



FEATURE ARTICLE

# Regime shifts in fish recruitment on the Northeast US Continental Shelf

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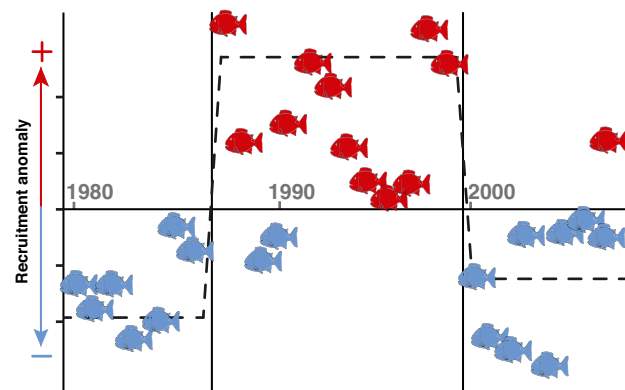
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**ABSTRACT:** There is accumulating evidence for decadal-scale regime shifts at the base of the food web on the Northeast US Continental Shelf. However, less evidence exists for regime shifts in fish recruitment success, particularly for synchronized regimes across multiple species. Here, we analyzed stock assessment output and survey data to test for regimes in the recruitment success of 18 commercially important marine species over a 29 yr timespan. We then tested whether recruitment regimes coincide with regimes in the zooplankton community, and whether the abundance of large spawners could explain the patterns in recruitment. We found evidence for 3 decadal-scale recruitment regimes: low recruitment success in the 1980s, high success in the 1990s, and a return to low recruitment success in the 2000s. This general pattern was found in all datasets of recruitment. The abundance of large spawners did not appear to be a broad-scale driver of recruitment success; however, recruitment regimes coincided with regimes in copepod abundance and size structure.

**KEY WORDS:** Fish recruitment · Northeast US shelf · Regime shift · Zooplankton

## INTRODUCTION

Marine ecosystems are known to experience rapid, persistent changes in state known as regime shifts, and there is accumulating evidence for regime shifts on the Northeast US Continental Shelf (NE Shelf). For example, there is evidence for phytoplankton



Recruitment success regimes of fish on the Northeast US Continental Shelf.

Graphic: C. Perretti and S. Schüller

productivity regime shifts over the past 30 yr (Kane 2011b, Greene et al. 2013), and regimes in zooplankton biomass and community structure are well documented (Kane 2007, 2011a, 2014, Turner et al. 2011, Greene et al. 2013, Bi et al. 2014, Morse et al. 2017). However, there is less evidence for regime shifts at higher trophic levels, particularly in fish recruitment. As recruitment is often the dominant component of variability in fish populations (Fogarty et al. 1991), and recruitment failures can have dramatic impacts on fisheries (e.g. Ljunggren et al. 2010, Whitmore et al. 2013), identifying regimes in fish recruitment is important.

Several studies have searched for synchrony in fish recruitment patterns on the NE Shelf (and more generally, in the Northwest Atlantic), and synchrony in

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productivity across stocks was a particular focus in early studies. Although synchrony in recruitment across stocks was initially suggested (Garrod & Colebrook 1978, Koslow 1984), follow-up analyses with additional data failed to find synchrony (Cohen et al. 1991, Myers et al. 1995). More recently, in an analysis of 12 New England groundfish stocks, Brodziak & O'Brien (2005) found significantly positive recruitment anomalies in several years, with 1987 being the most positive anomaly, and significantly negative anomalies in 2000 to 2001. In the Gulf of Maine, Pershing et al. (2005) found several statistically significant relationships between individual fish stocks, zooplankton abundance, and the North Atlantic Oscillation (NAO), with high zooplankton abundance regimes beginning in the late 1980s, and low abundance beginning in the early 2000s. Similarly, Mountain & Kane (2010) found evidence for a high abundance zooplankton regime beginning around 1990, and ending in the early 2000s. Together, these studies suggest that fish may exhibit regime-like productivity shifts in response to broad-scale environmental forcing, and on the NE Shelf in particular, a regime shift may have occurred in the late 1980s and the early 2000s.

In the North Sea, changes in the zooplankton community have been linked to regime-like dynamics in Atlantic cod recruitment (Beaugrand et al. 2003), and a suite of biological and physical variables exhibited regime dynamics in the late 1980s and potentially the late 1990s (Weijerman et al. 2005). Similarly, in the North Pacific, zooplankton regime shifts related to climate forcing have been linked to recruitment regimes in groundfish and salmon (Hare & Mantua 2000). The connection between zooplankton and the survival of young fish is a classic research topic with zooplankton phenology, community composition, and total abundance all potentially playing a role (Hjort 1914, 1926, Cushing 1974, 1990, Lasker 1978, 1981, Houde 1987). On the NE Shelf, zooplankton abundance has been shown to impact growth rates of some larval fish (Buckley & Durbin 2006), although the impact of zooplankton on recruitment is often conflated by other co-factors (e.g. Friedland et al. 2015).

Here, we build on earlier analyses centered on individual species (e.g. Mountain & Kane 2010, Richards et al. 2016) by using a multivariate approach that aims to identify regimes in fish recruitment per unit spawning stock biomass (a measure of recruitment success) and their underlying drivers. Using stock assessments and survey data, we test for coherent regime shifts in recruitment success of 18

species on the NE Shelf over a 29 yr timespan. To our knowledge, this represents the most extensive analysis of regimes in fish recruitment on the NE Shelf, both in number of species analyzed and timespan covered. We then investigate linkages between recruitment regimes, demographic structure, and the zooplankton community.

## MATERIALS AND METHODS

### Data sources

We estimated recruitment success using both stock assessment output and direct observations from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey. For the stock assessments, spawner biomass and recruit abundance ( $R$ ) was obtained for all stocks in which they were available (23 stocks, 18 species, Table 1). Spawning stock biomass (SSB) was lagged according to the age-at-recruitment ( $r$ ; Table 1) and we used recruit abundance in year  $t$  per spawner biomass in year  $t - 1$  ( $R_t/SSB_{t-r}$ ) as a metric of recruitment survival success (similar results were obtained using  $\log_e(R_t/SSB_{t-r})$ ). Stock-recruitment model residuals provide an alternative metric of recruitment success; however, previous studies have found model selection criteria are often unable to identify the correct stock-recruitment model under simulated conditions (de Valpine & Hastings 2002, Zhou 2007). As a result, stock-recruitment residuals could obscure patterns of recruitment if the residuals are driven by model misspecification. Therefore, we chose to use the relatively simple measure of recruits produced per spawner biomass as our metric of recruitment.

The range of years differs across stock assessments depending on data availability and the date of the last completed assessment. Therefore, we examined the full set of 23 stocks (18 species) with joint information available from 1986 to 2008. We also analyzed the set of 13 stocks (11 species) for which information was available from 1980 to 2008. We restricted our observations to 2008 in these 2 datasets because recruitment estimates from terminal years of a stock assessment are often the most uncertain and most likely to change in future assessments. Further, a number of stocks in the Northeast exhibit a 'retrospective pattern' in which convergence of estimates may take several years and more recent years are particularly unreliable (Legault 2008).

A number of different age-structured models provide the foundation for the stock assessments (Table 1). Although these models differ in form and

Table 1. Description of all stock assessments used in the analysis. Stock areas are single unit (Unit), Gulf of Maine (GOM), Georges Bank (GB), Mid-Atlantic Bight (MAB), Southern New England (SNE), and Cape Cod (CC). Assessment methods are Age Structured Assessment Program (ASAP), Virtual Population Analysis (VPA), Statistical Catch At Length (SCALE), and Statistical Catch at Age (SCA)

Scientific name	Common name	Stock area	Assessment timespan	Recruitment age $r$	Assessment method
<i>Sebastes fasciatus</i>	Acadian redfish	Unit	1913–2014	1	ASAP
<i>Hippoglossoides platessoides</i>	American plaice	GOM/GB	1980–2014	1	VPA
<i>Gadus morhua</i>	Atlantic cod	GB	1978–2011	1	ASAP
		GOM	1982–2014	1	ASAP
<i>Clupea harengus</i>	Atlantic herring	Unit	1965–2011	1	ASAP
<i>Scomber scombrus</i>	Atlantic mackerel	Unit	1962–2009	1	ASAP
<i>Lophius americanus</i>	Goosefish	Unit	1980–2009	1	SCALE
<i>Melanogrammus aeglefinus</i>	Haddock	GB	1960–2014	1	VPA
		GOM	1977–2014	1	ASAP
<i>Pollachius virens</i>	Pollock	Unit	1970–2014	1	ASAP
<i>Stenotomus chrysops</i>	Scup	Unit	1984–2010	0	ASAP
<i>Merluccius bilinearis</i>	Silver hake	Unit	1973–2009	1	ASAP
<i>Morone saxatilis</i>	Striped bass	Unit	1982–2012	1	SCA
<i>Paralichthys dentatus</i>	Summer flounder	Unit	1982–2012	0	ASAP
<i>Lopholatilus chamaeleonticeps</i>	Tilefish	Unit	1971–2012	1	ASAP
<i>Urophycis tenuis</i>	White hake	Unit	1963–2014	1	ASAP
<i>Pseudopleuronectes americanus</i>	Winter flounder	SNE/MAB	1981–2014	1	ASAP
		GB	1982–2014	1	VPA
<i>Glyptocephalus cynoglossus</i>	Witch flounder	Unit	1982–2014	3	VPA
<i>Anarhichas lupus</i>	Atlantic wolffish	Unit	1968–2014	1	SCALE
<i>Limanda ferruginea</i>	Yellowtail flounder	GB	1973–2012	1	VPA
		SNE/MAB	1973–2014	1	ASAP
		CC/GOM	1985–2014	1	VPA

assumptions, they all impose a structural filter on the data that influences the output (Brooks & Deroba 2015, Dickey-Collas et al. 2015). Accordingly, we repeated our analysis using NEFSC bottom trawl survey data (15 species), which is independent of these structural assumptions. Stock assessments and survey data both have unique strengths and weaknesses; however, by including both sources of information we hope to increase the robustness of our results.

The NEFSC bottom trawl survey spans the Northeast shelf from the Gulf of Maine to Cape Hatteras in both the spring and fall. The survey gear, sampling procedures and design details have been described by Azarovitz (1981) and Smith (2002). Because 3 different research vessels and gears were employed during the time period analyzed, we applied vessel and gear conversion coefficients derived using paired-tow calibration studies (Byrne & Fogarty 1985, Byrne & Forrester 1991, Miller et al. 2010). We also restricted the timespan to match the stock assessment time series as closely as possible (1980 to 2007). The survey series ends in 2007 because the NEFSC bottom trawl survey switched vessels in 2009 and length-specific catchability coefficients have not been estimated for many of the species in this analysis.

Therefore, for all species, our last observations of recruitment occurred in 2008, which corresponds to the 2007 year-class.

For the survey data, only a sample of fish are aged. Therefore we identified age-1 fish as those with length less than the expected length of an age-2 fish. To find the expected length-at-age, we used a generalized linear model where length was modeled as a Poisson random variable and age as the predictor variable:

$$\ln[E(L|A)] = b_0 + b_1 A \quad (1)$$

where  $L$  is length (cm) and  $A$  is age (yr), and the expected value of length conditional on age is a linear function of age on a log scale (i.e. a Poisson log-linear model with parameters  $b_0$  and  $b_1$ ). The Poisson model was chosen because length is recorded to the nearest cm in the survey and is strictly positive. Overdispersion was checked using the ‘dispersion-test’ function in the AER package in R, and was not found in any species. The age-1 threshold was then used to calculate a small and large fish index (numbers below and above the threshold, respectively) each year. As an additional check, we defined size thresholds based on the 20th percentile of the length

distribution across all years and found identical regime shift change points to the Poisson modeled results (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m574p001\\_supp.pdf](http://www.int-res.com/articles/suppl/m574p001_supp.pdf)).

Biomass was calculated using length–weight relationships directly from the survey data. Following Wigley et al. (2003), the length–weight relationship was modeled as:

$$\ln W = \ln a + b \ln L \quad (2)$$

where  $W$  is weight (kg),  $L$  is length (cm), and  $a$  and  $b$  are parameters fit via linear regression. The ratio of small fish numbers of the following year to larger fish biomass in the current year was used as a proxy for the assessment-based recruitment success index. The fall and spring recruitment success anomalies were averaged to provide an annual index of recruitment success. To reduce the number of missing observations, recruitment calculations were performed on the species level rather than the stock level. In doing so, we were able to include all species found in the stock assessment analysis except striped bass *Morone saxatilis*, tilefish *Lopholatilus chamaeleonticeps* and wolffish *Anarhichas lupus*, because each are poorly sampled by the trawl and had at least 3 years in which small fish were not captured.

### Regime shift detection

Regime shifts were detected using chronological clustering (Legendre & Legendre 2012), an algorithm designed to identify discontinuities in spatial and temporal data. Chronological clustering is flexible in that it does not impose a functional form on the relationship between the dependent variable (e.g. recruitment) and explanatory variable (e.g. time). Among other applications, it has been applied to multi-species time series of zooplankton (Legendre et al. 1985), spatial distributions of plants (Tuomisto & Ruokolainen 1994), and marine ecosystem time series in Northwest Europe (Weijerman et al. 2005).

We implemented chronological clustering using multivariate regression trees (MRT, Breiman et al. 1984, De'ath 2002, Borcard et al. 2011) via the 'rpart' package and the 'rpart' function in R using the default parameter values (Therneau et al. 2015). The clustering algorithm partitions the multivariate recruitment time series into temporal groups (i.e. regimes) where the groups are chosen to minimize the sum of squares within the groups (also known as minimizing the impurity measure, De'ath 2002). The sum of squares within a regime is given by:

$$\sum_{i,j} (x_{i,j} - \bar{x}_j)^2 \quad (3)$$

where  $x_{i,j}$  is the recruitment measure for species or stock  $j$  in year  $i$  of the regime, and  $\bar{x}_j$  is the mean of species or stock  $j$  in the regime. The sum is over all species and stocks in the dataset; therefore, all species are used simultaneously to determine the regime partitions. The final partitions are selected using  $k$ -fold cross-validation prediction error ( $k = 10$  here). Chronological clustering is performed by using time as the explanatory variable in the MRT, which enforces a temporal contiguity constraint.

### Sensitivity analysis

The chronological clustering algorithm uses information on all stocks simultaneously when determining the regime change points. Therefore, we estimated the sensitivity of each regime change point to the stocks included in the analysis by running the chronological clustering algorithm on a sample of stocks ranging from a single stock to all available stocks. We used all possible combinations of stocks for a given sample size up to a maximum of 10 000 combinations. The probability of detecting a change point for a given sample size was calculated as the proportion of runs in which a change point ( $\pm 1$  year) was detected. For example, for the 2001 change point, we calculated the proportion of runs in which a change point was detected in 2000, 2001, or 2002.

We also investigated the uncertainty associated with each change point using a bootstrap analysis. For each dataset, the bootstrap simulation randomly selected species with replacement to generate a bootstrapped dataset with the same number of time series as the original dataset. The change point algorithm was then applied to each bootstrapped dataset and the change points were recorded. This procedure was repeated 1000 times for each dataset. The distribution of change point years provides a measure of the uncertainty associated with the change point year.

### Copepod indices

Copepod abundance data from 1977 through 2013 was obtained from a long-term ecosystem monitoring program of the NE Shelf (Marine Resources Monitoring, Assessment, and Prediction, from 1977 to 1987, and Ecosystem Monitoring Program (EcoMon) from 1994 to the present). Samples were collected using

oblique tows of bongo nets with a mesh size of 333  $\mu\text{m}$  (Kane 2007). This mesh size does not capture the smallest copepod species; however, it provides a long-term shelf-wide index of the most common large copepod taxa. For each copepod taxa, a seasonally stratified area-weighted abundance (i.e. per net tow) was calculated. The samples were post-stratified to one-degree bins and copepod indices were calculated for separate geographic regions following Lucey & Fogarty (2013) to test whether particular regions (i.e. Gulf of Maine, Georges Bank, and the Mid-Atlantic Bight) were more likely to drive recruitment regimes.

We examined 2 previously developed indices of the copepod community: total abundance and size structure (Ecosystem Assessment Program 2011). For the total abundance index, annual abundance anomalies for the combined top 5 most abundant copepod taxa, consisting of *Calanus finmarchicus*, *Pseudocalanus* spp., *Centropages typicus*, *Temora longicornis*, and *Metridia lucens*, were calculated for each geographic region. Abundances of all included taxa were summed for a given year and an annual z-score was computed.

The size structure index was calculated as the difference between the mean of the anomalies of the small-bodied copepods and the anomaly of a large-bodied copepod (i.e. small copepod mean anomaly – large copepod anomaly). The small-bodied copepods were *Centropages typicus*, *Pseudocalanus* spp., *T. longicornis*, and *Centropages hamatus*, and the large-bodied copepod was *Calanus finmarchicus*. There is a seasonal cycle in copepod community structure, and the timing of the survey has changed over time. Therefore, anomalies were computed following the Kane (2007) method, which accounts for variability in the timing of sample collection. First, a cubic spline function is fit to the daily abundance for each taxon using data from the entire time series (see Fig. S2 in the Supplement). This provides an estimate of the expected abundance on any day of the year. The anomaly is calculated as the difference between the observed and the expected abundance given by the spline function. These anomalies are then averaged over each year to obtain an annual anomaly.

### Age truncation

Emerging evidence suggests that the progeny of older, experienced spawners may have higher survival rates than younger (particularly first-time) spawners (see Jakobsen et al. 2016 and contributions therein). Therefore, the removal of older fish may be

an important driver of recruit survival, particularly in the Northwest Atlantic where several stocks have experienced fishery-induced changes in size and age structure (Wigley 1999, Hutchings 2005, McBride et al. 2013). Using abundance-at-age data from all available age-structured stock assessments (19 stocks), we tested whether changes in the abundance of older fish explained changes in recruit survival. We identified old fish as those older than the 25th percentile of the age distribution of their stock (similar results were obtained when using the 20th percentile), where the age distribution was built using data over the timespan in which all stocks were assessed (1986 to 2008). We calculated the abundance anomaly of the old fish group in each year, and tested for change points corresponding to those found in the recruit survival index.

## RESULTS

We found evidence for 3 recruitment regimes: an initial regime of low recruitment success through the late 1980s, a switch to high recruitment success through the 1990s, and finally a return to low recruitment success through the early 2000s (Fig. 1). Recruitment success regime change points were similar in all datasets — the shift to high recruitment success occurs in 1987 in all datasets that extend back to 1980. The shift to low recruitment occurs in 2000 in both the 1980 to 2008 and 1986 to 2008 datasets. The similarity in change points found in the survey dataset and the assessment datasets suggests that both datasets are tracking the same recruitment processes, and that the recruitment regimes are unlikely to be driven solely by the assessment modeling process.

For all recruitment datasets, the mean coefficient of variation (CV) of recruit abundance was higher than that of spawner biomass (Table 2), as might be expected given the narrower age range of recruits and high variability of the recruitment process. Spawner biomass was generally low through the 1990s, then rebounded in the early 2000s after several years of high recruitment in the late 1990s (see Figs. S3, S4 & S5 in the Supplement) and, for some stocks, decreased fishing mortality.

The probability of detecting a change point increased steadily as more stocks were added to the analysis (Fig. 2). Less than half of the species exhibited a statistically detectable regime shift when analyzed in isolation (represented by the left-most point in each panel of Fig. 2). When 5 species were in-

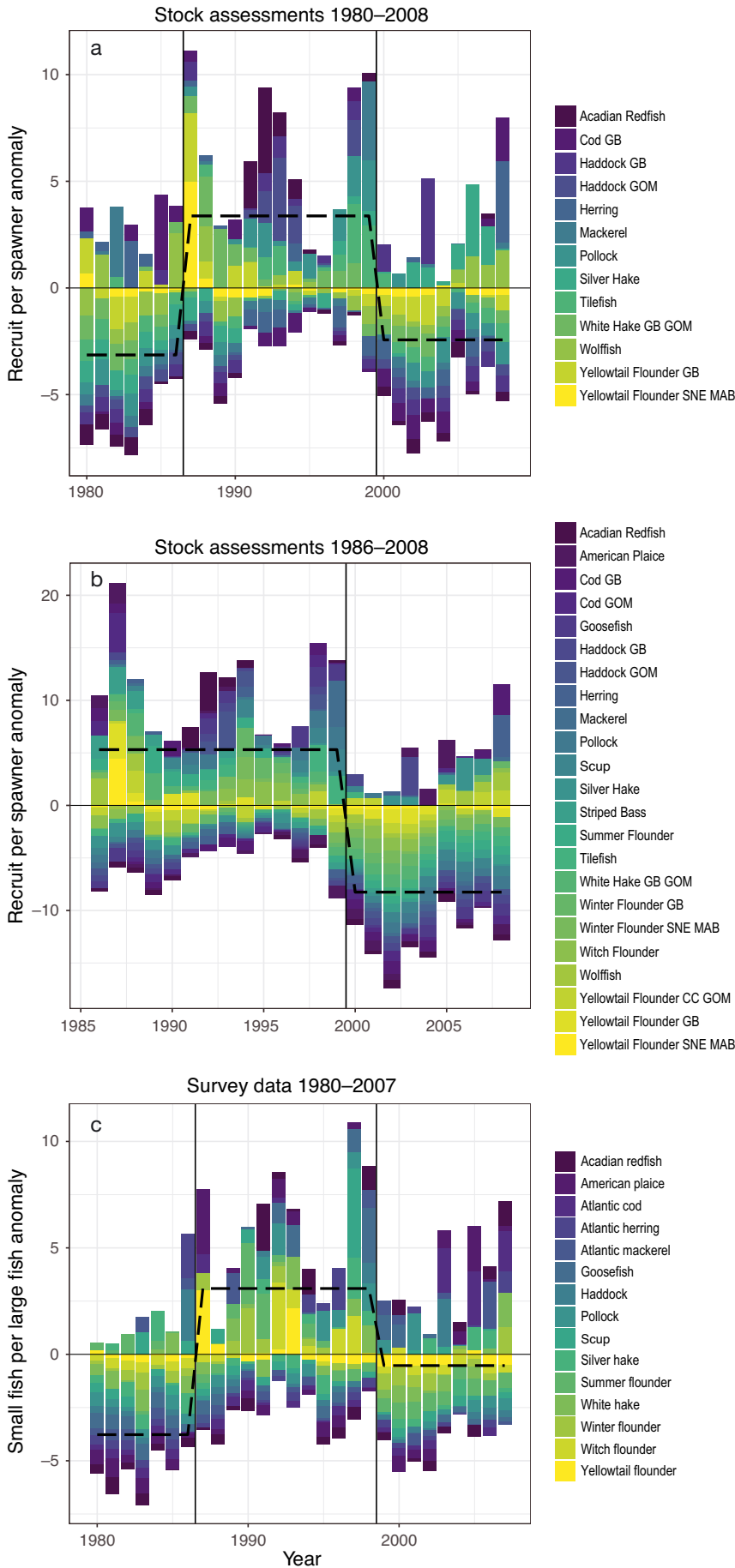


Fig. 1. Stacked bar chart of recruit per spawner anomalies for each recruitment dataset. (a) Stock assessments from 1980 to 2008, (b) stock assessments from 1986 to 2008, (c) survey data from 1980 to 2007. The vertical lines are the regime shift change points as determined by the chronological clustering algorithm. The dashed line is the average total annual anomaly within each regime. See Table 1 for abbreviations

Table 2. Coefficient of variation (CV) of recruit abundance and spawner biomass for all recruitment datasets

Recruitment dataset	Recruit abundance CV	Spawner biomass CV
Stock assessments 1980–2008	1.02	0.56
Stock assessments 1986–2008	0.80	0.38
Survey data 1980–2007	0.98	0.62

cluded, the probability of detecting a regime shift increased to approximately 75%; at 10 species, the probability was approximately 80% in the survey dataset and 95% in the stock assessment datasets. The 1987 change point was slightly more difficult to detect than the 2000 change point, as illustrated by its lower initial detection probability in all datasets. In general, the probability of detecting a change point in the survey dataset was lower than in the stock assessment datasets through most of the range of species, which is likely due to the greater year-to-year variability of the survey data compared to the stock assessment output.

In the bootstrap analysis, for all datasets, the modes of the bootstrap distribution corresponded to the observed change point years of the real datasets (i.e. 1987 and 2000 in the assessment datasets, and 1987 and 1999 in the survey datasets, see Fig. S6 in the Supplement). There was lower uncertainty in the stock assessment datasets, where at least 70% of

the bootstrap runs had the same change point as the real dataset, as compared to the survey dataset, while in the survey dataset approximately 60 and 45% of runs exhibited the 1987 and 1999 change points, respectively.

The proportion of large fish (our proxy for age truncation) began high, declined through the 1980s, was low through the 1990s, and increased through the 2000s (Fig. 3). The hypothesis underlying the age-truncation mechanism is that old fish are expected to have proportionally higher relative fecundity, higher quality eggs, and spawn over longer periods that are more likely to coincide with optimal conditions for larval survival. Therefore, low abundance of old fish should correspond to low recruitment success. However, in contrast to this, the period of low old fish abundance (the 1990s) corresponded to a period of high recruitment, and similarly, the period of high old fish abundance (2000s) coincided with a period of low recruitment success. Therefore, it seems unlikely that age truncation is driving patterns of recruitment in the stocks examined.

Copepod abundance regimes were similar to the recruitment regimes, particularly that of copepod community size structure (Fig. 4, see Fig. S7 in the Supplement). Overall, copepod abundance was below average in the 1980s, switched to above average in the 1990s, and returned to below average in the 2000s. The earliest and longest high abundance regime occurred in the Gulf of Maine, beginning in 1991 and ending in 2001. On Georges Bank, the high

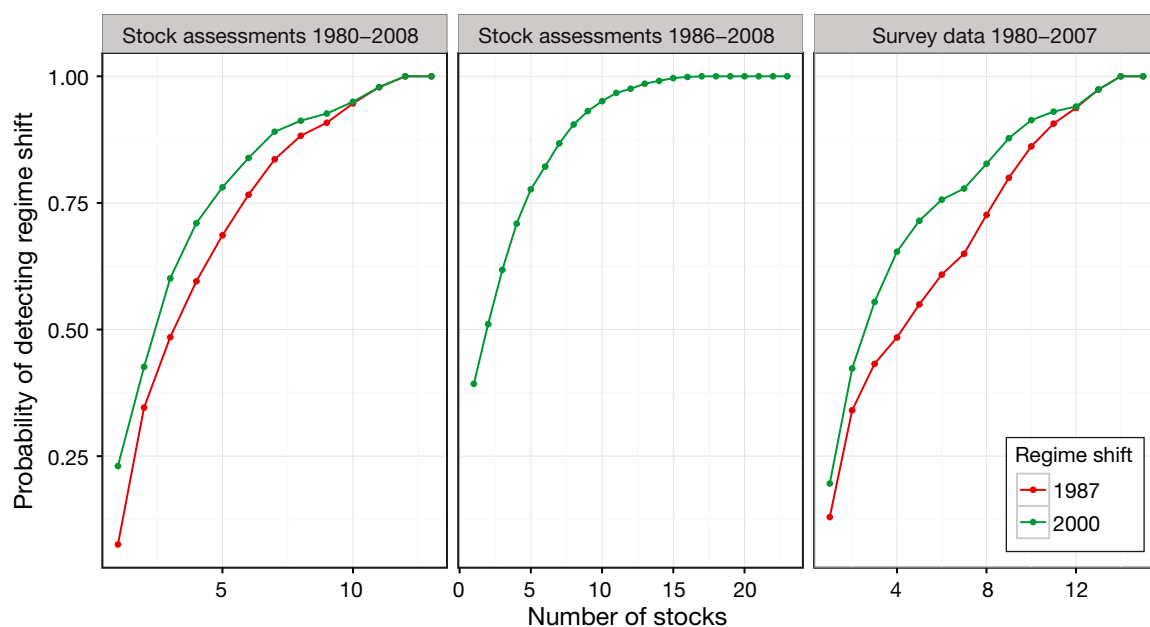


Fig. 2. Change point sensitivity analysis for each recruitment dataset

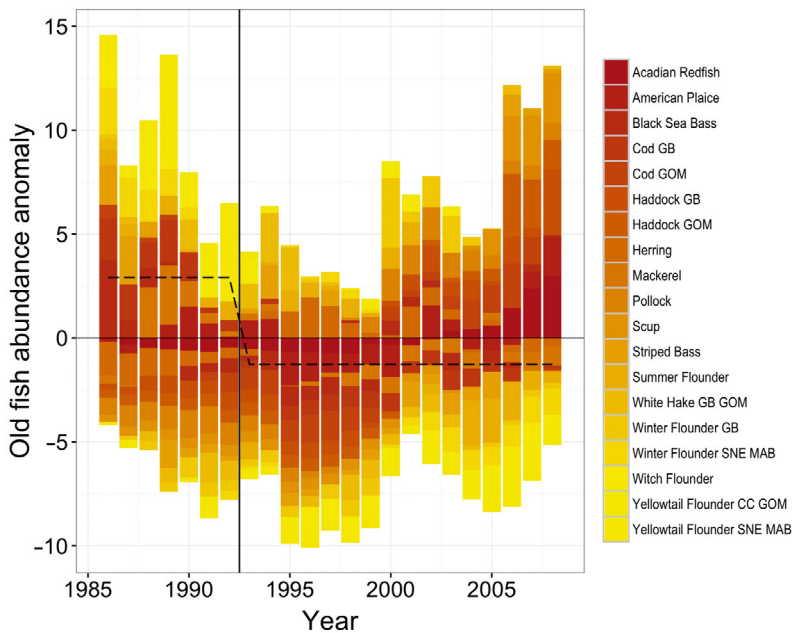


Fig. 3. Stacked bar chart of old fish abundance anomaly for each species with abundance-at-age data, chronological clustering breakpoint (vertical line), and average total annual anomaly within each regime (dashed line). See Table 1 for abbreviations

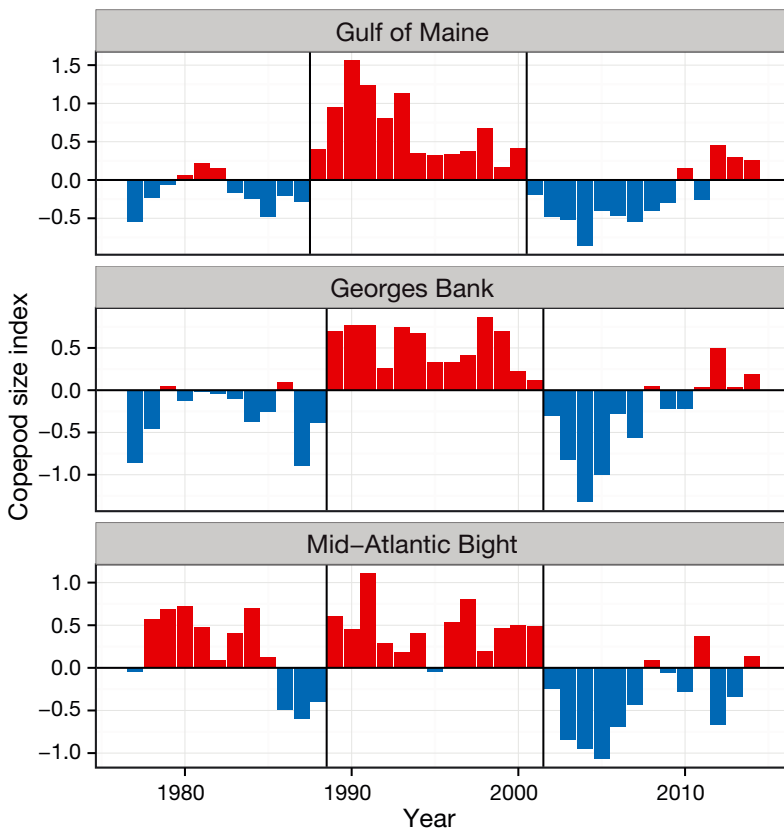


Fig. 4. Copepod size index (small copepod anomaly – large copepod anomaly) time series. Each bar represents the average annual anomaly, and vertical lines denote regime change points

abundance regime spanned from 1996 to 2003, and in the Mid-Atlantic Bight, it spanned from 1994 to 2001. In addition, 2 of the 3 most recent years exhibited positive anomalies, suggesting a return to a high abundance regime.

Even more closely mirroring the recruitment regimes were the copepod size regimes (Fig. 4). The early 1980s were dominated by large-bodied copepods (i.e. *Calanus finmarchicus*), then in the late 1980s, there was a shift to small-bodied copepods (e.g. *Pseudocalanus* spp.). The small copepod regime persisted until 2000 in the Gulf of Maine and 2001 in Georges Bank and the Mid-Atlantic Bight, after which the system switched back to a large copepod regime. The large copepod regime then persisted until 2010, but similar to copepod abundance, recently appears to have switched back to a small copepod regime.

## DISCUSSION

Using stock assessment output, trawl survey data, and a long-term zooplankton survey, we found evidence for regimes in recruitment success in fishes on the NE Shelf, which broadly coincide with changes in the copepod community. Our results build on previous work that found regimes across lower trophic levels on the NE Shelf emanating from changes in ocean circulation (e.g. Pershing et al. 2005, Mountain & Kane 2010, Greene et al. 2013), specifically linked to changes in Arctic climate (Greene & Pershing 2007, Greene et al. 2008). Here, we find that regime dynamics appear to impact higher trophic levels as well.

Several potential mechanisms could explain the link between regimes in fish recruitment and regimes at lower trophic levels. Increased zooplankton abundance, particularly of key prey of larval fish, could directly lead to increased larval growth and decreased



mortality (i.e. the stage-duration hypothesis, Houde 1987). For example, on Georges Bank, an increase in *Pseudocalanus* spp. during the late 1990s has been linked to increased larval growth rates in Atlantic cod and haddock (Buckley & Durbin 2006). Similarly, in the Gulf of St. Lawrence, the recruitment success of Atlantic mackerel has been linked to the abundance of preferred copepod nauplii (Castonguay et al. 2008).

An alternative explanation is that increased primary production led to increased benthic flux which led to increased benthic forage for adult groundfish (Townsend & Cammen 1988). This increased forage base could have led to higher parental condition, higher egg quality, and higher larval survival. Under this mechanism, the observed change in the zooplankton community would have been coincidental, and the real effect on recruitment would be through a benthic pathway. Given that the 1990s were a decade of high phytoplankton production (Kane 2011b), and, in some stocks, there appears to be a link between parental condition and phytoplankton bloom magnitude and phenology (Leaf & Friedland 2014), this mechanism deserves further investigation.

As mentioned above, although the high recruitment success of the 1990s coincided with a shift in zooplankton community structure and abundance, it also coincided with a period of low spawning stock biomass for many stocks (see Figs. S3, S4 & S5 in the Supplement). Recruitment success has been shown to increase during periods of low biomass in some stocks (Brodziak et al. 2001), and a link between recruitment and parental condition has been noted elsewhere (Blanchard et al. 2003). Since parental condition may play a role in determining recruitment success, and there is evidence for regimes in parental condition (L. Smith, NEFSC, pers. comm.), the high recruitment regime of the 1990s could have been driven by the combined effect of an increase in preferred copepod prey (particularly small copepods such as *Pseudocalanus* spp.) and an increase in parental condition due to a decrease in spawning stock biomass. Similarly, the low recruitment regime of the 2000s may have been driven by the increased spawning stock biomass following the high recruitment events of the late 1990s combined with the observed decrease in copepod prey. Further research is needed to understand the interplay of shelf-wide regimes in parental condition, zooplankton abundance, and recruitment success.

While there is evidence for age truncation in several fish populations on the NE Shelf, and there is

also evidence that large, old females tend to produce more and higher quality offspring (Berkeley et al. 2004, McBride et al. 2015), we did not find a clear link between recruitment success regimes and age truncation regimes. Rather, trends in age truncation appear to track trends in spawning stock biomass, both of which reached minimum values in the 1990s while recruitment success peaked, although some stocks had already experienced age truncation prior to the 1980s. Given that the high recruitment success of the 1990s occurred while many stocks were truncated, recruitment might have been even higher during the 1990s in the absence of age truncation, and similarly, the low recruitment success of the 1980s and 2000s could have been even lower if the populations had been truncated. In this way, big, old females may be particularly valuable during low productivity regimes. Additionally, despite being truncated, many stocks contained repeat spawners since the maximum age is typically much greater than the age at maturity for species in this region. As repeat spawners are known to spawn more and larger eggs (Palakovich Carr & Kaufman 2009) of higher quality (Kamler 2005) over a longer period (Fitzhugh et al. 2012), this may have provided a buffering effect despite the absence of the oldest individuals.

Although regimes are often difficult to detect in any single stock, once stocks are pooled together the regimes become increasingly clear. The difficulty in identifying regimes in individual stocks is somewhat expected, since each stock is subject to its own sources of variability and sampling error. This highlights the value of a multi-species meta-analytic approach for identifying broad scale ecosystem changes, while also highlighting the importance of stock-specific studies to illuminate remaining sources of variability. In this regard, a multi-species analysis such as this provides ecosystem context for single species analyses. This context is important, because if productivity shifts are unrecognized or ignored, particularly during periods of reduced productivity, risk to populations may be underestimated. However, if productivity shifts are recognized, managers can adjust harvest levels as they deem necessary.

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