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Temperature-modified stock-recruitment relationships for Northwest Atlantic fish stocks, a metapopulation approach

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Abstract

In a previous study, we documented poleward shifts in the distribution of many fish stocks that were correlated with large-scale oceanographic indices rather than changes in population abundance. However, shifts in spatial distribution varied spatially among stocks within a species and may have been exacerbated in heavily fish stocks. Stocks at the southern extent of their range experienced more dramatic movements than stocks at the northern extent of their range. We hypothesized that low recruitment in southern stocks relative to the northern stocks can at least partially explain the differences in spatial shifts observed within species. An analysis of stock-recruitment relationships among stocks within species that frequently occur in the US Northeast continental shelf ecosystem suggests that recruitment in southern stocks compared to northern stocks is as good (or better in some species). However, we developed and evaluated stock-recruitment relationships modified by environmental variables that can be used to improve stock assessment models. Including an environmental parameter improved the fit of these recruitment models, particularly in southern stocks, despite the penalty of an additional term and a possible additional source of variability. Incorporating an environmental variable into stock-recruitment relationships may be a promising method to consider the effects of fishing and the environment simultaneously, particularly as the effects of climate change continue to be a concern in management and policy.

Introduction

Poleward shifts in individual fish stocks have been observed in many marine ecosystems (Perry et al. 2005, Mueter & Litzow 2008, Brander 2009) and in the Northeast US continental shelf ecosystem (Weinberg 2005, Nye et al. in press). These patterns are to be expected as coastal and shelf waters warm as a result of natural warming cycles and of global climate change, but appear to occur more rapidly in marine ecosystems than in terrestrial ones (Rosenzweig et al. 2007, Rosenzweig et al. 2008). In the Northeast US continental shelf ecosystem, long-term shifts in distribution were most closely associated with the Atlantic Multidecadal Oscillation, however the mechanisms behind these spatial shifts are not fully understood and are likely different for each species depending on their biogeography, migration behavior and temperature preferences. Detection of these shifts can be used to inform management (Link et al. in review), but elucidation of the mechanisms underlying these shifts will help predict future shifts in distribution, predict changes in population dynamics, and augment quantitative management advice.

There are several possible mechanisms that explain the shifts in distribution observed in the Northeast US continental shelf. First, broadscale changes in temperature might induce directed movement of fish from warm waters to cooler waters within their preferred temperature range that are either deeper or poleward of their historical distribution. While directed movement to more favorable habitat occurs in many species (Tyler & Targett 2007) and has been documented in fish traditionally thought to be "sedentary" (Westwood & Cadrin 2004, NEFSC 2008), large movements on the order of hundreds of kilometers and reductions in the species range on the order of 20,000 km^2 are probably not the result of directed movement alone. Second, migration patterns and timing may change in response to increases in temperature. As the temperature regime warms, cold-water species may not migrate as far south in the winter such that we observe a poleward shift in distribution when sampled in the spring. Similarly, warm-water species may be able to move poleward and expand their range as summers are consistently warmer. To investigate the directed movement and migration in persistent distribution changes, otolith microchemistry techniques and large-scale tagging studies would be needed at large spatial and temporal scales to document migration patterns.

A third mechanism explaining large population shifts in distribution is a change in vital rates in general and in particular, an increase in mortality at the southern extent of a species' range, especially in early life stages. While hatching at lethal temperatures would increase mortality of eggs and larvae directly, reduced growth rate at suboptimal temperatures may indirectly increase mortality via an increase in predation and starvation (Houde 1987, 1989). Furthermore, changes in circulation may transport eggs and larvae to suboptimal nursery habitat and alterations in the phenology of oceanographic processes could also impact the recruitment success of these fishes. Mortality at the southern extent of a species range where temperature is most likely to be above the species preferred temperature may explain the shift in spatial distribution and would be reflected in stock-recruitment relationships. An analysis of stock-recruitment dynamics between northern and southern populations would determine whether there are spatial differences in mortality and recruitment among metapopulations within the same species. We hypothesize that stocks at the southern extent of their range have experienced unfavorable environmental conditions in recent years, leading to poor recruitment and the local extirpation of many of these stocks at the southern extent of their range. Conversely, stocks at the northern extent of a species range may have experienced a shift towards more conditions for recruitment leading to an increase in abundance and range expansion.

In this paper, we test the recruitment mortality hypotheses for three Northeast US fish species where a poleward shift in their distribution was detected (Nye et al. 2009); silver hake *Merluccius bilinearis*, red hake *Urophycis chuss* and yellowtail flounder *Limanda ferruginea*. All three of these species have at least two stocks within the Northeast US, typically a stock in the Gulf of Maine and another in the Southern New England and/or George's Bank region. We use the metapopulation structure of these species to test the hypotheses that mortality in the juvenile stage has caused (or contributed to) the poleward shifts in the center of biomass of these stocks.

Methods

Fish Data

Abundance and distribution data for six fish stocks were obtained from the Northeast Fisheries Science Center (NEFSC) fall trawl survey, which has operated on the northeast U.S. continental shelf since 1963 (Figure 1). The data collection and sample processing methods are described in Azarovitz (1981). Briefly, the survey employs a stratified random design with stations allocated proportionally to stratum area. A 12-mm mesh codend liner is used to retain smaller bodied and juvenile fish. All fish for each species were counted and weighed. Correction factors were applied for changes in vessel, gear, and door changes when appropriate. Only tows in which there were no gear or duration problems were used.

Spawning stock biomass and recruitment data for red hake and silver hake were obtained using NEFSC fall trawl survey data. Fish <20cm were labeled as “recruits” from the preceding year class for both of these species. Fish >20cm were considered spawners. For both silver hake and red hake, strata allocated to the northern stock were 01200-01300 and all other offshore strata were allocated to the southern stock. Recruitment and spawning stock biomass data for yellowtail flounder *Limanda ferruginea* were obtained from the most recent stock assessments (NEFSC) conducted using virtual population analysis (VPA) extending back in time to the 1970s. Estimates of SSB and R were then hindcast by first developing a relationship between the NEFSC survey estimates and VPA estimates and then applying the linear equation to estimate SSB and R in years for which VPA estimates are not available.

Two stock-recruitment (S-R) relationships were evaluated for each stock, the a) Beverton and Holt and b) Ricker curves respectively,

a) $R = \frac{aS}{1+bS}$ b) $R = Se^{a+bS}$

where R=recruitment in millions of individuals, S=Spawning Stock Biomass (mt), and a and b are fitted constants. These models were fit with and without lognormal errors, but the models with lognormal errors obtained the best fits and were thus, used in all cases.

The effect of four different environmental variables (E) were then incorporated into stock recruitment relationships by modifying the above equations to give,

a) $R = \frac{aS}{1+bS+cE}$ b) $R = Se^{a+bS+cE}$

where c is an additional fitted constant applied to the environmental variable.

Environmental metrics

Two indices of longer term climatological conditions were also used: the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). The NAO index is calculated as the difference between surface pressure of the subtropical (Azores) high and the Subpolar (Iceland) low. The mean winter NAO index was used because most of the variance in the NAO occurs in the winter months and is the only large-scale pressure and circulation pattern that is evident throughout the year in the northern hemisphere (Hurrell et al. 2003). Variability in the NAO has been associated with changes in precipitation, sea surface temperature, wind fields, sea ice formation and thus, with ecosystem change (Beaugrand et al. 2003, Drinkwater et al. 2003, Greene et al. 2003, Beaugrand 2004) and fish recruitment (O'Brien et al. 2000, Reid et al. 2001, Lindley et al. 2003).

The AMO is a 65-80-year cycle in the Atlantic thought to be driven by ocean thermohaline circulation (Sutton & Hodson 2005). We used AMO values that were not detrended (Sutton & Hodson 2005, 2007). The AMO is driven by thermohaline circulation and is associated with warmer land and ocean temperatures, decreases in summer precipitation and increases in the number of droughts. In the US, the area relevant to this study, these effects are most pronounced in the summer and somewhat less prominent in the autumn and winter climate at lower latitudes (Sutton & Hodson 2007).

Mean-stratified annual bottom temperature (BT) was calculated from the fall NEFSC survey where bottom temperature measurements were taken at each station. Prior to 1990 bottom temperatures were measured with water bottles and from then on bottom temperatures were measured with CTDs. Finally, we used the position of the north wall of the Gulf stream as defined by the 15^{o}C isotherm at 200m (Joyce et al. 2000, Joyce et al. 2009). The position of the Gulf Stream is related to the NAO and storm tracks, but may affect species at the southern extent of their range more directly than the NAO. All environmental variables were standardized before incorporating into S-R curves.

Statistical Analysis

ArcGIS software was used to create smoothed maps in twelve-year time blocks of red hake, silver hake, and yellowtail flounder using the inverse distance weighting (IDW) method using spring trawl survey data. For each species, raster size was maintained at a constant level and the smoothing power, p, was equal to 2. The spatial pattern of mean annual bottom temperature for each twelve-year time block also was depicted using IDW in ArcGIS. In this analysis we used inshore and offshore strata to visualize spatial trends.

Stock recruitment curves without the effects of environmental variables were fit to each of the species above. The residuals from the best fitting model were tested for correlation with environmental variables. To determine if there were differences in the northern vs. southern stocks in recruitment the residuals from the southern stock were subtracted from the northern stock and plotted over time for visual inspection.

All stock-recruitment curves were fit using ten different starting parameters to insure that the global minimum was found in each model fit using PROC NLIN (SAS 9.1.3). Evaluation of model fit was determined by calculating the AIC from the sums of squares, number of observations, and number of parameters, k, using the following formula (Burnham and Anderson 2002):

$$AIC_{SS} = 2k + n(\log(SS / n)$$

Results

Shifts in distribution are evident in maps of smoothed biomass of silver hake, red hake, and yellowtail flounder (Figure 1). However, by visual inspection of the recruitment time series there is no apparent difference in recruitment between the northern and southern stocks for silver hake and red hake (Figure 2). In fact, the recruitments in the southern stocks can be much larger, but are also more variable than recruitment in the northern stocks in both of hake species. The SSB for both hake species is larger in the northern stock than in the southern stock for at least the latter half of the time series.

Hindcast estimates produced good estimates of SSB and R in both stocks of Yellowtail flounder. However, there was more unexplained variability in the hindcast SSB estimates than in R (Figure 3). In both stocks of yellowtail flounder, SSB and R were much higher in the 60s and 70s and decreased thereafter (Figure 4). Similar to the two hake species, recruitment was more variable in the southern (SNE) stock than in the northern (GB) stock and had some of the highest recruitment events, but unlike the hake species there is considerable coherency between stocks in recruitment of yellowtail flounder, especially in the latter part of the time series (Figure 4b).

Beverton and Holt and the Ricker S-R relationships were fit for all six stocks and residuals were taken from the better fitting (with lower AIC) model (Table 1). The southern residual was subtracted from the northern residual to determine if recruitment was better in the northern stocks after correcting for differences in SSB. Thus, positive values indicate better recruitment in the north and negative values indicate better recruitment in the south. For silver hake and to a less extent red hake, recruitment has indeed become increasingly greater in the northern stock (Figure 5a, b). However, in yellowtail flounder there does not appear to be any temporal trend in the spatial aspects of recruitment (Figure 5c).

Residuals from the S-R relationships were tested for correlations against four environmental variables (Figure 6). Across all stocks, the highest correlations with recruitment were with BT and/or GI. Both stocks of yellowtail flounder were also correlated with the NAO and only red hake-N was correlated with the AMO. Interestingly, recruitment was negatively correlated with BT and to a lesser extent GI in both stocks of yellowtail flounder but positively correlated with the northern stocks of red hake and silver hake.

Problems with convergence for red hake and silver hake emerged when incorporating environmental variables into S-R relationships, probably as a result of high variation in the data and a weak S-R relationship. Therefore, we focus on the environmentally-modified S-R relationships for yellowtail flounder (Figure 7). In yellowtail flounder, incorporation of either BT or GI improved the S-R relationships in both the SNE and GB stocks (Table 1, Figure 8). The S-R model with BT obtained the lowest AIC values in the SNE stock and GI produced the best fits in the GB stock (Table 1). Recruitment predicted by each model can be compared with observed recruitment (Figure 8). For both stocks, the model with BT incorporated captures the high recruitment in the early part of the time series better than the other environmental variables which may explain why this model is statistically the best fit.

Although the best temperature modified S-R relationship was obtained by incorporating BT, the Gulf Stream index visually explains how these two variables affect recruitment particularly for the SNE stock. The highest recruitments occurred at moderate stock sizes in both the SNE and GB stock (Figure 9). A dome-shaped response to SSB can almost be discerned for the SNE stock (Figure 9a, c). The lowest recruitments occur when the GI index is positive or when the position of the Gulf Stream is pushed northward onto the shelf. Similarly, the highest recruitments occur when BT is low and poor recruitment when BT is high, but the relationship is less clear (Figure 9c).

Discussion

For red hake and silver hake, northward shifts in overall distribution can be at least partially explained by higher recruitment in the northern stocks versus the southern stocks, but not in yellowtail flounder. Even so, temperature variables, particularly BT and GI, were correlated with recruitment and by incorporating these variables into S-R relationships of yellowtail flounder we could more precisely predict recruitment under different conditions of stock size and environment. Both stocks of yellowtail flounder are currently recovering from severe overfishing, but are still overfished and overfishing is occurring (NEFSC 2008). Since the 1990s, the GB stock has increased in size more so than the SNE stock, but neither stock has recovered to the levels of the 1960s. Here we have shown that recruitment in the SNE stock, the stock at the southern limit of the species range, is more variable and more sensitive to climatic factors than the more northern (GB) stock. Similarly (Myers 2001) found that stocks at the edges of their range had more variable recruitment, supporting the hypothesis that density-independent regulation is more important at the edge of species range.

Recruitment in SNE yellowtail flounder was previously correlated with the NAO and the pool of cold water available to young flounder (Sullivan et al. 2005). Similarly, we found that recruitment was correlated with NAO and moreover, that recruitment could be predicted by incorporating mean coastwide BT or GI into traditional S-R relationships. While many environment-recruitment correlations tend to break down once additional years of data are available (Walters & Collie 1988, Myers 1998), this study confirms a previously established environment-recruit relationship that recruitment of SNE yellowtail flounder is affected by bottom temperature, which in turn is affected by larger scale oceanographic phenomena, the position of the Gulf Stream and the NAO. Some hypothesize that stocks at the edges of a species range are likely to be more sensitive to climate change, thus making them more vulnerable to the effects of fishing, suggesting that populations at the edges of their range should be managed more conservatively (Brander 2009). As such, for a fish stock like yellowtail flounder that is recovering from overfishing in an environmentally unfavorable (warm) climate, fishing mortality should be adjusted to account for these conditions in addition to what would be suggested by stock assessments that do not incorporate the effects of these environmental variables.

Considerable improvements to these environmentally-modified stock-recruitment relationships can be made by incorporating temporal autocorrelation, lagged effects of environmental variables, and the combined effects of multiple environmental variables. However, we have shown the efficacy of incorporating environmental variables to improve prediction of recruitment. The utility of doing so is particularly useful when the effects of environmental variables on recruitment in multiple stocks within a species are compared (Myers 1998, 2001, Stige et al. 2006).

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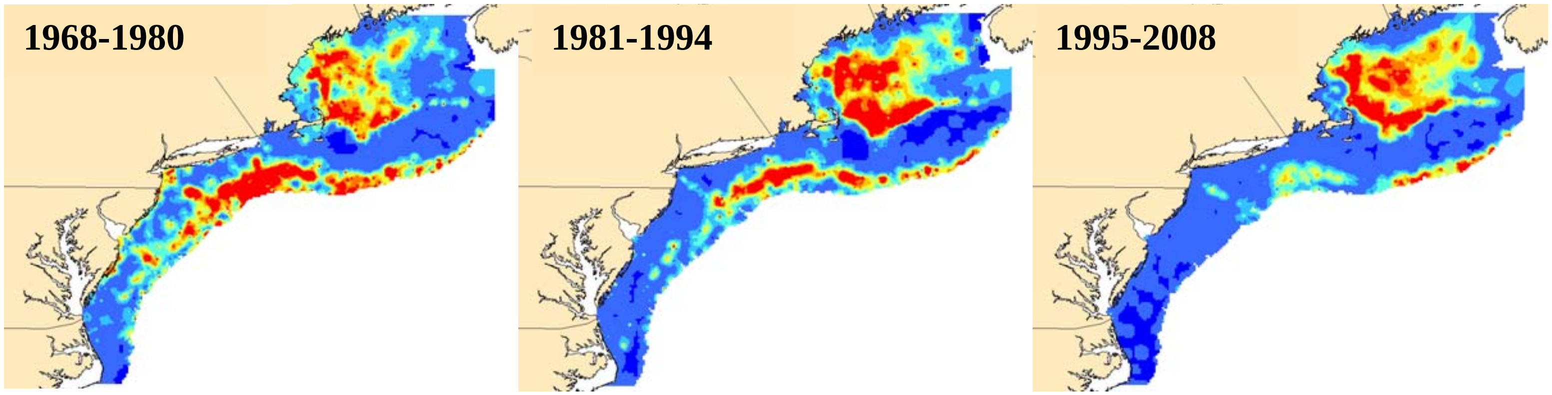
Table 1: AIC values for Stock-Recruitment curves for northern and southern stocks within in three species of fish in the Northeast US coast.

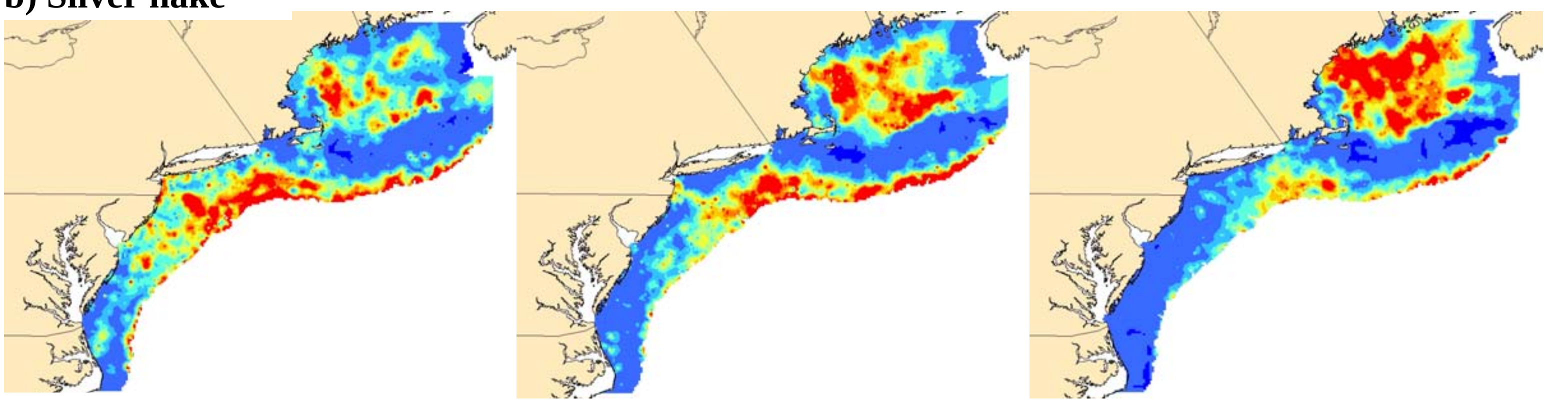
Stock	Recruitment model					
	Ricker	Beverton and Holt	NAO	AMO	BT	GI
Silver hake-Northern	14.27	14.6	-	-	-	-
Silver hake-Southern	8.36	8.06	-	-	-	-
Red hake - Northern	14.59	14.05	-	-	-	-
Red hake-Southern	10.11	9.22	-	-	-	-
Yellowtail flounder-GB	-10.61	-10.66	-10.41	-8.76	-10.02	-11.35
Yellowtail flounder-SNE	9.51	9.76	11.01	11.73	7.64	8.31

Figure 1: Shifts in spatial distribution of three species of fish a) red hake, b) silver hake, and c) yellowtail flounder in the Northeast US continental shelf ecosystem for three twelve year time periods. Maps are the smoothed surfaces of the log transformed biomass per tow of the spring NEFSC trawl survey where warmer colors indicate high densities

a) Red hake



b) Silver hake



c) Yellowtail flounder

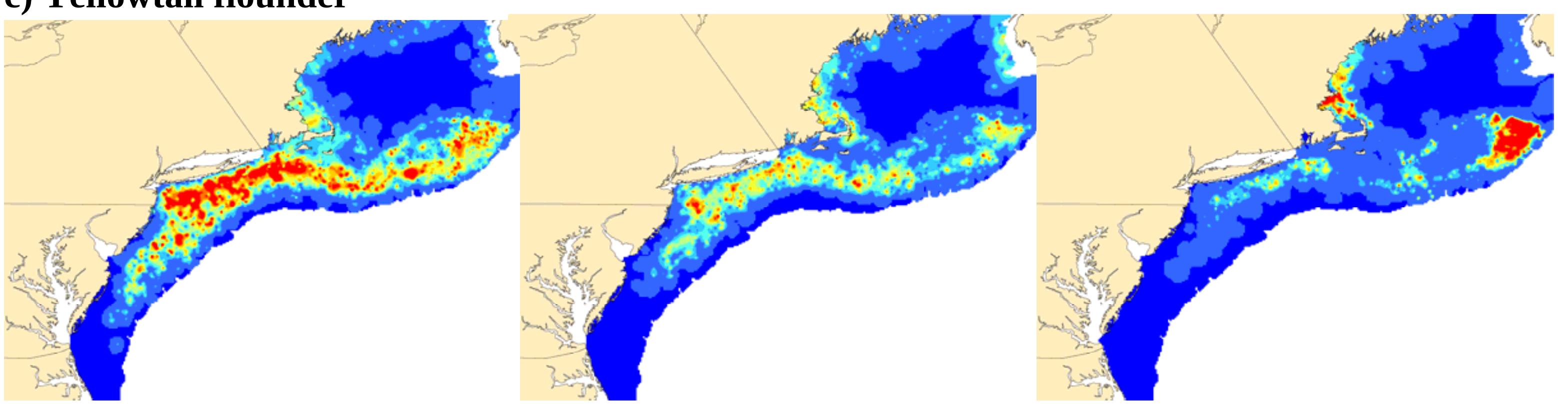


Figure 2: Minimum swept area estimates of the Northern and Southern stocks of a) recruitment and b) spawning stock biomass for silver hake and c) recruitment and d) SSB for red hake

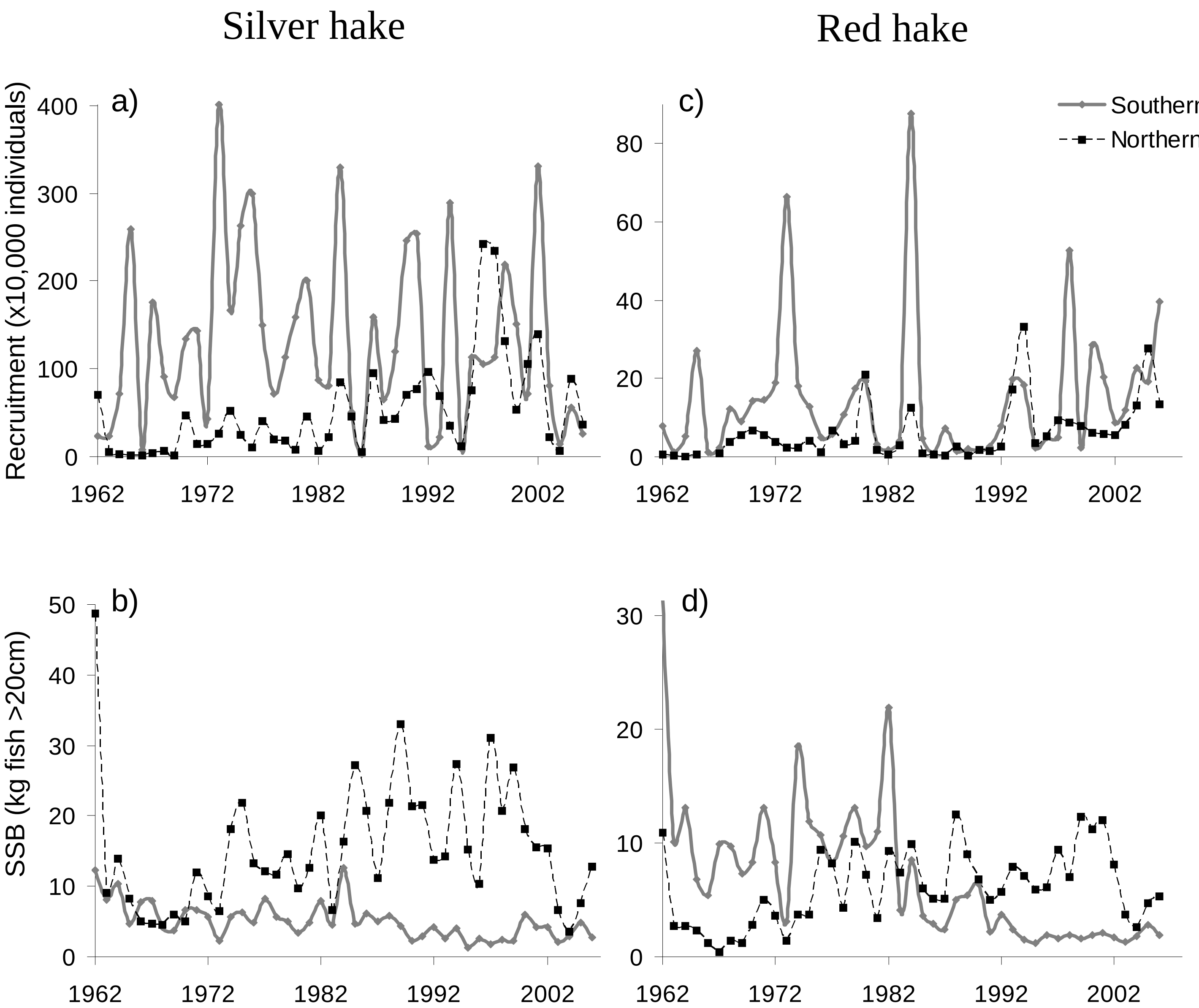


Figure 3: Hindcast estimates of Spawning Stock Biomass and Recruitment for the GB stock (a,b), SNE stock (c,d)

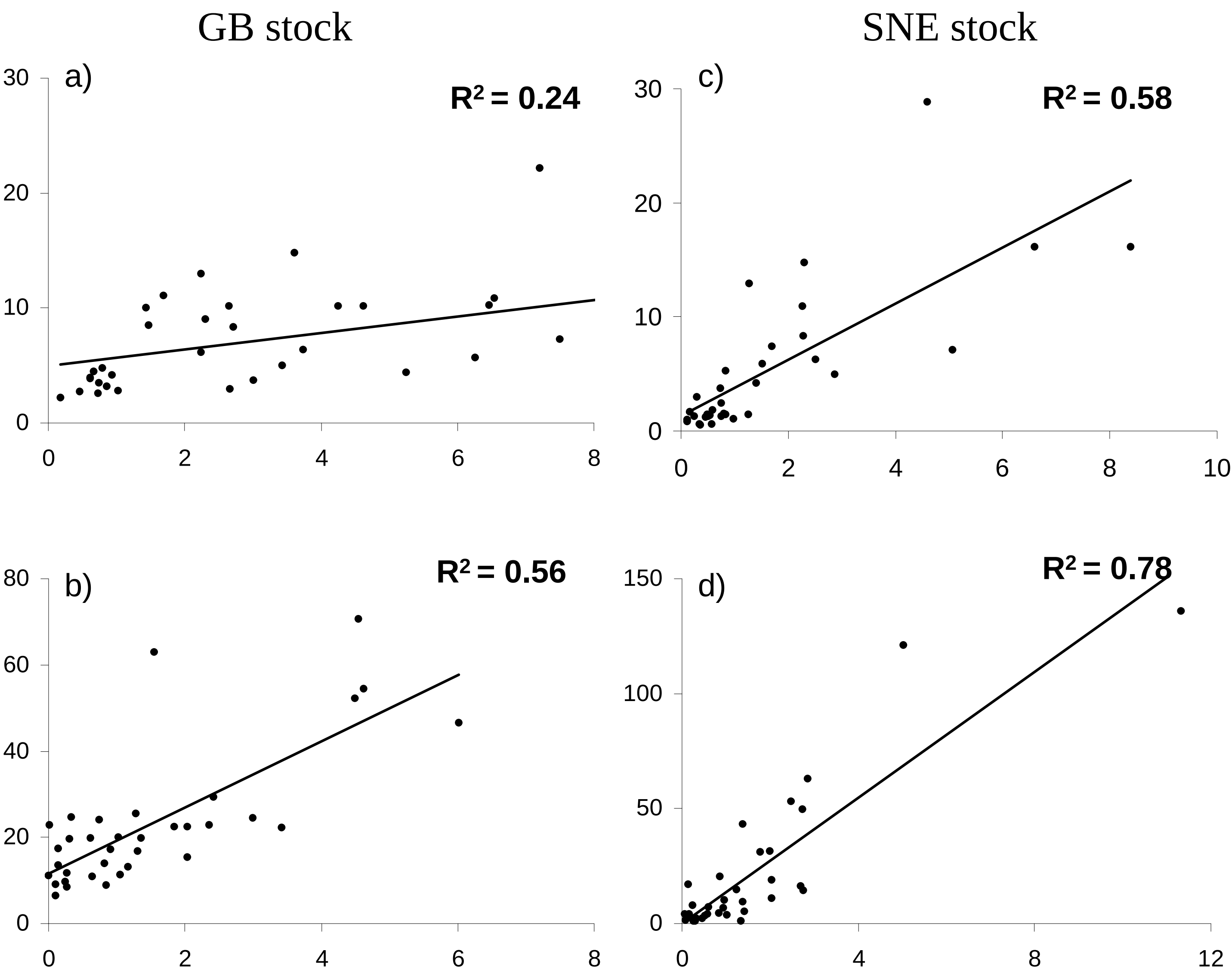


Figure 4: Time series for a) Spawning stock biomass and b) Recruitment for three stocks of YT flounder. GB and SNE values were hindcast from VPA and survey data. The VPA estimates of the shorter time series of the GOM-Cape Cod stock are shown for comparison, but not used in the analysis.

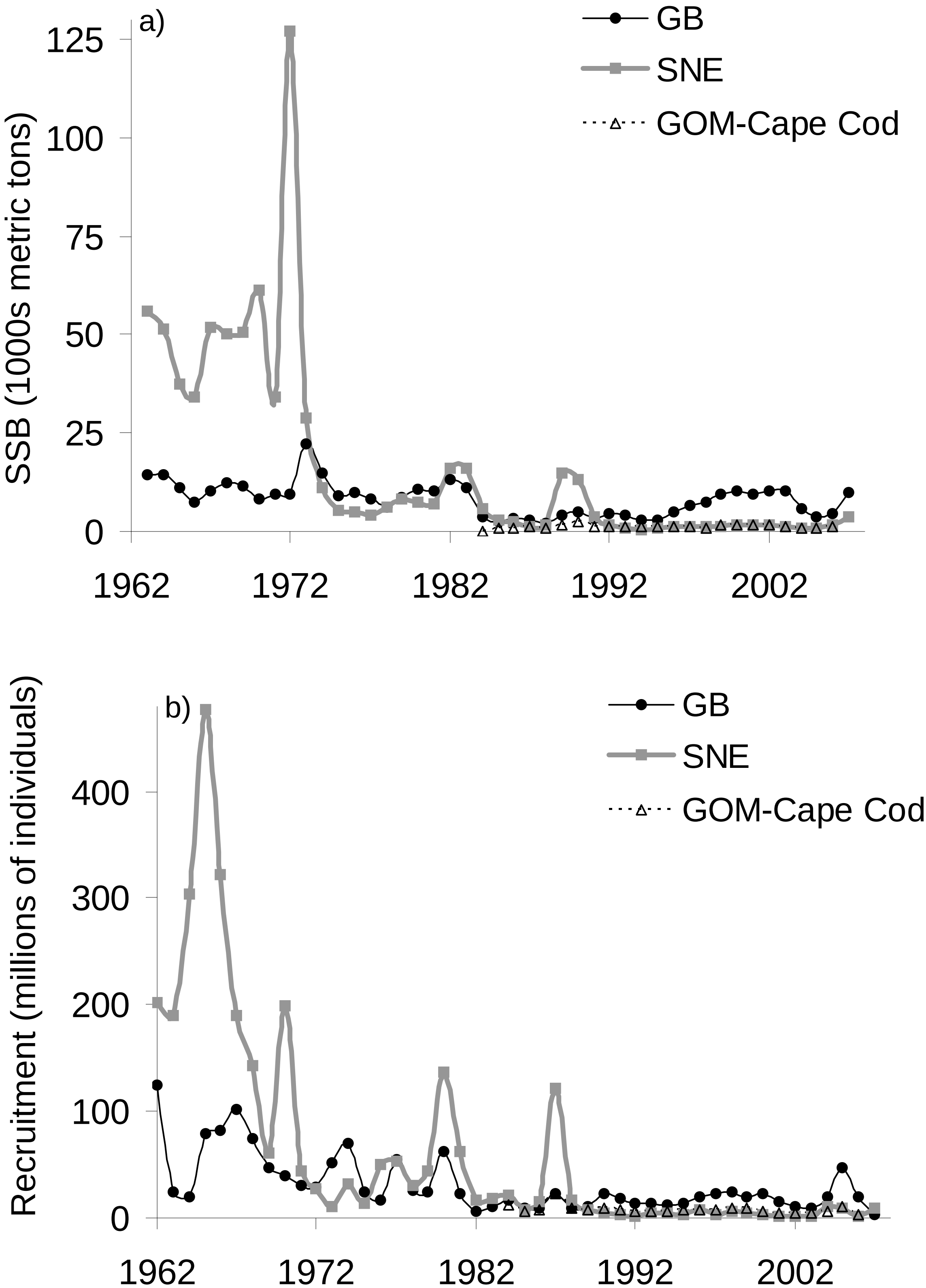


Figure 5: Difference in recruitment anomalies between the northern and southern stocks of a) red hake, b) silver hake, and c) yellowtail flounder

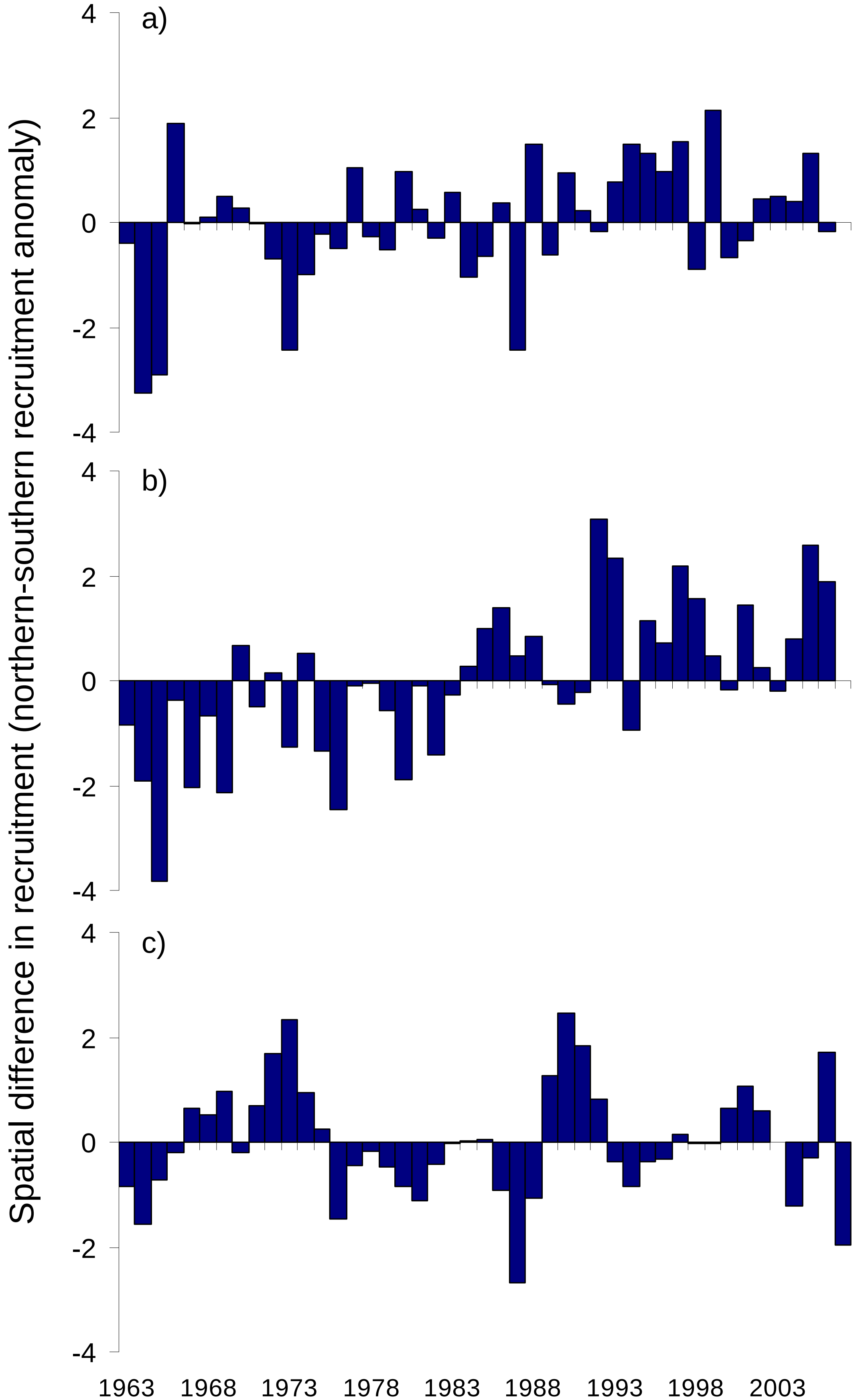


Figure 6: Correlations of recruitment anomalies with four environmental variables

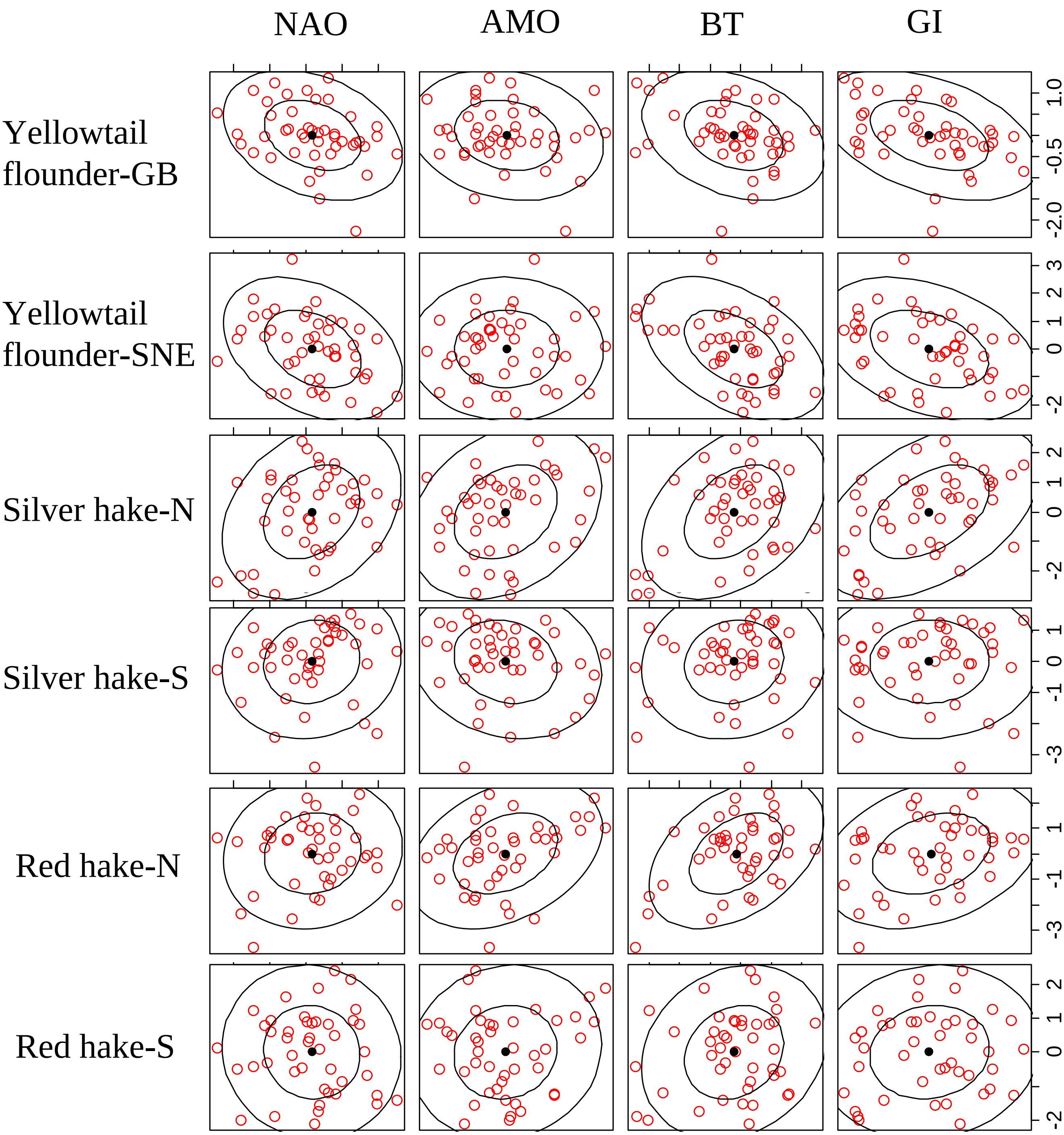


Figure 7: Stock recruitment relationships for a) Southern New England and b) Georges Bank stocks of Yellowtail flounder. Solid line indicates the Beverton and Holt S-R relationship. Dashed line indicates the Ricker S-R curve without the effect of the environmental variable. Open circles are the observed recruitment

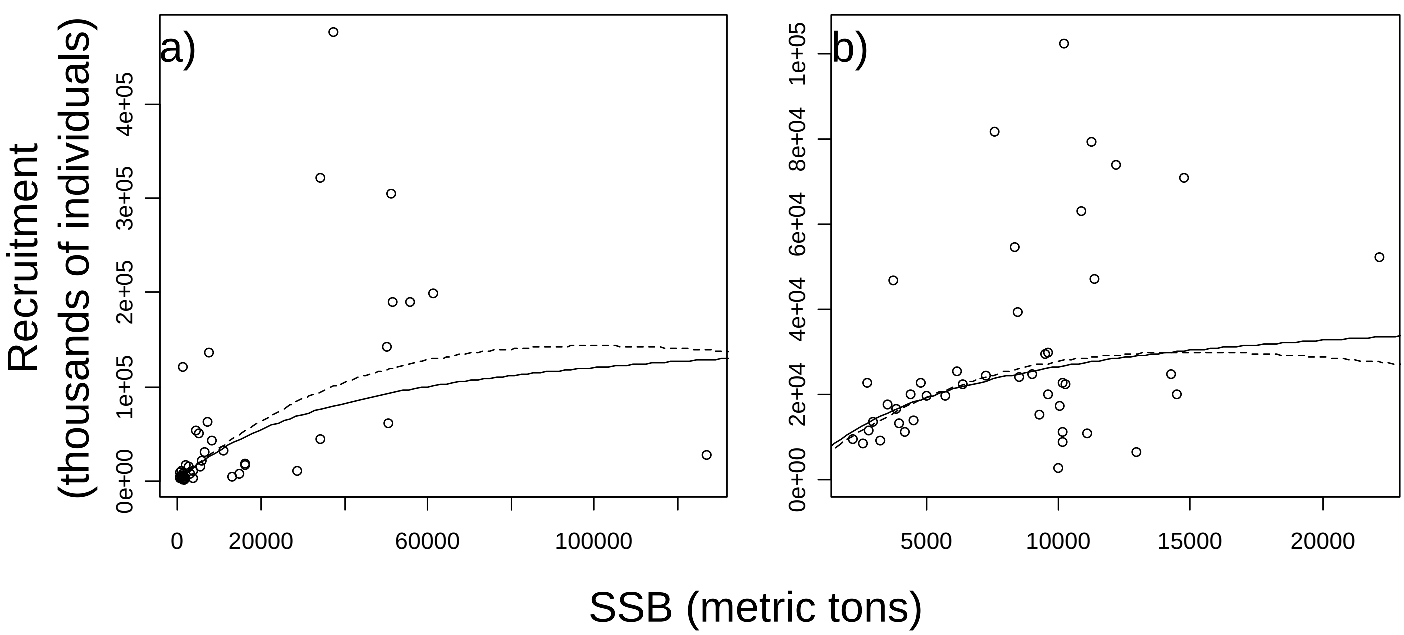


Figure 8: Comparison of observed and predicted recruitment of the a) GB stock and b) SNE stock of yellowtail flounder from Beverton and Holt stock-recruitment relationships in which only SSB was incorporated (pink) and where GI (red) and BT (green) were incorporated as additional explanatory variables.

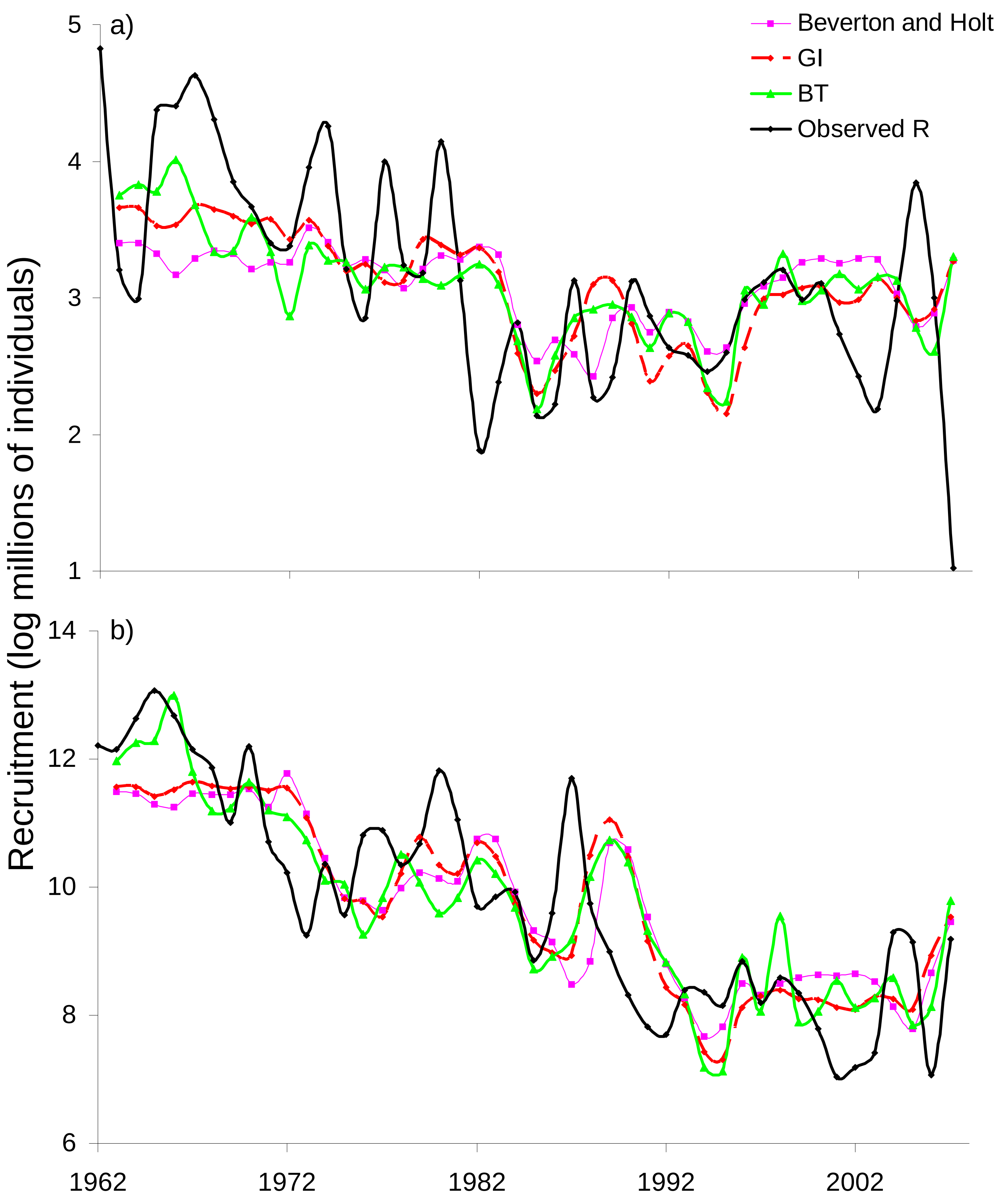


Figure 9: Relationship of yellowtail flounder recruitment with SSB (thousands of metric tons), the position of the Gulf stream (a,b) and bottom temperature (c,d). Note that the scale of the y-axes has been reversed because of the negative correlation of recruitment with both GI and BT and are shown as anomalies.