no national borders, yet for a plethora of reasons, we delineate fish into distinct population or stock units that often reflect human institutional borders more so than biological factors. Across a wide variety of taxa, population dynamics can be synchronous over a range of spatial scales. Common patterns are generally attributed to a meta-population structure supported through dispersal, or a common response to large scale environmental forcing. In the NW Atlantic, common species occur in the broader Gulf of Maine Area (GOMA), yet the area is managed in the south by the US and in the north by Canada. Many species occurring in the GOMA are subject to common forcing resulting in coherent patterns of recruitment and growth among distinct populations. To evaluate these issues, we compared six survey biomass time series of 19 representative species from US and Canadian waters. We further explored the biomass trends of aggregate groups such as the top 13 groundfish or total fish biomass. Many of these individual species and aggregates species groupings showed synchronous trends. For instance, Canadian and US populations of haddock, thorny skate and white hake have comparable trends within species. Conversely, some species show differing survey time series trends and asynchronous event timing, suggesting forcing processes may influence these species differently. Collectively our results demonstrate the value of comparing time-series for common species from contiguous ecosystems, with the potential to elucidate the relative importance of major factors affecting such species.

Introduction

For many animals, population dynamics can be synchronous over a range of spatial scales but the mechanisms that generate such synchronicity are often difficult to determine. Common temporal patterns among spatially distinct density-dependent populations are generally attributed to one or more of the following: a meta-population structure supported through dispersal, a common response to large scale environmental forcing or a common response to prey populations which are also synchronous (reviewed in Liebhold et al. 2004).

In marine systems, there is good evidence that large-scale environmental forcing influences recruitment success (Myers 1997; Myers et al. 2001), and the assumption is that synchronous recruitment dynamics translates into synchrony in the abundance of adult populations. The strength of this connection between recruits and adult depends on life history traits (Tedesco and Hugueny 2006). Importantly, the effect of environmental forcing on marine populations has provided context as to how exploited populations have responded to fishing (Frank et al. 2007). Across the North Atlantic, populations within their range respond differently to intense fishing depending on the governing temperature regime. Warmer, species rich, southern fish communities can withstand higher depletion rates than colder, less species rich fish communities because of their higher demographic rates and a greater pool of potentially compensating species (Frank et al. 2006, 2007)

Within the realm of marine resource management, there has been a global call for an Ecosystem Approach to Management (EAM, Hall and Mainprize 2004; McCloud *et al.* 2005; Pikitch *et al.* 2005). This includes consideration of the effects of fishing on the broader ecosystem *and* the effects of the ecosystem and the environment on species

dynamics. One way to help facilitate the implementation of EAM is via comparative ecosystem studies, either focusing on single species (e.g., Brander 1994, 1995) or whole ecosystems (e.g., Hunt and Megrey, 2005; Moloney et al., 2005; Bundy et al *In press*). Comparisons of similar ecosystems can serve as *ad hoc* replicates, mimicking an experimental set-up where common, unique and fundamental features, as well as important drivers that influence the processes in marine ecosystems, can be explored. These comparative analyses allow the opportunity for taking a broader ecosystem perspective and permit the ability to draw generalizations important to successful implementation of EAM.

An Ecosystem Approach to Management requires some understanding and agreement on the bounds of the ecosystem. Definition of boundaries can be context, scale and question specific. With regard to fisheries management, the Gulf of Maine Area (GoMA) in the Northwest Atlantic (Figure 1) has been traditionally managed in the north by Canada, and in the south by the USA, due to the national border which divides the area. This anthropogenic boundary has determined the nature of fisheries and ecosystem management in the GoMA, but arguably this is an ecosystem comprised of the following contiguous systems: the Gulf of Maine, Georges Bank, the Bay of Fundy and the western Scotian Shelf (Figure 1). Given the adjacency of these four systems, it can be expected that the population dynamics of some species may be synchronous, responding to large scale environmental influences. If this is the case, there are implications for the management of fisheries and their ecosystems across the whole Gulf of Maine area.

Three transboundary species, George's Bank cod, haddock and yellowtail flounder are already being assessed jointly by the USA and Canada under the TRAC

process, and more are under consideration (<http://www.mar.dfo-mpo.gc.ca/science/TRAC/trac.html>). Although still a single species approach, this is in keeping with an EAM at the spatial scale by considering each species in the context of the larger Gulf of Maine Area in assessments and management.

For the first time, we explore whether there is population synchronicity within a broad range of finfish populations and in total biomass in the Gulf of Maine Area by comparing species dynamics across its four contiguous ecosystems. We hypothesize that long-term trends in biomass do not vary independently across the four regions in the GOMA, but may exhibit local variation. For each species, we ask if there are any significant trends, and which populations are primarily responsible for each trend. We then ask whether the trends are coherent across ecosystems and test whether environmental factors contribute to coherency among populations. Our expectation is that species within the mid range and/or northern limits of their spatial distribution will respond positively to warmer waters, while those on the southern limit of their range will respond negatively.

The value of comparing the dynamics of fish populations in the contiguous ecosystems of the Gulf of Maine Area is that it furthers our understanding of factors affecting population dynamics and enables the elucidation of patterns common across species. Furthermore it provides the essential contextual information for building an ecosystem approach to management at the scale of the ecosystem, rather than at the level of a single stock.

Methods

Description of surveys and survey areas

The four regions of the GOMA are surveyed separately by Canada and the US (Figure 1). These multi-species surveys are designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. All surveys have a stratified random design, and have a survey time series of over 35 years (with the exception of the Canadian survey of eastern Georges Bank). The surveys are conducted in depths from approximately 27 to 366 m; however, greater depths are occasionally sampled in the canyons along the continental shelf break. Within each depth-region stratum, stations are assigned randomly and the number of stations allotted to a stratum is in proportion to its area (with a minimum of 2 per strata). Once onboard, fish are sorted to species, weighed (0.1 kg), length measured (cm), sex and maturity determined, and subsamples of key species eviscerated for feeding ecology studies.

In Canadian waters, the Bay of Fundy (BoF) and the western Scotian Shelf (WSS) have been surveyed by Canadian vessels once per year in July since 1970 and Eastern Georges Bank has been surveyed since 1986 in February. The surveys used a #36 Yankee bottom trawl from 1970-1981, and a Western IIA trawl since 1982 (Simon and Comeau (1994), which is towed at approximately 5.5 km h^{-1} for 30 minutes at each station.

The Gulf of Maine (GoM) and Georges Bank (USGB) are surveyed via US vessels twice a year, once each in the spring and in the autumn. These broad-scale trawl surveys cover continental shelf waters from Cape Hatteras, North Carolina to Nova Scotia (approximately $290,000 \text{ km}^2$), with strata assigned to the major regions along the eastern US seaboard. All four seasons are sampled, but the major focus has been in

spring (March-May) and autumn (September-November), with winter and summer surveyed more sporadically. The surveys generally utilize a #36 Yankee (or similar) bottom trawl towed at approximately 6.5 km h^{-1} for 30 min at each station. A more detailed description of the bottom trawl survey design and protocols are provided in Azarovitz (1981) and NEFSC (1988).

There were 7 survey series in total and we studied the trends of 19 fish species that were common to all seven surveys: cottidae (longhorn sculpin *Myoxocephalus octodecemspinosus*, sea raven *Hemitripterus americanus*), gadoids (Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, pollock *Pollachius virens*, silver hake *Merluccius bilinearis*, white hake *Urophycis tenuis*, red hake *Urophycis chuss*); elasmobranches (little skate *Leucoraja erinacea*, thorny skate *Amblyraja radiata*, spiny dogfish *Squalus acanthias*, winter skate; *Leucoraja ocellata*); flatfish (American plaice *Hippoglossoides platessoides*, winter flounder *Pseudopleuronectes americanus*, witch flounder *Glyptocephalus cynoglossus*, and yellowtail flounder *Limanda ferruginea*); pelagics (Acadian redfish *Sebastes spp.*, Atlantic herring *Clupea harengus*) and goosefish *Lophius americanus*. In addition, we studied the trends of the total biomass of all species caught in the surveys.

Relative abundance (weight per tow) from each survey was first $\log(x+1)$ transformed. To correct for differences in catchability among the surveys, we standardized each survey time series (subtracted the mean and divided by the standard deviation) before conducting statistical analysis.

Environmental data

The temperature regime was estimated using the extended reconstructed sea surface temperature (ERSST version 3) dataset. This dataset is based on the SST compilation of the International Comprehensive Ocean-Atmospheric Data Set and uses interpolation procedures to reconstruct SST in regions with sparse data (Smith and Reynolds 2004). While the dataset extends back to 1854, we used values from 1970-2007 where the 95% confidence uncertainty of ERSST data is 0.1°C or less (Smith and Reynolds 2004). The spatial resolution of the data is 2° longitude by 2° latitude. There is considerable coherency among 2° x 2° grids in the Northwest Atlantic (Friedland and Hare 2007) so we averaged the monthly ERSST over the area of interest. We used wind stress data as an additional environmental variable derived from National Centers for Environmental Prediction (NCEP) files recorded from four points in the Georges Bank, Gulf of Maine region. Wind stress was computed using the method of Large and Pond (1981). We calculated the number of “wind events” greater than 12 m s⁻¹ in each year and used this in our statistical analyses.

We used two indices of longer term climatological conditions that affect GoMA, the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation. The mean winter NAO index was used because most of the variance in the NAO occurs in the winter months and is the only teleconnection pattern that is evident throughout the year in the northern hemisphere (Hurrell et al. 2003). The NAO index we used is calculated as the difference between surface pressure of the subtropical (Azores) high and the Subpolar (Iceland) low. While variability in the NAO has been associated with changes in precipitation, sea surface temperature, sea ice formation and thus, with ecosystem change (Drinkwater et al. 2003; Greene et al. 2003) and fish recruitment (O'Brien et al. 2000;

Reid et al. 2001; Lindley et al. 2003), its effects are stronger at high latitudes of the northern hemisphere and occur at time scales of about 10 years (Hurrell et al. 2003?).

The Atlantic Multidecadal Oscillation (AMO) represents sea surface temperature (SST) variability that has occurred in the Atlantic ocean over the time scale of 20-40 years and its effects are strong in the northern hemisphere. The mechanism that causes the AMO has not been completely worked out, but is related to the global thermohaline circulation, driven by global density differences caused by temperature salinity changes as water circulates the globe (Sutton and Hodson 2005). Despite the lack of a clear mechanism, the AMO is a measure of warm phases and cold phases in SST in the Atlantic. The AMO index used herein is based on the detrended Kaplan SST dataset (5 x 5 degree latitude x longitude grids) from 0-70°N. The linear effects of anthropogenic climate change are removed from this time series in order to represent the natural variation in sea surface temperatures that has been observed over the last 150 years and correlated with natural fluctuations that have occurred over the last millennium (Sutton and Hudson 2005). The AMO can camouflage or exacerbate the effects of human induced warming. All environmental variables were standardized before analysis. There was no significant correlation between these variables (Figure 2).

Statistical analysis of multiple time series

To identify coherent trends in survey time series, we used two techniques. First, we used Loess (locally weighted regression smoother) smoothing to visualize long term trends among survey abundance indices for each species. Loess smoothing is a technique that fits a regression to sections of the data by weighting points relative to their distance from the target value. We used a span of 0.50, meaning that 50% of the data were used to

arrive upon the smoothed estimate for each year. The smoothed mean trend of all survey time series is simply the average of the smoothed trends calculated for each time series.

We hypothesized that if species had strongly coherent survey time series then, statistical techniques would identify only one trend to describe all six time series. To identify the number of common trends we used Dynamic Factor Analysis (DFA) in the Brodgar software (www.Brodgar.com). DFA minimizes variance among multiple time series and can be seen as a data reduction technique to reduce the number of time series to a smaller number of similar time series (Zuur et al. 2003). Explanatory variables were incorporated into the DFA analysis to determine if environmental variables could predict trends in species abundance. Model selection was based on Akaike's information criterion (AIC). For each species, thirty possible models were tested and the model with the lowest AIC was chosen to best represent the common trend(s) among surveys and its dependence on environmental variables. Thirty possible models resulted from varying the number of common trends (1, 2, or 3 common trends), incorporation of explanatory variables (none, NAO, ERSST, AMO, Wind), and error covariance matrix structure (symmetric vs. diagonal). We choose the most parsimonious model with the lowest AIC, unless a more complicated model improved the AIC by at least a value of 2 (Burnham and Anderson 2004). Factor loadings and canonical correlations indicated how well the common trends identified by DFA represent each individual trend. To identify coherent trends, we considered survey time series with canonical correlation values greater than 0.45 to be "coherent" with the common trend. We hypothesized that if all survey time series were strongly coherent with one another, DFA would identify one common trend with each survey time series loading to, and closely fitting, this common trend. Lack of

coherence was characterized by the extraction of more than one common trend with only a few survey time series associated with each trend. We provide examples of these two cases. Between these two extremes, we illustrate several species where one common trend was found, but dominated by one survey time series or where multiple trends were found but with strong coherence of all survey time series with each of the common trends.

We used all seven survey time series in the Loess smoothing technique, but excluded the Eastern George's Bank survey time series in the DFA analyses because it was much shorter than the other six time series. In DFA, we analyzed the survey time series starting in 1970 to obtain better model fits even though the USGB and USGOM fall survey time series extended as far back as 1963. In DFA, missing values remain blank and too many missing values can cause instability in the algorithm and higher AIC values.

Results

Visual inspection of the seven standardized survey time series for each species reveals that interannual variability was high, but that several species clearly displayed common trends (Figure 3). An overall declining trend was apparent for cod, white hake, witch flounder, thorny skate and goosefish (Figure 3b,d,n,r,t). An overall increasing trend was visible in Atlantic herring, winter flounder, longhorn sculpin, and spiny dogfish (Figure 3i,l,o,p). Sea raven, red hake and yellowtail flounder also appear to have increased, but the trends are noisy (Figure 3j,e,k). Haddock and Acadian redfish both

exhibit a decrease in abundance during the first half of the survey time series, followed by an increase through the 1990s (Figure 3g,h).

Loess smoothing clarified many long-term trends (Figure 4), and the 19 species can be grouped in 4 main classes of response: (i) declining trends were apparent for cod, white hake, witch flounder, thorny skate, and goosefish (Figure 4b,d,n,r,t), and variable long-term declines were also detected in pollock and American plaice (Figure 4c,m); (ii) increasing trends were exhibited by red hake, Atlantic herring, spiny dogfish, little skate, sea raven, yellowtail flounder and longhorn sculpin (Figure 4e,i,j,k,o,p,q); (iii) a “U” shaped response where biomass decreased from the 1980s to around 1990, then subsequently increased was again seen for haddock and redfish and also for winter flounder (Figure 4g,h,l) and (iv) a inverted “U” where biomass first increased, then decreased (silver hake, and winter skate Figure 4f,s).

Many species exhibit a decrease in the most recent few years of these surveys (total biomass, spiny dogfish, pollock, Atlantic herring, winter flounder, Acadian redfish, sea raven, yellowtail flounder, witch flounder, and goosefish). The degree to which the mean smoothed curve represents each survey time series can be discerned visually, but is also represented as the sum of the squared differences between each smoothed survey time series and the mean curve (Table 1). The species with most coherence (smallest mean residual) were thorny skate, Atlantic herring, haddock, white hake Acadian redfish, witch flounder and silver hake. The species with highest greatest variance among survey time series includes spiny dogfish, yellowtail flounder, total biomass and winter flounder. Because the EGB is a short time series, model fit was poor for some species (thorny skate, herring, witch flounder and goosefish), but for other species the fit is as good as

for the other survey time series that have more observations and contribute more to the loess smoothing.

DFA identified trends on a shorter time scale than loess smoothing and also allowed for the assessment of the role of environmental conditions on population trends. Environmental variables used were not significantly correlated with each other and displayed slightly different trends over time (Figures 2,5). For most species, the best fits were estimated without inclusion of an explanatory variable. However, in seven of the twenty species an environmental variable improved fit, the AMO in six species (total biomass, winter skate, little skate, Acadian redfish, sea raven, and yellowtail flounder) and SST in one species, herring (Table 2). The ability of the DFA model to fit the variability for each survey time series is represented by the diagonal of the error covariance matrix (Table 3). Low values indicate good model fit to the common trends identified.

The trends estimated by DFA are similar to those identified by loess smoothing (Figure 6). For the nineteen species and total biomass, the DFA identified 1 common trend for 7 species and total biomass, 2 common trends for 8 species, and 3 common trends for 4 species (Table 2). Of the 7 species with 1 common trend, only goosefish displayed coherence among all six time series (Figure 7), i.e., all six survey time series were positively loaded on this common trend, with canonical correlations between the actual time series and the common trend >0.45 . Of the remaining 6 species, five of the white hake time series were coherent (not BoF), 4 of the winter skate time series were coherent (not BoF or WSS), 3 of the Acadian redfish, yellowtail flounder and total biomass time series were coherent and 2 of the little skate and silver hake time series

were coherent. In most cases, the models that fit the data best, averaged across all survey time series for each species (Table 3), are those with a higher number of common trends identified; the five worst fitting models are for Acadian redfish, goosefish, little skate, total biomass and silver hake, all of which have one common trend (Table 2). The 3 best fitting models are for Thorny skate, Atlantic herring and winter flounder, all of which have 3 common trends.

Of the 8 species with 2 common trends, haddock, witch flounder, Atlantic cod and spiny dogfish had 3 or more survey time series highly correlated with the two common trends (Table 2). Longhorn sculpin, red hake, sea raven and pollock had between 2 and 4 survey time series highly correlated with the two common trends. Four species had 3 common trends identified by the DFA: thorny skate, Atlantic Herring, American plaice and winter flounder. In general, the best fits of the DFA models occurred for the Georges Bank and Gulf of Maine surveys (Table 3).

The results display a range of coherency among the species for the different survey series. A closer look at four of these species (goosefish, silver hake, Atlantic herring, and winter flounder) illustrates this further (Figures 7-10). According to our hypothesis, goosefish displayed the most coherence among the six survey time series; the DFA identified one common trend (Figure 7a); the factor loadings for all six survey time series were high (Figure 7b); the canonical correlations between the six survey time series and the common trend were all >0.45 (Figure 7c, Table 2), and the curves estimated by DFA fit well with the data (Figure 7d). The USGB (Fall) and GoM (Fall) survey series were most highly loaded on the common trend and these survey time series

have the best fits (Figure 7d, Table 3). The USGB (Spring) and GoM (Spring) had low loadings on the common trend and fit the least well. (Figure 7d, Table 3).

Similar to goosefish, one common trend was identified in silver hake (Figure 8a, Table 2). All survey time series were positively loaded on this common trend (Figure 8b), but these loadings were all less than 0.30. Only two survey time series, USGB (Spring) and USGB (Fall), had canonical correlations that were >0.45 (Figure 8c, Table 2). The estimated trends for USGB (Spring) and USGB (Fall) fit the data well (Figure 8c, Table 3) but the fit of the estimated trends for the other survey series is much poorer. The trends created by DFA were strongly influenced by these two survey time series and do match well with the trends found by loess smoothing (Figure 8c, Figure 4).

Although three common trends were identified for Atlantic herring, this species represents a clear case of coherency across all six survey time series. Because three common trends were identified in contrast to silver hake and goosefish where 1 common trend was identified, this result could be misinterpreted as non-coherent (Figure 9a, Table 2). However, all of the survey time series were positively loaded with each of the three common trends (Figure 9b,) indicating consistency and most have high canonical correlations with each survey time series (Figure 9c, Table 2). Although the long-term trend in abundance across the entire GOMA region is adequately described by one common trend, the lowest AIC value was obtained when three common trends were used to fit the data. The common trends extracted are similar to each other (Figure 9a), but the DFA is able to fit both the long term-trend and short-term local variation in each survey time series by using the three common trends (Figure 9d).

The results for winter flounder indicate that there is little coherency among the survey series across the GoMA: there are three common trends (Figure 10a, Table 2); these trends have variable loadings for each survey time series (Figure 10b), few of which are correlated with the estimated trend (Figure 10c). The model fits are reasonably good (Table 3, Figure 10d), but the good fit is the result of fitting three very different trends (Figure 10a). The first common trend is similar to the mean trend estimated by loess smoothing where there was a sharp dip in abundance in the 1990s (Figure 10a, Figure 4l), but the second and third trends are very different, the second showing a steady increasing trend that characterized the WSS and BOF survey time series (Figure 10d), and the third a slight downward trend, with a peak in the early 1980s and around 2000.

As exhibited by loess smoothing and DFA, the population trends of haddock are remarkably similar in all surveys and show a decrease from 1980-1990, followed by an increase from 1990-2000 (Figure 4h, 6h). Similar peaks occurred between 1980 and 2000 in total biomass and in other species, particularly, pollock, little skate, winter skate, winter flounder, yellowtail flounder and Acadian redfish. However, peaks in one survey time series occur at the same time as dips in other survey time series for the same species. For instance, there is a dip in total biomass between 1980 and 2000 in the majority of the survey time series, particularly the GoM (Spring) and GoM (Fall) with a concurrent increase in USGB (Spring). This trend in total biomass is reflective of similar trends observed in individual species such as pollock, little skate, winter skate, winter flounder, yellowtail flounder. However, the peaks and dips do not occur in the same survey time series across all species. For instance, there is a peak in abundance of yellowtail flounder in the BoF during this time period, but a dip in the remainder of the surveys. A similar

pattern occurs in winter flounder. In contrast, a peak occurs in winter skate in the USGB and USGOM surveys, but a simultaneous dip occurs in the WSS survey time series. A similar dip on the WSS occurs in sea raven. Acadian redfish decreased in abundance during this time in the spring on USGB and GoM with an increase on the WSS and EGB.

When survey time series are very coherent, loess smoothing and DFA yield similar results as in the case of thorny skate, Atlantic herring, and haddock. The best fits were obtained in these three species with both DFA and loess smoothing (Tables 1,3). The mean trend identified by loess smoothing is similar to the trend estimated in DFA (Figures 4,6). The poorest fits in loess smoothing were obtained for winter flounder, total biomass, yellowtail flounder, and spiny dogfish and indeed either poor fits or multiple common trends were identified using DFA. However, DFA has the added benefit of using multiple survey time series to obtain good fits for even non-coherent time series. This is illustrated by the winter flounder results where 3 very different trends were extracted, but the average covariance for winter flounder was low.

Discussion

Despite differences in surveys, gear, season, and sampling areas, there was considerable synchrony and coherence among the seven survey time series that we examined for most of the species occurring in the GOMA ecosystem. Given the adjacency of the four areas of the GOMA, we hypothesized that the long-term trends in biomass of fish species would not vary independently across the four regions of the GOMA, but that they may exhibit local variation. We further suggested this synchronicity of population dynamics could be due to large scale environmental forcing.

The results of the “visual” examination of survey trends, the loess analysis and the DFA are largely confirmatory, with the DFA teasing out nuances in the trends and providing a statistical basis for determining when survey trends are coherent. Based on the “visual” inspection and loess smoothing, the species survey trends can be grouped into 4 groups: decreasing; increasing; decrease followed by an increase (a “U” shaped response) and an increase followed by a decrease (an inverted “U” shaped response). The DFA added detail to these groupings and identified species which belong to more than one group due to multiple responses across survey series, such as red hake which had 2 common trends, (one increasing and one an inverted “U”) and winter flounder which had 3 common trends (“U”, increasing and variable stationary).

The time series of survey estimates for many species were coherent across at least part of the GOMA. Goosefish was the only species that the DFA identified with one common trend, coherent across all 6 survey time series. However, the results demonstrate that the identification of one common trend is not sufficient to determine coherency among survey series for two reasons: (i) one common trend may only be correlated with a few survey series (eg., little skate), or (ii) that the common trend may be positively correlated with one survey series and negatively correlated with other series. In the case of yellowtail flounder, for example, although the DFA identified one common trend, the canonical correlation results indicate that the biomass trend of yellowtail flounder in the BOF in the summer is opposite to that on GB(Spring) and GB (Fall), see below. In addition, more than one common trend can be coherent across all survey series. For example, 3 common trends were identified for thorny skate, yet all survey series were positively correlated with each of the 3 trends (with the exception of USGB (Fall) with

the second trend), indicating that the common trends were similar. Coherency is thus identified by a combination of the number of common trends **and** their canonical correlations with the original data.

Given this definition of coherency, 5 species were coherent across the GOMA: goosfish, thorny skate, herring, haddock and Atlantic cod. White hake and winter skate were coherent across the GOMA excluding the BOF, and WSS respectively, and spiny dogfish across USGB (Fall and Spring), GOM (Fall) and BoF. While sea raven exhibit opposite trends in the BOF and USGB spring, there was coherency among the GOM and GB survey series. There was less coherency in the dynamics of the other 10 species examined. Four species with one common trend were among the species which showed the least coherency across the GOMA (yellowtail flounder, total biomass, little skate and silver hake). The one common trend was only coherent across two survey series, and in the case of yellowtail flounder and total biomass, the common trend was also correlated with the data in the opposite direction.

Total biomass is a conservative property of an ecosystem; as species are fished and their biomass reduced, other species increase in abundance and “replace” these species in the foodweb. With the removal of top predators lower trophic levels can be expected to increase. Thus changes in total biomass can be reflective of changes in ecosystem productivity, which can include outbursts of short-lived species, changes at lower trophic levels due to oceanographic conditions, or changes in ecosystem structure caused by fishing. There was considerable variation in the survey trends of total biomass across the GOMA. Since this is an aggregate of many species, it was not surprising that this was one of the poorest fitting models in the LOESS and DFA analysis. The DFA

resulted in one inverted “U” shaped common trend which did not fit the BOF or WSS survey time series (total biomass has increased in these areas), but was positively correlated with the USGB Spring survey data and negatively correlated with the GOM (Spring) and GOM (Fall). There are no declining trends among the survey areas, and no overall declining trend, suggestion that biomass is conserved across the GOMA. Similarly, Link et al. (2002) found little variation in total biomass of the US GOMA ecosystem, but that fish biomass across different functional groups varied.

We hypothesized that environmental forcing factors may drive broadscale synchrony across populations and regions. We explored 4 potential environmental variables and only the AMO and SST added explanatory power to these models for 7 of 19 species plus total biomass. We had hypothesized that species within the mid range and/or northern limits of their spatial distribution would respond positively to warmer waters (thus to a positive AMO), while those on the southern limit of their range would respond negatively. Our results give scant support for this hypothesis. The AMO increased from the mid 1970s and has been above the long term average since 1995. The species which have a more southerly distribution are winter skate, little skate and yellowtail flounder. Of these yellowtail flounder and little skate increased, supporting the hypothesis. Redfish, American plaice and sea raven are more northerly species, so their biomass should decrease according to this hypothesis. However, only the biomass of sea raven decreased and redfish increased. In the case of ERSST, herring biomass has increased since the mid-1980s, coinciding with an increase in ERSST only in the most recent years. However, the trend in the ERSST is reflected, not in the long-term increase

of herring stocks extracted by the first common trend in the DFA, but rather in the localized peaks evident in the second trends.

A more parsimonious explanation of the AMO may be that it is simply a trend that helps explain the patterns observed in the data (either positively or negatively). In the case of Acadian redfish, yellowtail flounder, little skate and total biomass, their pattern of increase is comparable to the AMO. In the case of winter skate, the biomass trend is opposite the AMO trend. These 4 species and total biomass have only one common trend, but are among the poorest fitting models, so the AMO may have simply helped the fit. In the case of sea raven and American plaice, which have 2 and 3 common trends respectively, and are also among the poorest fitting models, the first common trend is opposite the AMO trend. Again, the AMO may have simply helped the fit.

This lack of clear link between coherent (or not so coherent) population dynamics across GOMA and environmental variables suggests that some other factor must be at play. We have focused on large scale environmental forcing in this paper, but other explanations could include (i) other large scale forcing factors such as fishing, and (ii) a meta-population structure supported through dispersal.

(i) Fishing

Fishing has occurred throughout the GOMA for centuries, with an intense level of effort since the 1950s. Fishing, that is, the sustained removal of a large proportion of a fish population over decades, is a major forcing factor affecting the population dynamics of a species. Fishing reduces the abundance of populations, and if fishing pressure is too high (ie., removals greater than surplus production), the population will decline. Of the ten species with coherent survey trends over all or part of the GOMA, five have

experienced considerable declines across the GOMA: goosefish, white hake, thorny skate, Atlantic cod, witch flounder. Pollock and American plaice have also declined across GOMA, but their survey trends are less coherent. All of these species have been subject to high fishing mortality, either as a target species, bycatch or both. They are also larger-bodied species, with later age at maturity and size at maturity and will take a longer time to recover from overfishing. Since the 1990s and a wide-spread reduction in fishing effort, the rate of decline of these species has been reduced, and in some cases reversed (eg., pollock, American plaice and goosefish). This, and the lack of influence of an environmental factor in the DFA is a clear indication that fishing has been the main forcing factor on the population dynamics of these 7 species across the GOMA, resulting in coherent changes in biomass estimates from all surveys. The same argument may be made for haddock which also decreased to around the 1990 across the GOMA. However, since the reduction in exploitation in the early 1990s, the biomass of haddock in all areas has increased back to earlier levels, although the BoF has since decreased again.

Of the other species with coherent survey trends across the GOMA, three had increasing trends, Atlantic herring, Spiny dogfish and Sea Raven, and winter skate had an inverted “U” across Georges Bank and the GoM. It is not clear what factors may be contributors to these trends, but is likely a compensatory response or release from predation. Other than herring, none of these species has been traditionally fished, although spiny dogfish landings have increase five-fold since 1987 (Rago et al. 1998) and little skate is a likely to be the primary skate species taken in the New England bait fishery (<http://www.nefsc.noaa.gov/sos/spsyn/op/skate/>). Herring is a small pelagic, which matures and reproduces at younger ages than the larger fish described above.

Further more, these forage fish may benefited from predatory release, due to the reduction of predators (Link et al 2002, Bundy and Fanning 2005)

(ii) Metapopulation Structure and dispersal

The survey trends and DFA results indicate that some of the survey trends are opposite which suggests that there may be movement between different areas of the GOMA. In the case of yellowtail flounder for example, there is a peak in biomass in the BoF, centered on the late 1980s, while there is a trough in the biomass trends for all other surveys. Since then the biomass in the BoF decreased while it had increased elsewhere. This is supported by the negative correlation of the common trend from the DFA with the BoF survey data and the positive correlation with the USGB data for Spring and Fall. This suggests that there may be some movement of yellowtail flounder between Georges Bank and the BoF. Opposite trends in relative abundance were also seen in pollock, winter skate, winter flounder, and Acadian redfish. There was a lack of coherency among the survey time series for all of these species, and movement between areas could contribute to this. Although it is not possible to make any firm conclusions about the spatial movement of these fish, or the possibility of metapopulation structure, the study of connectivity and spatial distribution of these species is an area of important research.

In reality, fishing and multiple environmental factors act upon these fish populations. We did not incorporate multiple explanatory variables into the DFA. While it is possible to incorporate multiple explanatory variables into DFA the number of parameters to fit increases exponentially (adding one extra explanatory variable means 6 additional parameters must be fit, one for each time series). Low AIC values are rarely obtained simply by adding more explanatory variables. However, this work lays the

foundation for additional ecosystem studies that will elucidate mechanisms that generate coherency identified in some species and incoherency in others.

In this DFA, we took the model with the lowest AIC as the best fitting model, whether from the asymmetric or the diagonal matrix. Often, these identify the same model as the best. However, in some cases, two different models are identified, such as in the case of yellowtail flounder. Here, the lowest AIC was obtained using a symmetric error covariance matrix, specifying 1 common trend and using the AMO as an explanatory variable. However, a low AIC value was obtained using no explanatory variables, and identifying 2 trends. While biological knowledge can be used to specify the DFA model, we objectively choose the most parsimonious model with the lowest AIC (Burnham and Anderson 2004).

Our results demonstrate that many species in the GOMA have coherent, synchronous population trends across the BoF, the WSS, the GoM and George's Bank. Among those showing greatest coherency are those which have clear declining trends in all areas and all surveys. The value of this comparative approach across contiguous ecosystems is that it provides a robust basis from which to draw conclusions regarding changes in biomass and potential drivers. A comparative approach is a particularly important contribution to EAM since ecosystems are non-linear networks of interacting species which are difficult to understand. It enables a form of replication, which, if the same results are seen in the replicates, provides robust conclusions which fisheries managers would be foolhardy to ignore. In this case, we have seen that 5 large bodied, long-lived fish species have decreased across the whole GOMA: the implications for management are clear. The situation where forage fish (herring) are concurrently

increasing across the area, a possible response to predatory release, indicates changes in ecosystem structure and possibly in functioning. We also provided evidence of potential movement between areas of the GOMA for some species. These results point clearly to the need for the assessment and management of these resources at the GOMA scale, rather than the stock unit and national boundaries currently in use. The success of rebuilding depleted stocks across GOMA will be dependent on a conservative area-wide strategy that considers that each ecosystem could be a source of recruitment to another.

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Table 1: Model fit of the mean abundance trend calculated by loess smoothing. Values are the sum of squared residuals for each time series from the mean smoothed trend (Mean smoothed values-smoothed individual time series values)

Species	WSS Summer	EGB Feb	BoF Summer	GoM Spring	USGB Spring	GoM Fall	USGB Fall	Average
Total biomass	3.31	14.52	8.26	19.47	10.04	20.94	10.53	12.44
Spiny dogfish	4.46	16.04	9.21	12.32	10.09	13.56	11.29	11.00
Thorny skate	4.87	11.54	2.84	2.51	2.82	1.80	5.26	4.52
Winter skate	26.69	4.98	10.76	2.77	6.03	1.14	10.18	8.51
Little skate	10.72	5.54	9.64	4.11	6.20	3.81	25.64	9.38
Atlantic cod	8.20	8.55	13.65	5.84	3.07	6.16	2.35	6.83
Haddock	3.65	2.85	15.13	3.12	2.13	3.12	5.75	5.11
White hake	4.43	5.82	9.06	5.68	3.11	3.24	4.45	5.11
Silver hake	3.53	3.17	7.12	7.64	3.40	12.19	4.83	5.98
Pollock	22.00	5.30	6.66	10.36	9.97	12.35	5.46	10.30
Atlantic Herring	5.74	9.35	2.61	4.19	4.82	3.93	2.66	4.76
Red hake	9.63	4.22	16.41	7.46	9.18	7.91	18.84	10.52
Acadian redfish	5.68	6.15	4.78	5.18	5.45	7.74	1.94	5.27
Sea raven	12.81	4.38	22.87	6.45	11.64	5.08	7.70	10.13
American plaice	8.89	6.22	9.79	14.42	7.39	11.25	11.85	9.97
Yellowtail flounder	5.84	4.29	34.88	3.83	11.64	6.76	13.94	11.60
Winter flounder	15.98	10.42	18.98	2.96	14.39	2.69	22.05	12.50
Witch flounder	5.56	10.30	6.88	4.84	4.51	3.46	6.18	5.96
Longhorn sculpin	5.50	5.73	8.98	9.85	10.23	8.59	12.81	8.81
Goosefish	2.07	9.87	4.07	4.55	3.43	2.14	7.10	8.46

Table 2: Number of common trends, canonical correlations of each common trend with each time series and relevant explanatory variables in DFA analyses. Species used in examples are in bold

Species	Common trend	WSS Summer	BoF Summer	GoM Spring	USGB Spring	GoM Fall	USGB Fall	Exp variable
Total biomass	1	-	-	-0.59	0.45	-0.88	-	AMO
Atlantic cod	1	0.86	0.45	-	0.66	0.61	0.61	-
	2	-	-	0.62	-	0.83	0.54	
Pollock	1	-0.77	-	-	-	0.48	-	-
	2	-	-	-0.76	-0.80	-0.71	-	
White hake	1	0.60	-	0.70	0.60	0.80	0.90	-
Red hake	1	0.67	0.53	-	-	0.74	-	-
	2	-	-0.56	0.69	-	-	0.70	
Silver hake	1	-	-	-	0.54	-	0.64	-
Haddock	1	0.64	0.64	0.82	0.78	0.83	0.56	-
	2	-	-	0.65	0.70	0.79	0.84	
Acadian redfish	1	-	-	0.80	-	0.96	0.35	AMO
Atlantic Herring	1	0.96	0.76	-	0.59	0.80	0.69	SST
	2	0.45	0.54	0.65	0.87	0.61	0.72	
	3	0.73	0.64	0.57	-	0.95	0.81	
Sea raven	1	-	0.74	-	-0.54	-	-	AMO
	2	-	-	0.70	0.81	0.64	0.48	
Yellowtail flounder	1	-	-0.66	-	0.79	-	0.84	AMO
Winter flounder	1	0.83	0.66	-	-	0.57	-	-
	2	-	0.66	-	-	-	-0.74	
	3	-0.55	-0.64	-	0.61	-	0.57	
American plaice	1	-	0.72	-	0.69	-	-	AMO
	2	-	0.53	0.69	-	0.60	-0.42	
	3	-	-	0.70	0.62	0.54	-	
Witch flounder	1	-	0.46	0.81	0.88	0.62	0.79	-
	2	-	0.77	0.82	0.47	0.71	0.19	
Longhorn sculpin	1	0.73	-	0.61	0.62	0.80	-	-
	2	-	0.55	-	-	0.59	-	
Spiny dogfish	1	-	0.74	-	0.47	0.61	0.62	-
	2	-	0.54	-	-	0.77	0.64	
Little skate	1	-	-	0.58	0.74	-	-	AMO
Thorny skate	1	0.94	0.87	0.81	0.74	0.74	0.70	-
	2	0.55	0.72	0.85	0.54	0.54	-	
	3	0.72	0.68	0.92	0.94	0.82	0.78	
Winter skate	1	-	-	0.52	0.87	0.54	0.92	AMO
Goosefish	1	0.60	0.49	0.45	0.45	0.70	0.84	-

Table 3: Model fit for DFA as represented by the diagonal of the error covariance matrix

Species	WSS Summer	BoF Summer	GoM Spring	USGB Spring	GoM Fall	USGB Fall	Average
Total biomass	0.97	0.97	0.75	0.81	0.23	0.93	0.78
Spiny dogfish	0.81	0.43	0.91	0.55	0.39	0.51	0.60
Thorny skate	0.16	0.21	0.01	0.14	0.30	0.26	0.18
Winter skate	0.89	0.94	0.73	0.21	0.62	0.19	0.60
Little skate	0.80	0.81	0.65	0.40	0.86	0.62	0.69
Atlantic cod	0.34	0.71	0.49	0.44	0.02	0.44	0.41
Haddock	0.62	0.40	0.32	0.33	0.22	0.34	0.37
White hake	0.64	0.85	0.53	0.65	0.40	0.24	0.55
Silver hake	0.88	0.96	0.96	0.72	0.95	0.64	0.85
Pollock	0.50	0.88	0.45	0.33	0.45	0.93	0.59
Herring	0.13	0.35	0.51	0.01	0.09	0.16	0.21
Red hake	0.60	0.61	0.28	0.95	0.46	0.55	0.58
Acadian redfish	0.90	0.82	0.33	0.73	0.11	0.82	0.62
Sea raven	0.67	0.51	0.19	0.34	0.20	0.48	0.40
American plaice	0.84	0.27	0.10	0.39	0.30	0.70	0.43
Yellowtail flounder	0.79	0.56	0.74	0.29	0.94	0.18	0.58
Winter flounder	0.37	0.30	0.35	0.43	0.43	0.13	0.33
Witch flounder	0.82	0.43	0.11	0.27	0.40	0.43	0.41
Longhorn sculpin	0.51	0.64	0.61	0.52	0.24	0.72	0.54
Goosefish	0.65	0.76	0.80	0.80	0.54	0.34	0.65

Figure 1. Map of the Gulf of Maine Area. GB = Georges Bank, BoF = Bay of Fundy, WSS = Western Scotian Shelf, GoM = Gulf of Maine proper. Red lines and labels = Canadian survey strata, green lines and labels = US Survey Strata. Dotted line = Canada/USA International border.

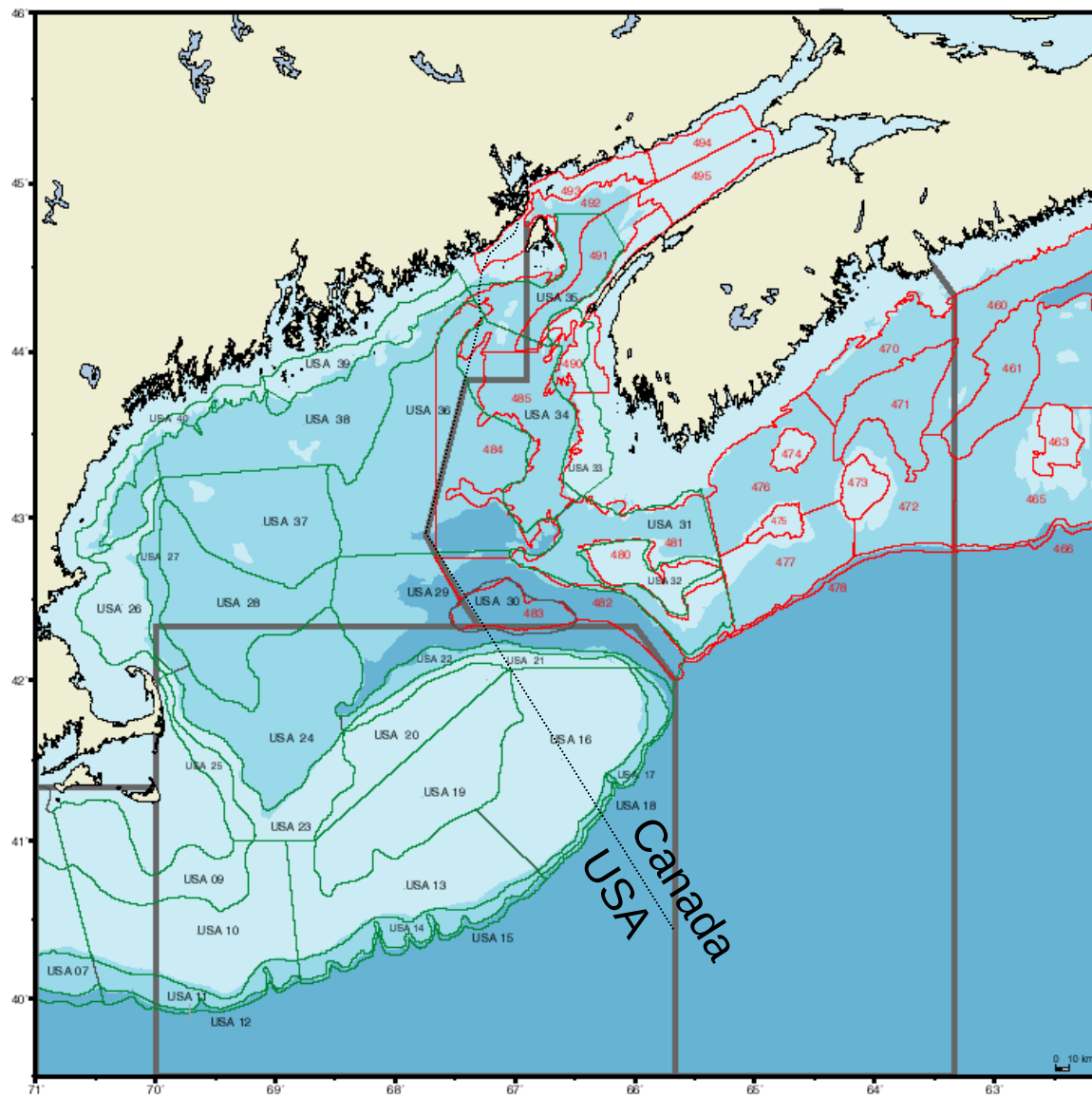


Figure 2: Correlation matrix of standardized environmental variables used in DFA analysis.

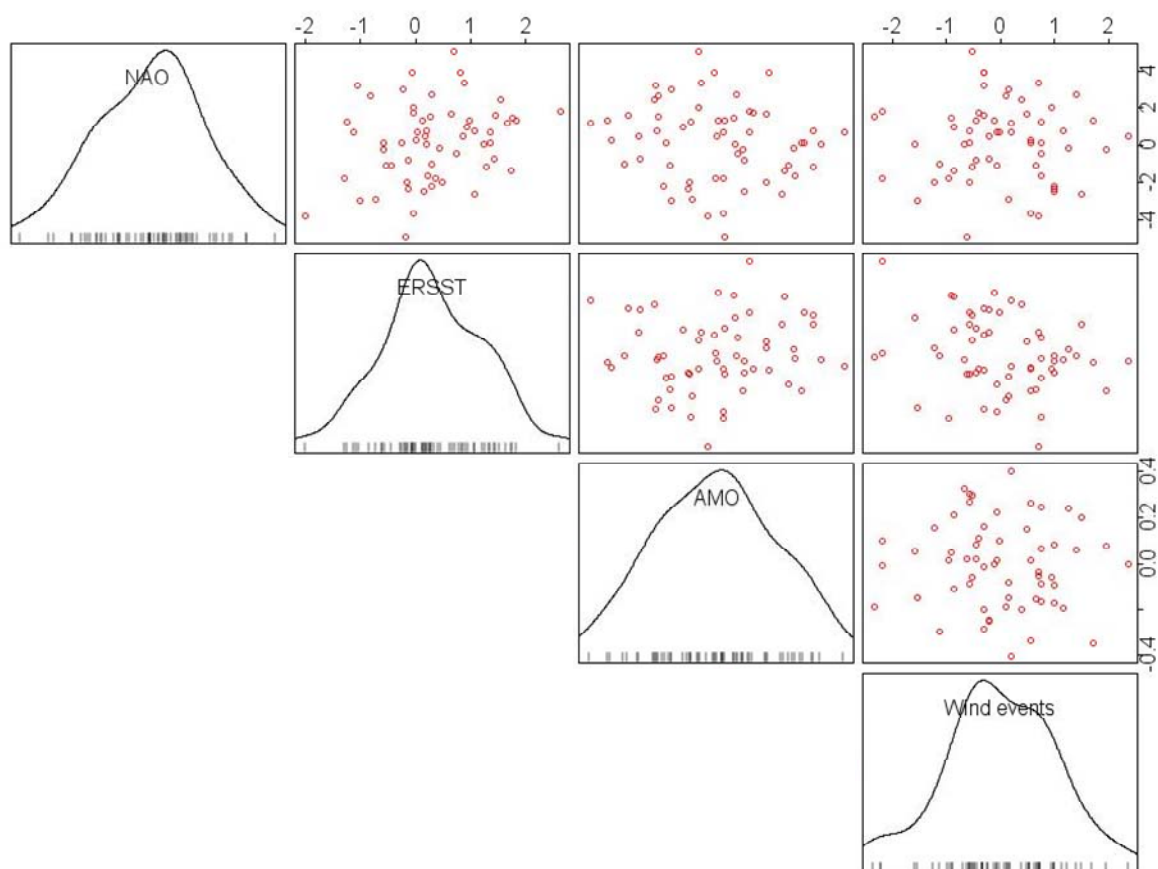
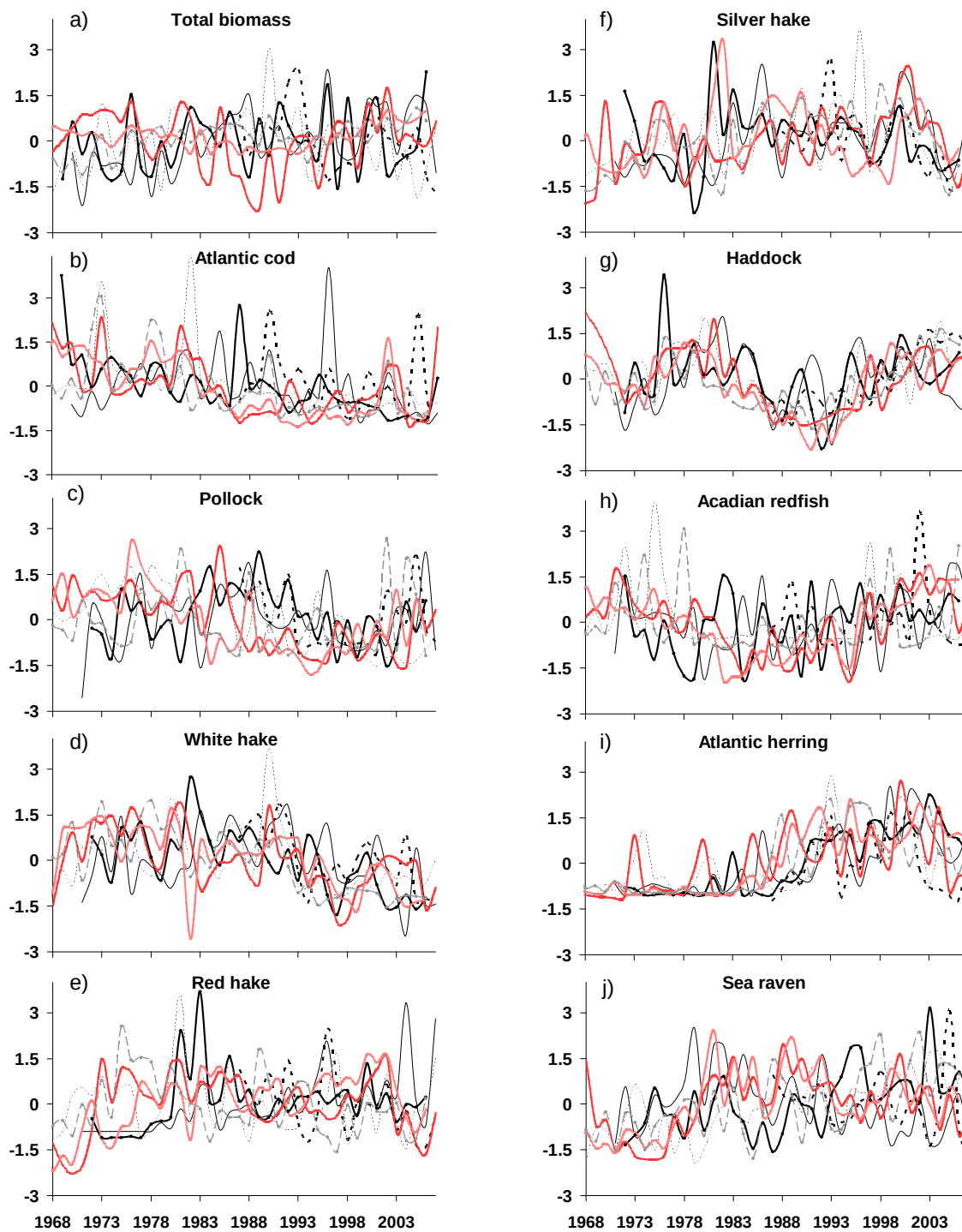


Figure 3: Seven time series of standardized relative abundance of total biomass of each survey and 19 representative finfish species in the GOMA ecosystem.

—●— WSS - - - EGB — BoF — GoM Spring - - - USGB Spring — GoM Fall - - - USGB Fall



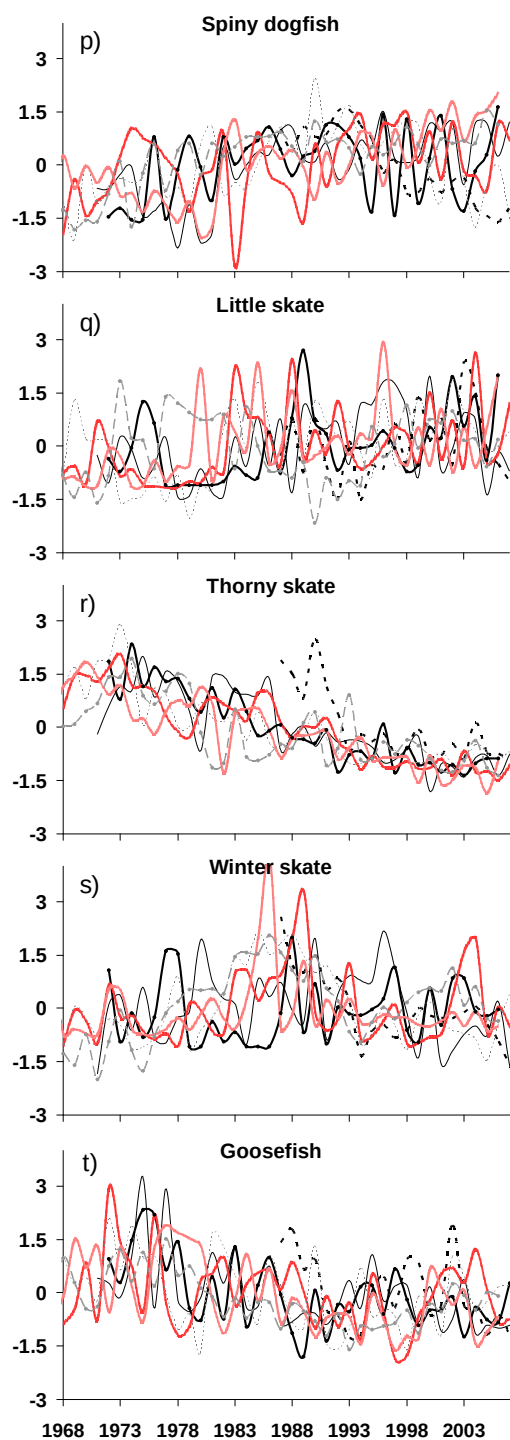
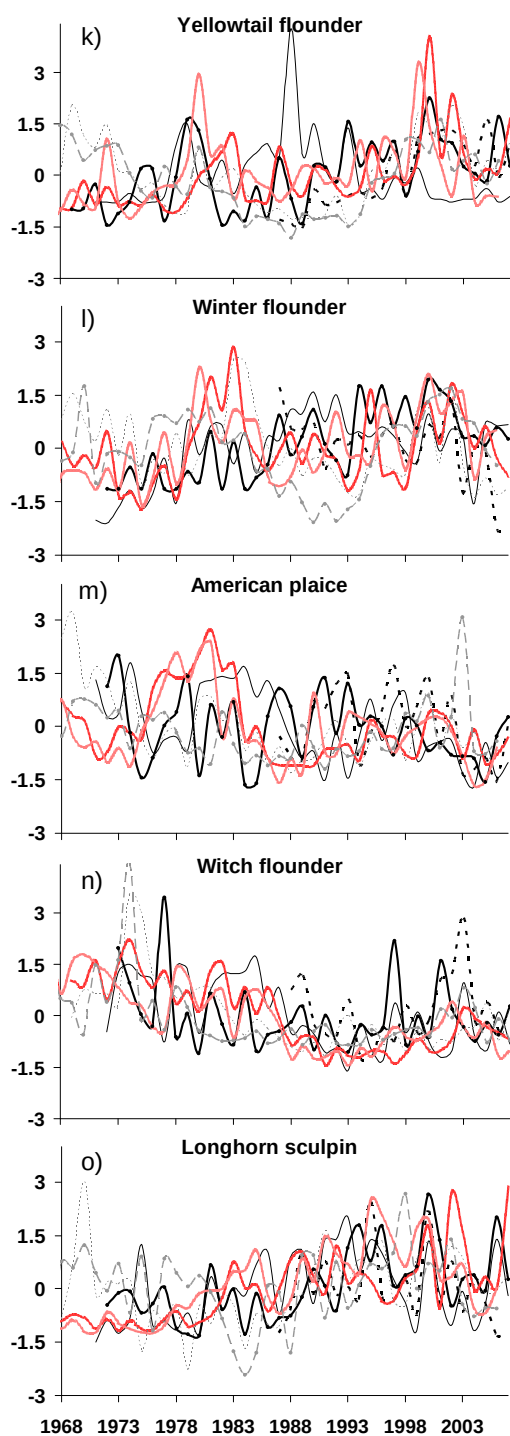


Figure 4: Trends in relative abundance smoothed using loess regression. Different time series are represented by (—) WSS, (---) BOF, (· · ·) EGB, (·····) GOM Spring, (· · · · ·) USGB Spring, (---) GOM Fall, (· · · · ·) USGB Fall, (—) mean.

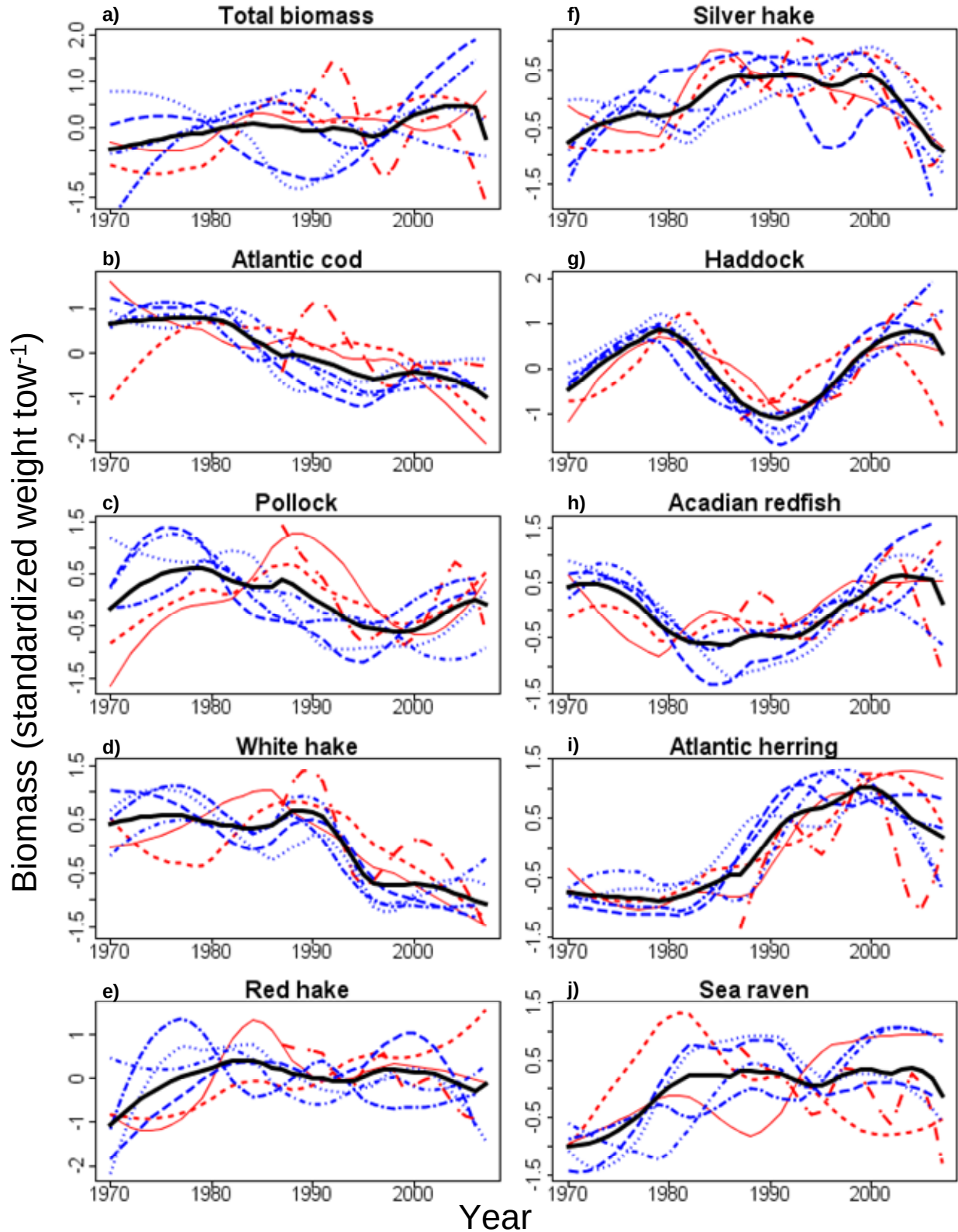


Figure 4: Trends in relative abundance smoothed using loess regression. Different time series are represented by (—) WSS, (---) BOF, (·-·-·) EGB, (·····) GOM Spring, (·-·-·) USGB Spring, (-·-·-) GOM Fall, (-·-·-) USGB Fall, (—) mean

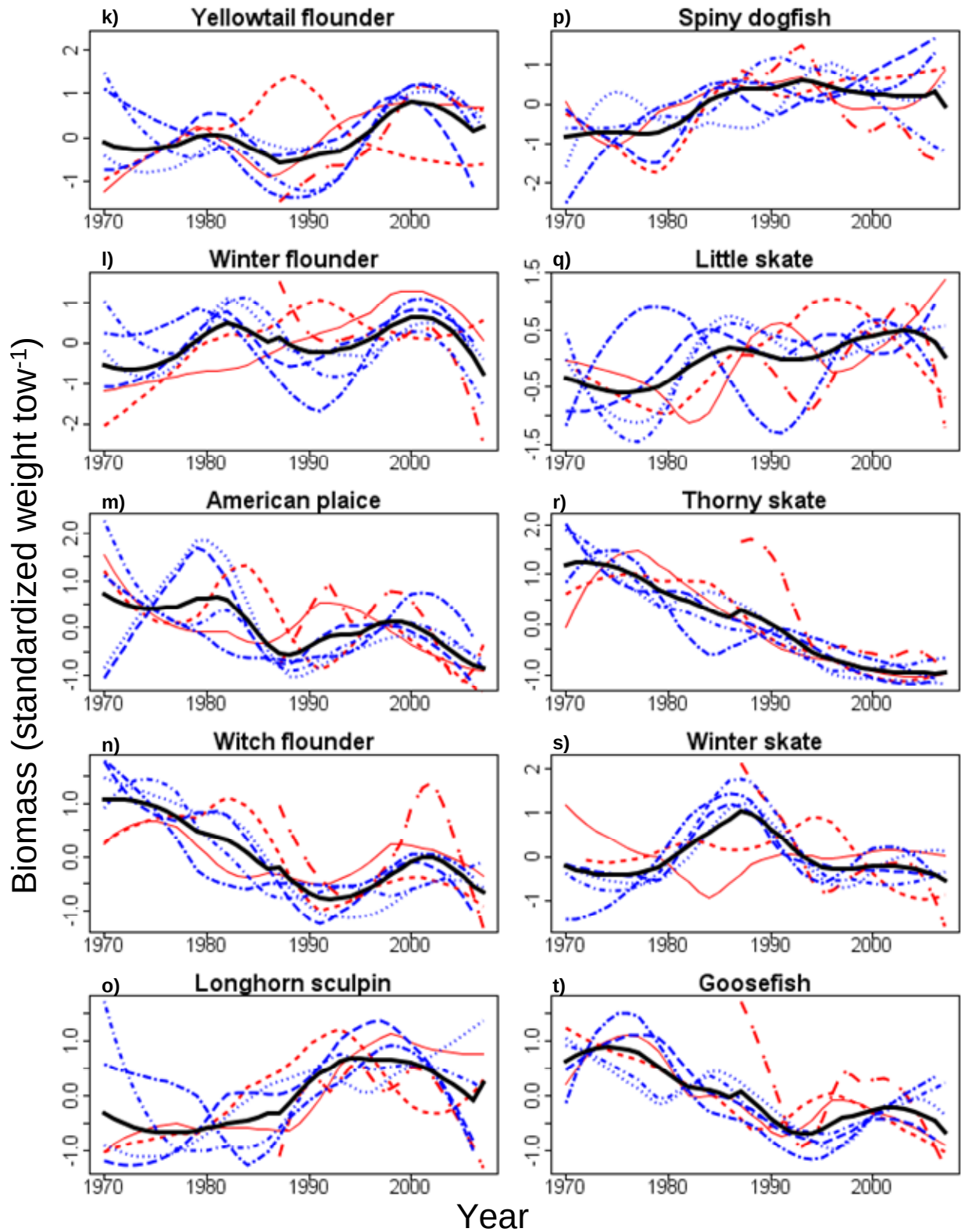


Figure 5 : Standardized time series of a) ERSST, b) Annual wind events, c) NAO, d) AMO. Note the different units on the y-axis

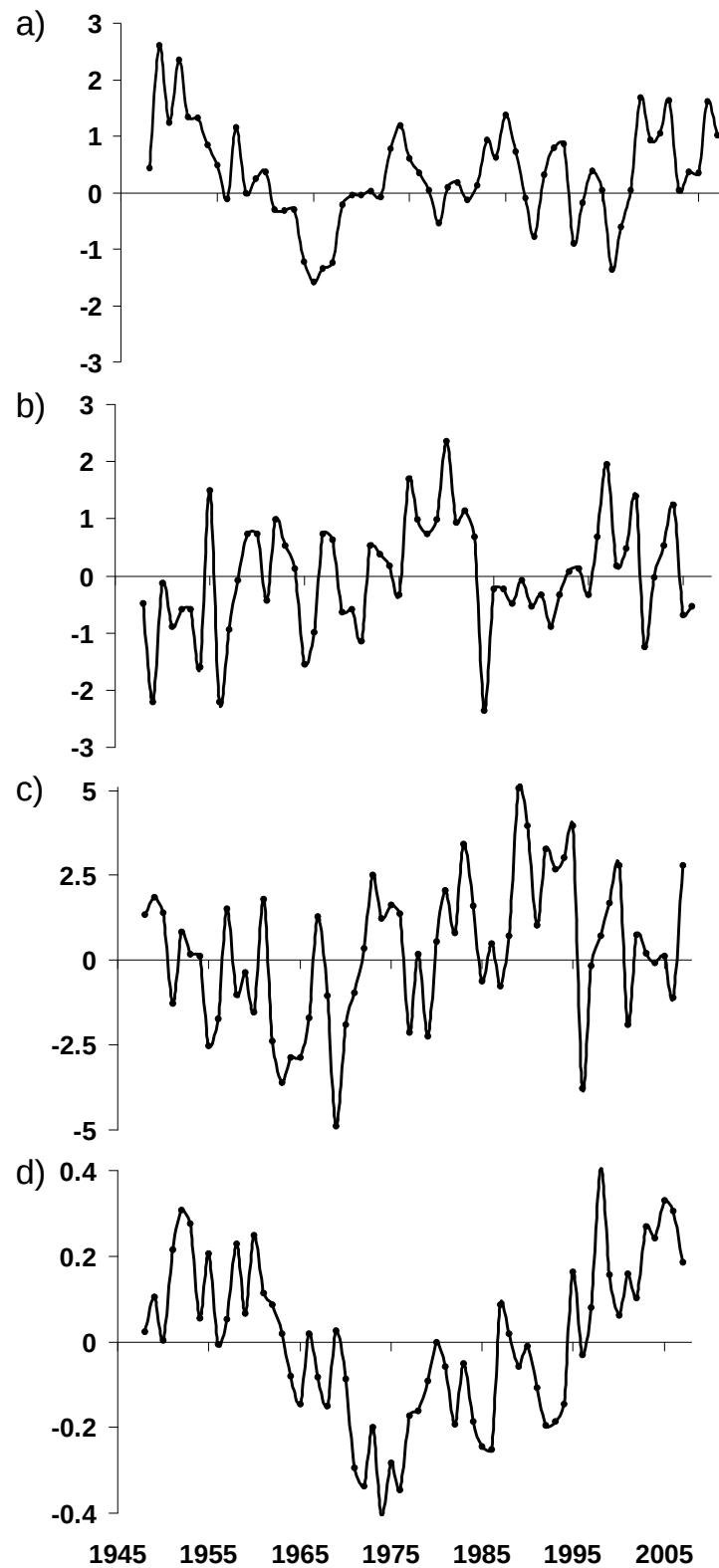
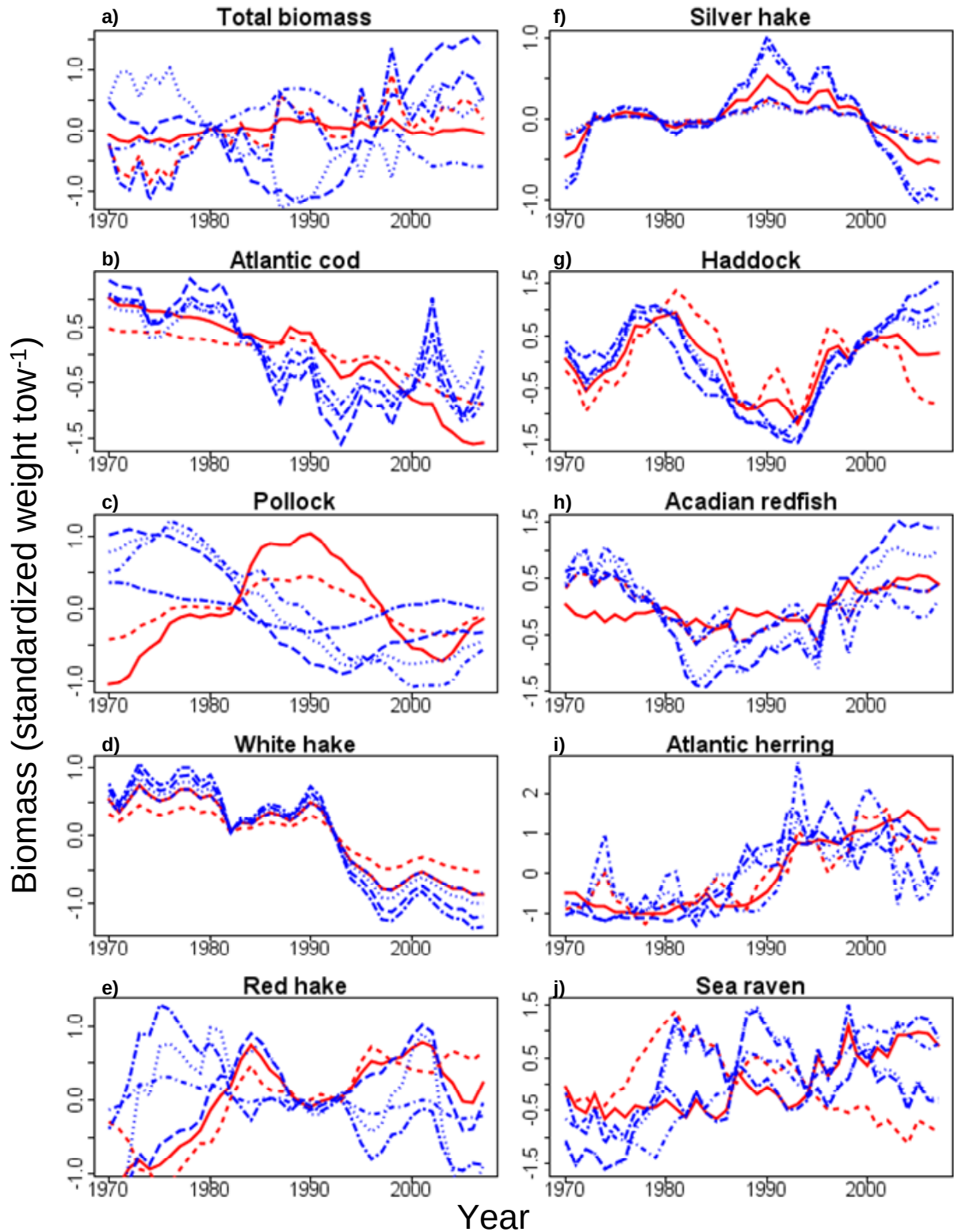


Figure 6 : Fitted trends resulting from common curves identified in DFA. (—) WSS, (---) BOF, (.....) GOM Spring, (-.-.-) USGB Spring, (-.-.-) GOM Fall, (-.-.-) USGB Fall.



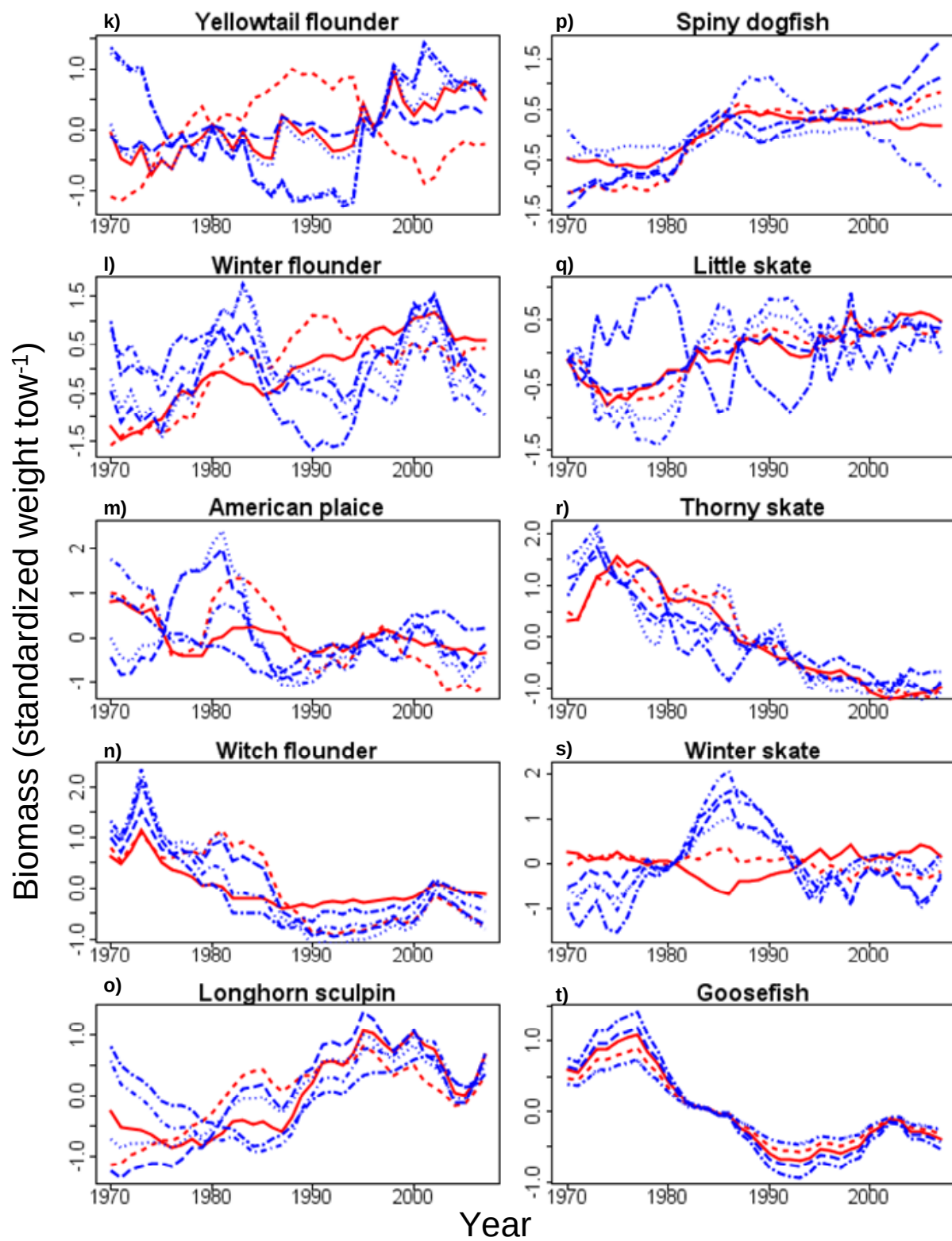


Figure 7: DFA results for a strongly coherent species with one common trend, goosefish (a) the common trend with confidence intervals, (b) the factor loadings of the survey series on the common trend (c) DFA fitted curves for the six time series shown together where green time series indicate series with >0.45 canonical correlations with the common trend and (d) DFA model fits for 6 time series where points are observations and lines are the model fit.

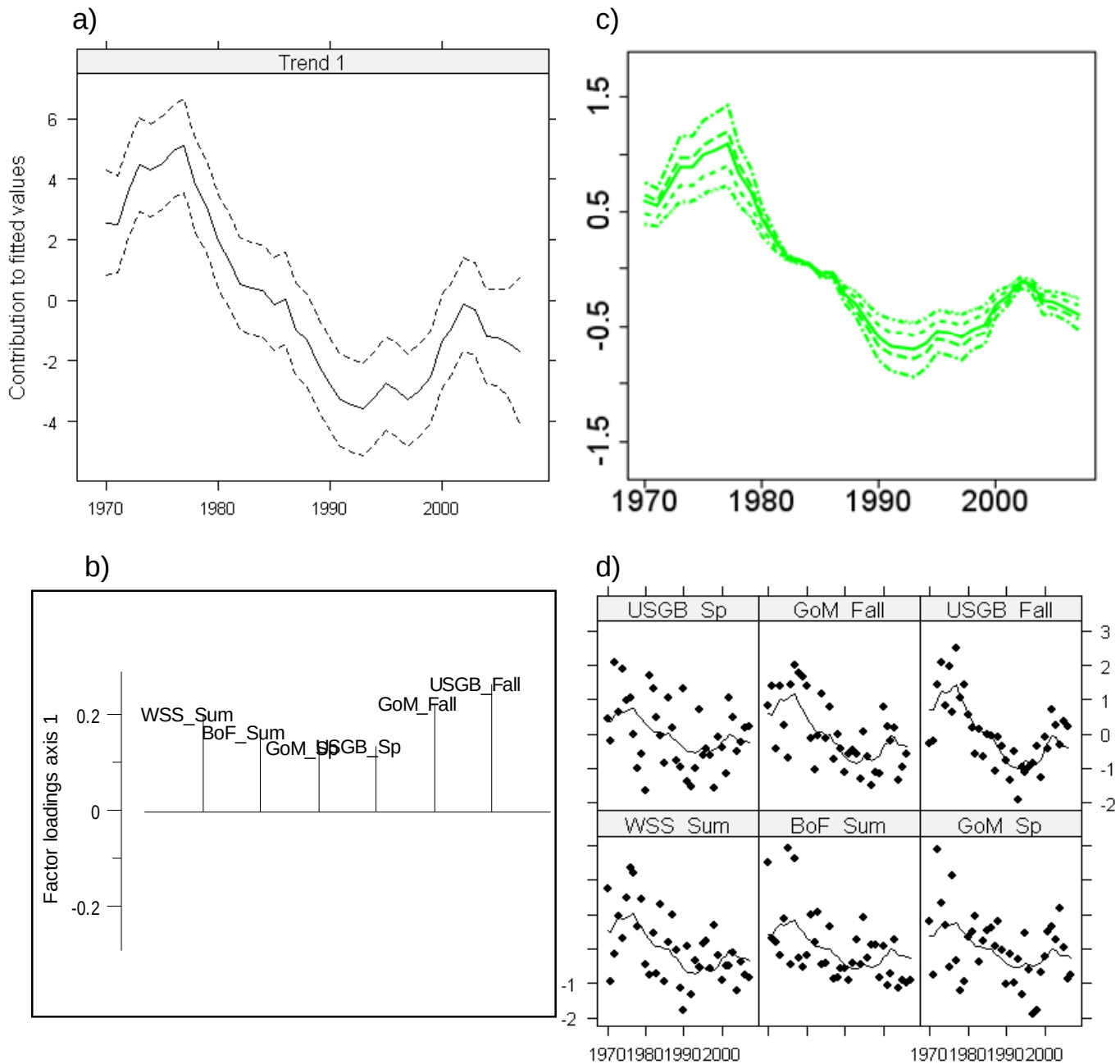


Figure 8: DFA results for a weakly coherent species with one common trend, silver hake (a) the common trend with 95% confidence intervals, (b) the factor loadings of the survey series on the common trend (c) DFA fitted curves for the six time series shown together where green time series indicate series with >0.45 canonical correlations with the common trend and (d) DFA model fits for 6 time series where points are observations and lines are the model fit.

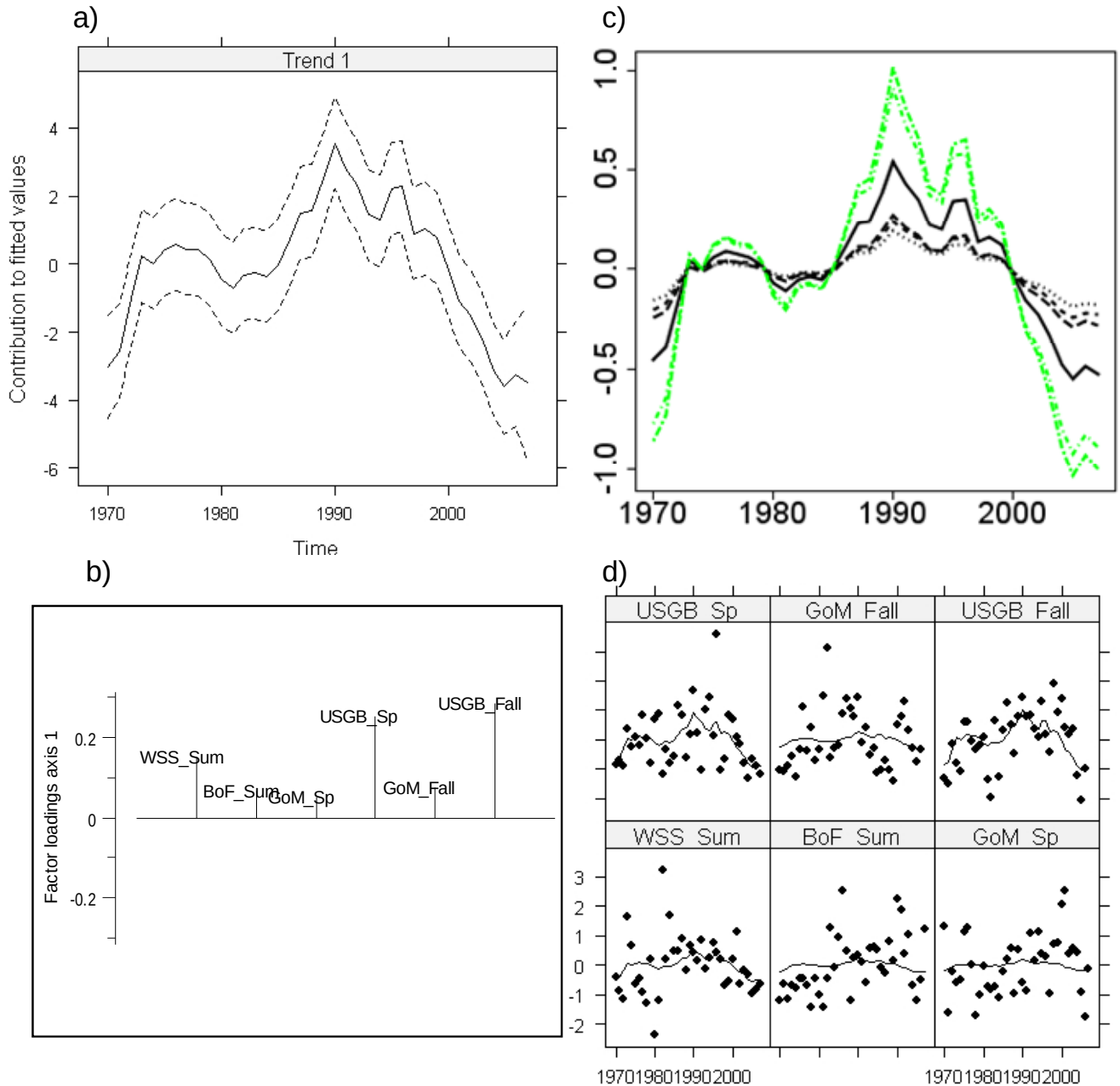


Figure 9: DFA results for Atlantic herring. Three common trends were identified (a) and all survey time series were positively loaded (b) with each common trend, indicating coherence among the surveys

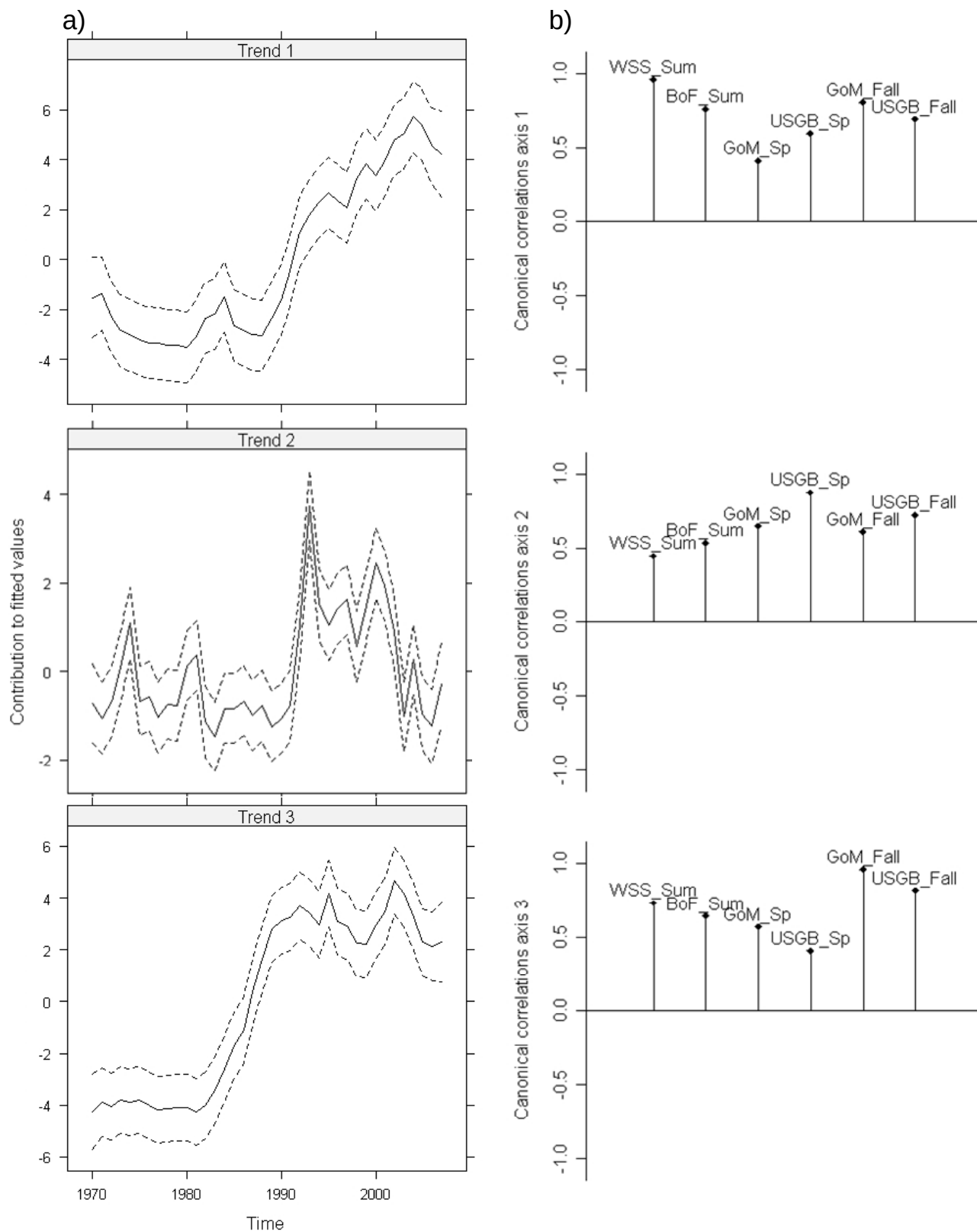


Figure 9: DFA results for herring. Fitted curves (c) for the six time series shown together where green time series indicate series with >0.45 canonical correlations with the common trend and (d) DFA model fits for 6 time series where points are observations and lines are the model fit.

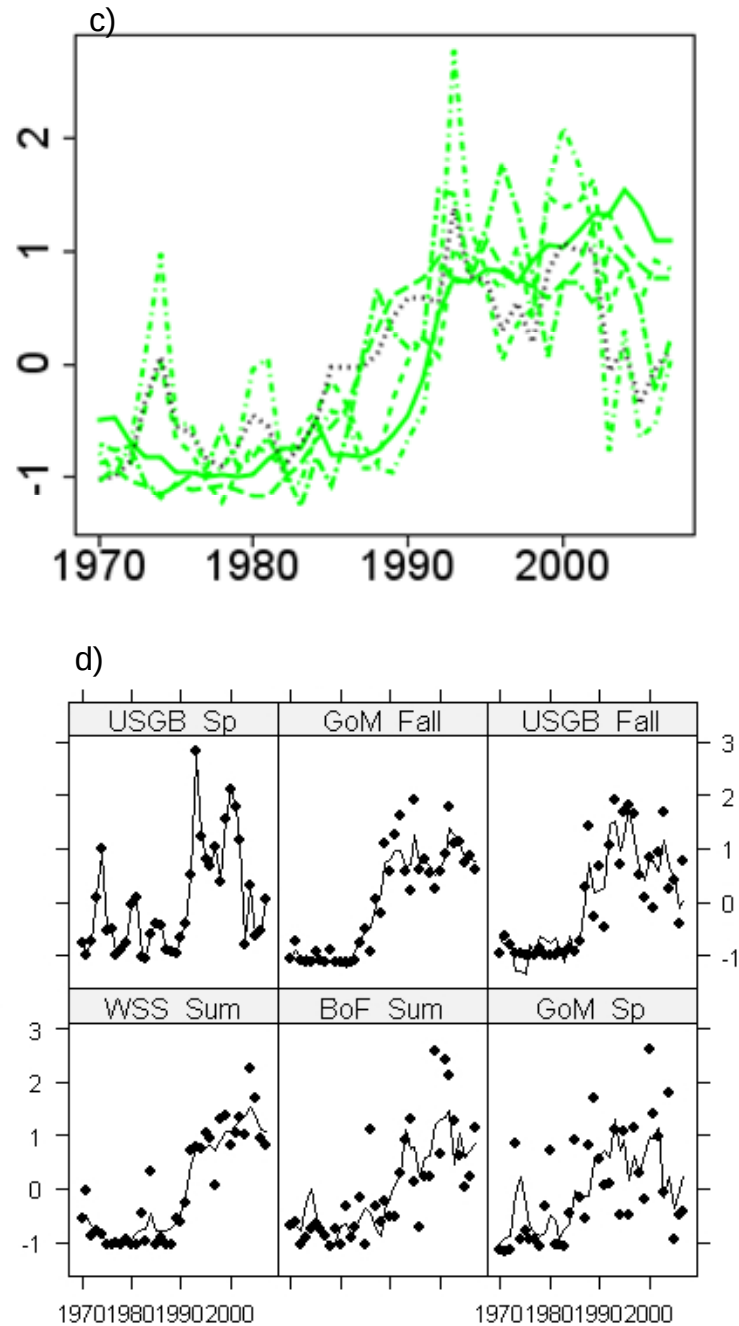


Figure 10: DFA results for winter flounder. Three common trends were identified (a), but only a few of the survey time series were positively loaded (b) with each common trend, indicating lack of coherence among the surveys.

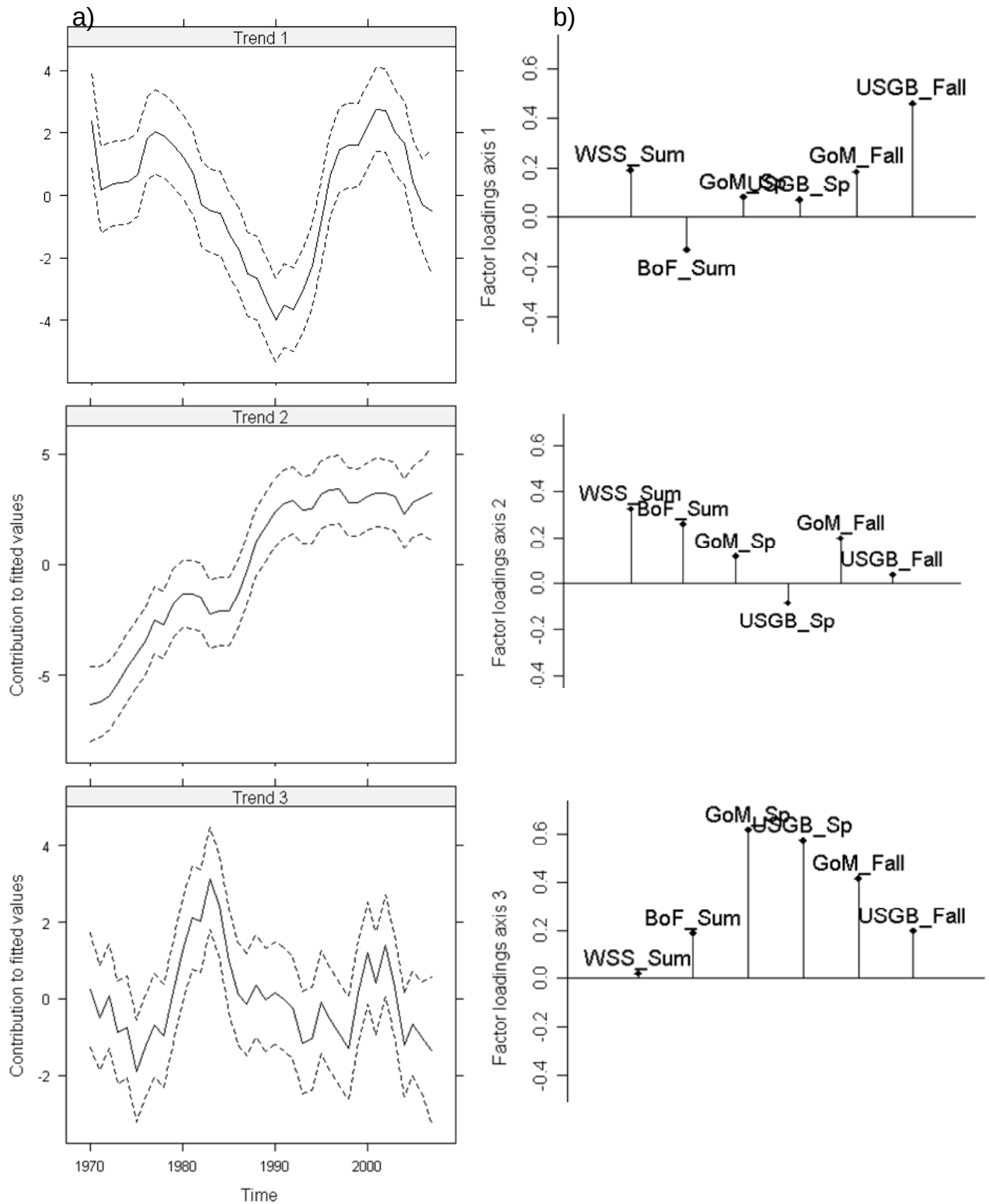


Figure 10: DFA results for winter flounder. Fitted curves (c) for the six time series shown together where green time series indicate series with >0.45 canonical correlations with the common trend and (d) DFA model fits for 6 time series where points are observations and lines are the model fit.

