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Original Article

Age-specific differences in the seasonal spatial distribution of butterfish (*Peprilus triacanthus*)

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The spatial distribution of butterfish (*Peprilus triacanthus*) in the Northwest Atlantic Ocean was investigated using a suite of spatial indicators based on Northeast Fisheries Science Center spring and fall bottom trawl survey data, 1982–2013. In the spring, ages 2 and 3 were found farther northeast and deeper than age 1 butterfish, while in the fall, age 3 butterfish were found farther northeast and deeper than ages 0 and 1. There was no significant northward movement of butterfish in spring or fall over the course of either time-series. However, there was a significant increase in the area occupied by ages 1–3 in the spring that was correlated with surface temperature. This illustrates that responses to climate change may be manifested as range expansions, rather than poleward movement of the centre of gravity (i.e. bivariate weighted mean location of the population). Two changes were observed over the course of the fall time series, both for ages 1 and 2: increased spatial dispersion; and a decrease in depth. The former result would have been masked, while the latter would have been erroneously generalized to all age classes, if an age-specific analysis had not been done. This study demonstrates the importance of an age-based and seasonal analysis. It is also shown how a spatial distribution analyses can inform stock assessments by providing insights into diverging survey indices and availability to surveys in general. Similarly, spatial distribution analyses can be used to verify the spatial equilibrium assumption for the calculation of biological reference points.

Keywords: area occupancy, butterfish, centre of gravity, *Peprilus triacanthus*, spatial distribution.

Introduction

Butterfish (*Peprilus triacanthus*) in the Northwest Atlantic Ocean between Cape Hatteras and the Gulf of Maine (Figure 1) are considered to be a unit stock for management purposes (Adams *et al.*, 2015). Butterfish begin schooling around 6 cm (Collette and Klein-MacPhee, 2002). They are a short lived, fast growing species, overwintering offshore, and then moving inshore and northwards in the summer (Cross *et al.*, 1999). Spawning occurs from May to September, but peaks in June and July (O'Brien *et al.*, 1993). They are fully recruited by their third summer at age 2 (DuPaul and McEachran, 1973).

Historically, butterfish catch peaked in 1973 at 40 000 mt, primarily because of foreign fleets targeting longfin squid (*Doryteuthis pealeii*) in offshore areas (Adams *et al.*, 2015). Butterfish catch declined sharply following the implementation of the Fishery Conservation and Management Act of 1976 (Murawski and Waring, 1979). Foreign landings were completely phased out by 1987 (Adams *et al.*, 2015). From 2002 to 2012 there was no directed fishery, and landings, primarily as bycatch in the small mesh (<10.2 cm) bottom trawl longfin squid fishery, dropped to a low of 400 mt in 2005. However, a directed fishery was re-established in 2013, and harvest limits were increased (NMFS, 2015) following the most recent stock assessment (Adams *et al.*, 2015).

The Northeast Fisheries Science Center (NEFSC) conducts spring and fall bottom trawl surveys along the northeastern continental shelf of the United States (Politis *et al.*, 2014). One of the concerns raised in the most recent butterfish stock assessment was conflicting survey trends: the spring series has generally been increasing over time, while the fall series has been decreasing. Although the spring

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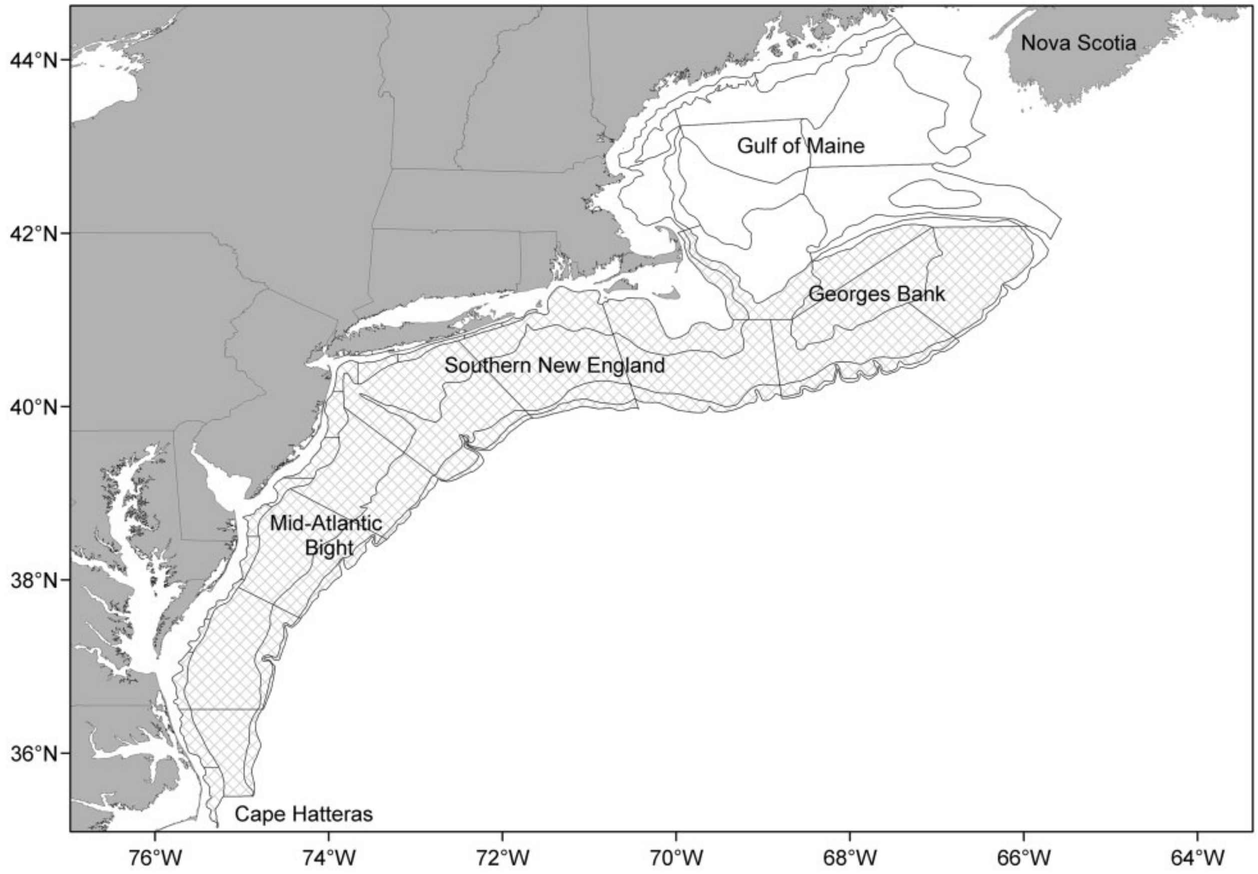

Figure 1. Northeast Fisheries Science Center bottom trawl survey strata from Cape Hatteras, NC, USA to Nova Scotia, Canada. Strata used in this study include the butterfish stock assessment offshore strata (cross hatch), as well as Gulf of Maine and outer Georges Bank strata (white).

series tracked cohorts more clearly through the age structure, butterfish are more widely distributed throughout the survey area during the fall. Thus, fall survey trends are thought to more accurately represent patterns in overall abundance. Accordingly, only the fall survey data were used in the assessment. Research into the spatio-temporal distribution of butterfish may provide insights into these divergent trends (Adams *et al.*, 2015).

The primary objective of this study was to quantify the spatio-temporal distribution of butterfish by age and season, from 1982 to 2013. The most recent butterfish stock assessment (Adams *et al.*, 2015) used a statistical catch-at-age model that relies in part on NEFSC survey abundance indices and age composition. Thus, NEFSC survey-based spatial indicators for butterfish were calculated at age to inform future stock assessments. Spatial indicators, such as the centre of gravity (CG), can be used to detect changes over time in the distribution of fish stocks (Woillez *et al.*, 2007). The CG has been used in fisheries for several decades, where it is also referred to as the centroid of distribution or centre of mass (e.g. Koslow *et al.*, 1985; Heath and MacLachlan, 1987; Murawski and Finn, 1988; Kendall and Picquelle, 1989).

A secondary objective of this study was to examine environmental (i.e. temperature and salinity) and density-dependent effects on the spatial distribution of butterfish. The CG has also been used to link changes in fish distribution to climate change (e.g. Nye *et al.*, 2009). In the case of butterfish, there was no effect of abundance, bottom temperature or surface temperature on the weighted mean latitude in the spring (1968–1990) or fall (1967–1989) NEFSC survey data (Murawski and Mountain, 1990). However, there was a significant effect of abundance when spring NEFSC survey data were restricted to the Mid-Atlantic Bight (Figure 1), 1980–1989 (Mountain and Murawski, 1992). Thus, this secondary objective serves as a re-evaluation of environmental and density-dependent effects on the spatial distribution of butterfish.

Material and methods

Data sources

The NEFSC has conducted spring and fall bottom trawl surveys on the continental shelf of the Northeast United States since 1968 and 1963, respectively. Butterfish otoliths were first collected in the NEFSC survey in 1982. Thus, data used in this analysis were from 1982 to 2013. Exact survey dates are given in Supplementary Table S1. The survey employs a random stratified design. Strata are defined primarily by depth, and the number of stations allocated to each stratum is proportional to stratum area. Sampling originally occurred at depths between 27 and 366 m, but shallower strata were added in 1972 and 1979. In spring 2009, the survey vessel FRV *Albatross IV* (AIV) was replaced by the FSV *Henry B. Bigelow* (HBB). These and other changes in gear and protocols over the course of the time-series are documented in Johnston and Sosebee (2014).

Because of the deeper draft of the HBB only strata with depths >18 m have been surveyed since 2009 (Johnston and Sosebee, 2014). During the most recent stock assessment for butterfish (Adams *et al.*, 2015) these strata were referred to as the offshore strata. To maintain the same footprint over the course of the time-series, a choice had to be made between including the shallow strata and ending the time-series in 2008, or including data from 2009 forward and restricting the footprint to the offshore strata. Given the observed changes in the distribution of many species in response to climate change (e.g. Nye *et al.*, 2009), the latter was chosen so as to incorporate the most recent available data. Additionally, several of the offshore strata that were not sampled consistently throughout the time-series were omitted. To investigate possible northward shifts in distribution, Gulf of Maine strata, as well as several outer Georges Bank strata, were added to provide more reliable estimates of the distribution centres over time (Brown *et al.*, 2011). Assessment offshore strata and the strata used in this spatial analysis are listed in Supplementary Table S2 and shown in Figure 1.

Age determination methods for butterfish are documented in Dery (1988). Age–length keys from each cruise were used to transform the length frequencies observed at each trawl station into age frequencies. Butterfish abundance at each station was disaggregated into age 0 to 4+ for the fall, and age 1 to 4+ for the spring. Data for 2009–2013 were converted to AIV units using the length-based calibration in Miller (2013) to account for the aforementioned vessel and gear changes.

Conductivity, temperature and depth data are collected at all NEFSC trawl stations (Politis *et al.*, 2014). However, salinity data are currently only available in the NEFSC survey database going back to fall 1997, and most 2008 data are also not available. Additionally, in spring 2005 salinity measurements were not recorded at $> 5\%$ of stations. Altogether this reduced the number of years with sufficient hydrographic data to $n = 14$ for the spring, and $n = 16$ for the fall. Thus, the environmental analysis was restricted to 1998–2013 for the spring (minus 2005 and 2008), and 1997–2013 for the fall (minus 2008).

Spatial indicators

The CG characterizes one property of the spatial distribution of a fish population. This and other properties of the spatial distribution of a fish population have been formalized into a suite of spatial indicators related to transitive geostatistics by Bez *et al.* (1997) and Woillez *et al.* (2007, 2009). In this section it is only described how each indicator is calculated in practice.

Geographical referencing

Distances between points must be computed in a Euclidean reference system (Bez, 2007). This was done by setting the minimum longitude and latitude of the strata used in this analysis (75°48′W, 35°09′N) as (0, 0) and converting all coordinates to kilometres according to Rivoirard *et al.* (2000). The cosine of the midpoint latitude (39°49′N) was used to convert longitude. Geographically referenced longitude and latitude are hereafter referred to as the *X*- and *Y*-components of the CG.

Centre of gravity

The CG is the mean location of the surveyed population:

$$\mathrm{CG} = \frac{\sum_{i=1}^{n} x_i w_i z_i}{\sum_{i=1}^{n} w_i z_i} \tag{1}$$

where x_i is location (XCG or YCG), w_i is the area of influence, and z_i is the number of butterfish. In the case of irregular sampling, spatial indicators are weighted with an area of influence (Bez *et al.*, 1997; Woillez *et al.*, 2007, 2009). Given the random stratified survey design (as opposed to a grid), a Dirichlet tessellation (Legendre and Legendre, 1998) was used as a non-subjective method to calculate areas of influence, with areas along the edge of the study area clipped to the boundary of the strata. Prior to analysis, the CG of sample locations (unweighted by z_i) was calculated to verify that changes in the CG over time were not because of changes in sampling design (Woillez *et al.*, 2009). Abundance weighted mean depth was also calculated with (1) (Faraj and Bez, 2007).

Inertia

The inertia (variance) describes how dispersed the population is around its CG:

$$I = \frac{\sum_{i=1}^{n} (x_i - \mathrm{CG})^2 w_i z_i}{\sum_{i=1}^{n} w_i z_i} \tag{2}$$

I can be decomposed into two orthogonal axes describing the maximum and the minimum components of the inertia. The square root of *I* for a given axis gives the standard deviation of the respective axis. As *I* has units of square kilometres, axes of inertia are plotted in CG maps as the standard deviation, which has units of kilometres. After back transformation to longitude and latitude, the axes may no longer appear orthogonal in CG maps (Bez, 2007; Faraj and Bez, 2007).

Positive area

The positive area (PA) is the area (in square kilometres) occupied by fish abundances greater than zero:

$$\mathrm{PA} = \sum_{i=1}^{n} w_i [z_i > 0] \tag{3}$$

Intra-season analysis

As a preliminary, basic age-specific differences in spatial distribution within each of the two seasons were characterized. This was done with a Kruskal–Wallis test for each spatial indicator, followed by a non-parametric multiple comparison test (Siegel and Castellan, 1988). For both tests, significance was set at $\alpha = 0.05$. Age 4+ butterfish were omitted from this analysis as there was a number of years in the time-series when this age class was not observed ($n = 10$ in the spring; $n = 21$ in the fall).

Spatial distribution over time

To quantify the spatial distribution of butterfish over time, each of the spatial indicators for each age class within a season was regressed as a function of year. A Durbin–Watson test was used to check each linear model for serial correlation and, if present, a first-order autoregressive model was fit instead (Neter *et al.*, 1996).

Environmental and density-dependent effects

To examine environmental and density-dependent effects on the spatial distribution of butterfish, each of the spatial indicators for each age class within a season was fit to a multiple linear regression model. Candidate predictor variables were: stratified mean number per tow from the survey (hereafter referred to as stratified mean number); bottom temperature, surface temperature, bottom salinity, and surface salinity. Note that all hydrographic parameters were also calculated as the stratified mean. Stratified mean number was log transformed for analysis. Prior to multiple linear regressions, a variance inflation factor analysis (Neter *et al.*, 1996) was used to detect collinearity among the candidate predictors. A conservative cut-off of 5 was used (e.g. Puerta *et al.*, 2014). A backward elimination procedure (Neter *et al.*, 1996) was then used to reduce each model to predictor variables that were significant at the level of $\alpha = 0.05$. Residuals were tested for autocorrelation with a Durbin–Watson test, and, if present, a first-order autoregressive model was fit instead (Neter *et al.*, 1996).

Software

Several R (R Core Team, 2015) packages were used in this analysis: spatial indicators were calculated in RGeostats (Renard *et al.*, 2014); Dirichlet tessellae were calculated in spatstat (Baddeley and Turner, 2005); non-parametric multiple comparison tests were done in pgirmess (Giraudoux, 2014); and variance inflation factor analysis was done in usdm (Naimi, 2015). Autoregressive models were calculated in PROC AUTOREG (SAS Institute, Inc., Cary, NC, USA).

Results

Intra-season analysis

The spatial distribution of butterfish varied by age class in the spring. There was a significant difference between age classes for XCG ($H = 25.73$, d.f. = 2, $p < 0.001$), YCG ($H = 20.68$, d.f. = 2, $p < 0.001$), depth ($H = 29.10$, d.f. = 2, $p < 0.001$) and PA ($H = 35.71$, d.f. = 2, $p < 0.001$). Multiple comparison tests revealed that ages 2 and 3 butterfish were significantly farther northeast and deeper than age 1 butterfish (Figure 2). These age-specific differences in distribution can also be visualized by toggling through the CG maps in the online supplementary material (Supplementary Figure S1). Multiple comparisons tests also showed that ages 1 and 2 butterfish had a significantly larger PA than age 3 butterfish (Figure 2).

The spatial distribution of butterfish also varied by age class in the fall. There was a significant difference between age classes for XCG ($H = 27.30$, d.f. = 3, $p < 0.001$), YCG ($H = 15.04$, d.f. = 3, $p = 0.002$), depth ($H = 19.52$, d.f. = 3, $p < 0.001$) and PA ($H = 80.37$, d.f. = 3, $p < 0.001$). Multiple comparison tests for XCG revealed that ages 1–3 were significantly farther east than age 0 butterfish, while age 3 butterfish were significantly farther north than ages 0 and 1 butterfish (Figure 2). In this case, age-specific differences are best observed in the maps (Supplementary Figure S1) by noting that the CGs for age 0s are generally more inshore. Multiple comparison tests found that ages 1–3 were significantly deeper than age 0 butterfish (Figure 2). Finally, age 0 butterfish had a significantly larger PA than ages 1–3, while ages 1 and 2 had a significantly larger PA than age 3 butterfish (Figure 2).

Spatial distribution over time

Spatial indicators showed interannual variation in the spring for all age classes (Figure 3). There was a significant increase in area occupancy for ages 1, 2, and 3 butterfish over the course of the time-series. However, there was no change in the CG, inertia or depth for any age class in the spring.

Spatial indicators also showed interannual variation in the fall for all age classes (Figure 4). There was no change in the CG over the course of this time-series either. In this case, however, there was a significant increase in inertia for ages 1 and 2 butterfish. There was also a significant decrease in depth for the same two age classes. Finally, there was no change in area occupancy over the course of the fall time series.

A simple *post hoc* analysis was done to examine whether age-specific effects observed in the fall would have been masked using the total number of fish. As noted above, significant changes for inertia and depth over time were observed for ages 1–2, but not age 0 butterfish. Thus, regressions were also run for these two cases using the sum of all ages. There was no change in inertia over the course of the fall time series ($\beta = 468.70$, $t(30) = 1.42$, $p = 0.166$). This indicates that the significant slopes for ages 1 and 2 shown in Figure 4 would have been masked. Conversely, there was a significant decrease in depth for the total number of butterfish ($\beta = -0.51$, $t(30)$ $p = 0.032$), when this was actually only true for ages 1 and 2 (Figure 4).

Environmental and density-dependent effects

There were clear environmental relationships with the spatial distribution of butterfish in the spring (Table 1). There was a highly significant correlation between surface temperature and area occupancy for all age classes. There was also a correlation between surface temperature and the YCG for age 1 butterfish. The negative relationship between surface salinity and depth for age 2 butterfish was barely significant ($p = 0.047$) and thus should be viewed with caution. There were no significant density-dependent relationships.

Environmental relationships with the spatial distribution of butterfish in the fall were more complicated (Table 1). For age 0 recruits, there was a highly significant correlation between bottom temperature and the XCG; and a correlation between surface salinity and the YCG. Area occupancy of recruits was positively correlated with bottom temperature and negatively correlated with surface temperature. The YCG of age 1 butterfish was positively correlated with bottom temperature. Depth of age 1 butterfish was positively correlated with bottom temperature and negatively correlated with surface temperature. For ages 2 and 3 butterfish there was a positive relationship between bottom temperature and depth. There was also a correlation between the abundance of age 3 butterfish and area occupancy. The relationship between the stratified mean number of age 4+ butterfish and the YCG was barely significant ($p = 0.047$) and may be an artefact of the low sample size ($n = 7$).

Discussion

The primary objective of this study was to quantify the spatio-temporal distribution of butterfish by age and season, from 1982 to 2013. The intra-season analysis revealed age-specific differences for all spatial indicators of butterfish distribution in both seasons. The clearest signal observed during the time-series analysis was increased area occupancy for ages 1–3 in the spring. The secondary objective of this study was to examine environmental and density-dependent effects on the spatial distribution of butterfish. This revealed a highly significant relationship between the increased spring area occupancy and surface temperature.

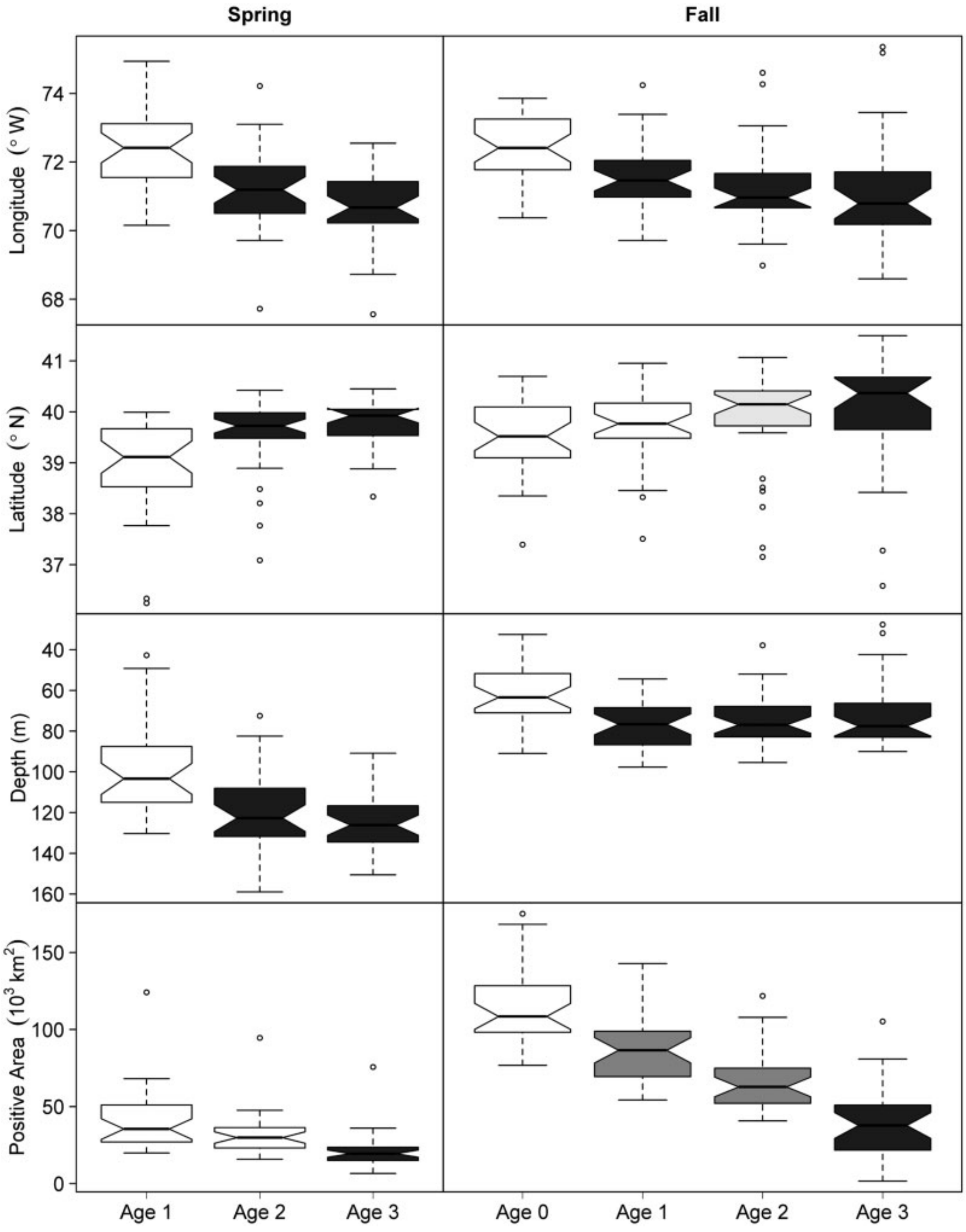

Figure 2. Notched box plots showing medians of selected spatial indicators for spring ages 1–3 and fall ages 0–3 butterfish. Hinges are the first (Q_1) and third (Q_3) quartiles. Whiskers are within 1.5 times the range between Q_1 and Q_3. Outliers are shown as circles. Within each season, black boxes are significantly different from white boxes; grey boxes (i.e. PA for fall ages 1 and 2) are significantly different from black and white boxes; while light grey boxes (i.e. latitude for fall age 2) are not significantly different from other boxes. Significance level for all multiple comparisons was $\alpha = 0.05$. Note that Kruskal–Wallis tests were done on XCG and YCG, not the back-transformed longitude and latitude, which are shown here to aid interpretation.

Intra-season analysis

This study revealed age-specific differences in the CG of butterfish from 1982 to 2013. In the spring, ages 2 and 3 were found farther northeast and deeper than age 1 butterfish. This is likely a response to upwelling conditions, as butterfish are associated with fronts on the outer continental shelf during winter and early spring (Manderson *et al.*, 2011). In the fall, age 3 butterfish were found farther northeast and deeper than ages 0 and 1, while ages 1 and 2 were found farther east (XCG only) and deeper than age 0s. This more complicated spatial segregation may be because the water column is warm and stratified during the fall, and butterfish associations with fronts are weak or absent (Manderson *et al.*, 2011). Area occupancy decreased with age in both spring and fall. In both seasons, the PA was significantly less for age 3 butterfish than younger age classes. Woillez *et al.* (2007) found that the PA for European hake (*Merluccius merluccius*) in the Bay of Biscay was relatively stable until age 3, and then dropped for ages 4 and 5+.

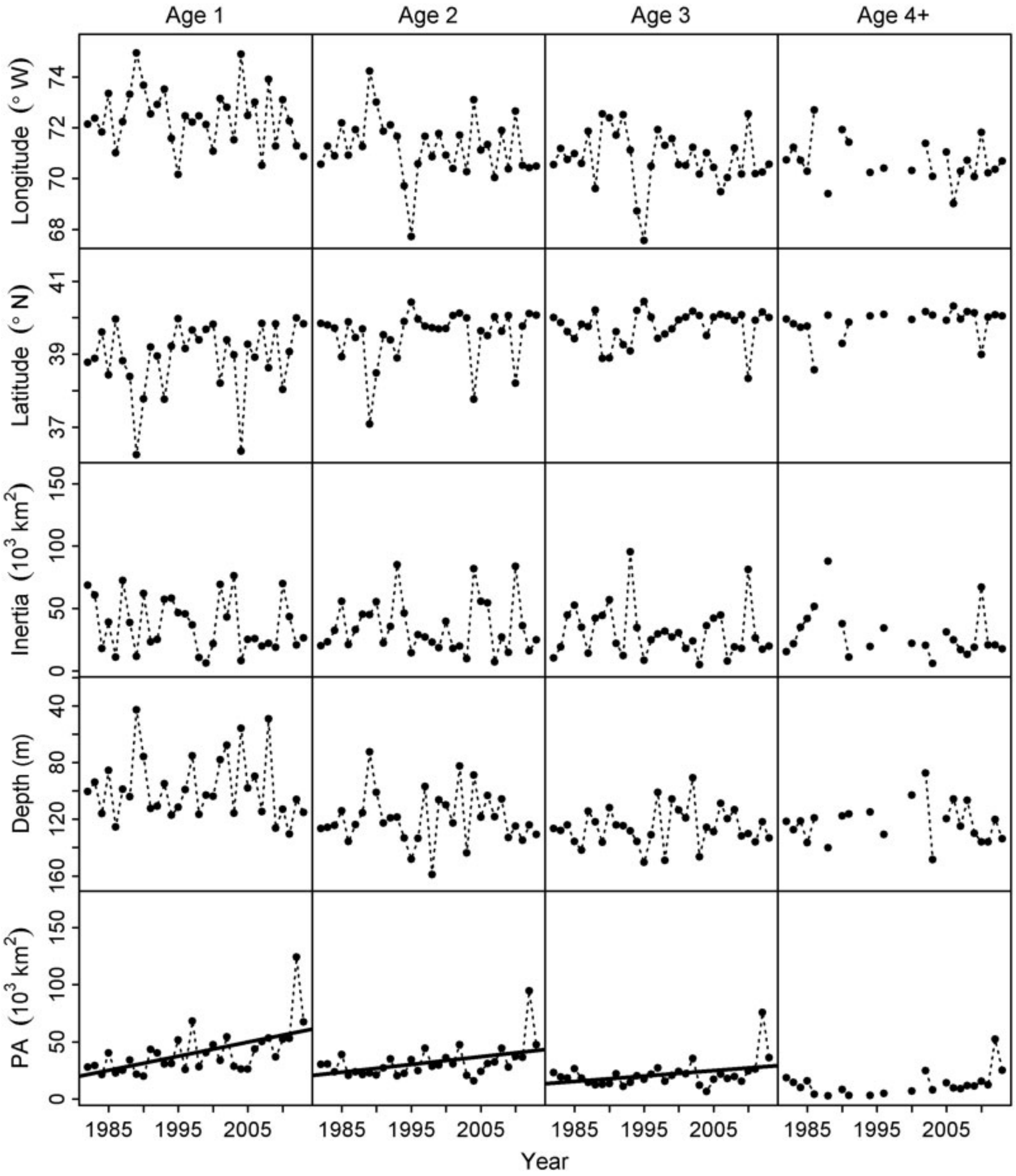

Figure 3. Spring time series of spatial indicators for butterfish ages 1 to 4+. Solid lines indicate a significant linear fit at the level of $\alpha = 0.05$. Note that linear models were tested on XCG and YCG, not the back-transformed longitude and latitude, which are shown here to aid interpretation.

Spatial distribution over time

The finding of no northward movement of butterfish in spring or fall over the course of the 32-year time-series is consistent with another recent analysis. Using an alongshelf measure, Walsh *et al.* (2015) also found no poleward movement of adult butterfish in the spring or fall during the period 1999–2008 when compared with 1977–1987. However, they did report that adult butterfish were found more inshore (e.g. cross shelf) in both spring and fall in the Mid-Atlantic Bight during 1999–2008. A comparable result would have been observed in the present study as a decrease in the XCG over time (i.e. westward movement). Although none of the slopes was significant, this was the general trend for fall ages 1–3 butterfish (Figure 4).

There were two changes in spatial distribution over the course of the fall time-series. The increase in inertia for fall ages 1–2 indicates that these age classes have become more scattered over time. An increase in inertia with age has also been observed in European hake (Woillez *et al.*, 2007). The other change over the course of the fall time-series is that age 1–2 butterfish have occupied shallower habitat. Walsh *et al.* (2015) also found that adult butterfish were shallower in the fall during the period 1999–2008 when compared with 1977–1987.

The importance of using age-specific indices was illustrated with the *post hoc* fall time-series analysis. In this case, age-specific changes in spatiotemporal distribution would have been masked or misrepresented if the data were not disaggregated by age. The increased dispersion of ages 1 and 2 butterfish over the course of the fall time-series would have been masked if only the total number of butterfish was analysed. Conversely, it would have been erroneously reported that butterfish have occupied shallower depths in the fall, when this was actually only true for ages 1 and 2.

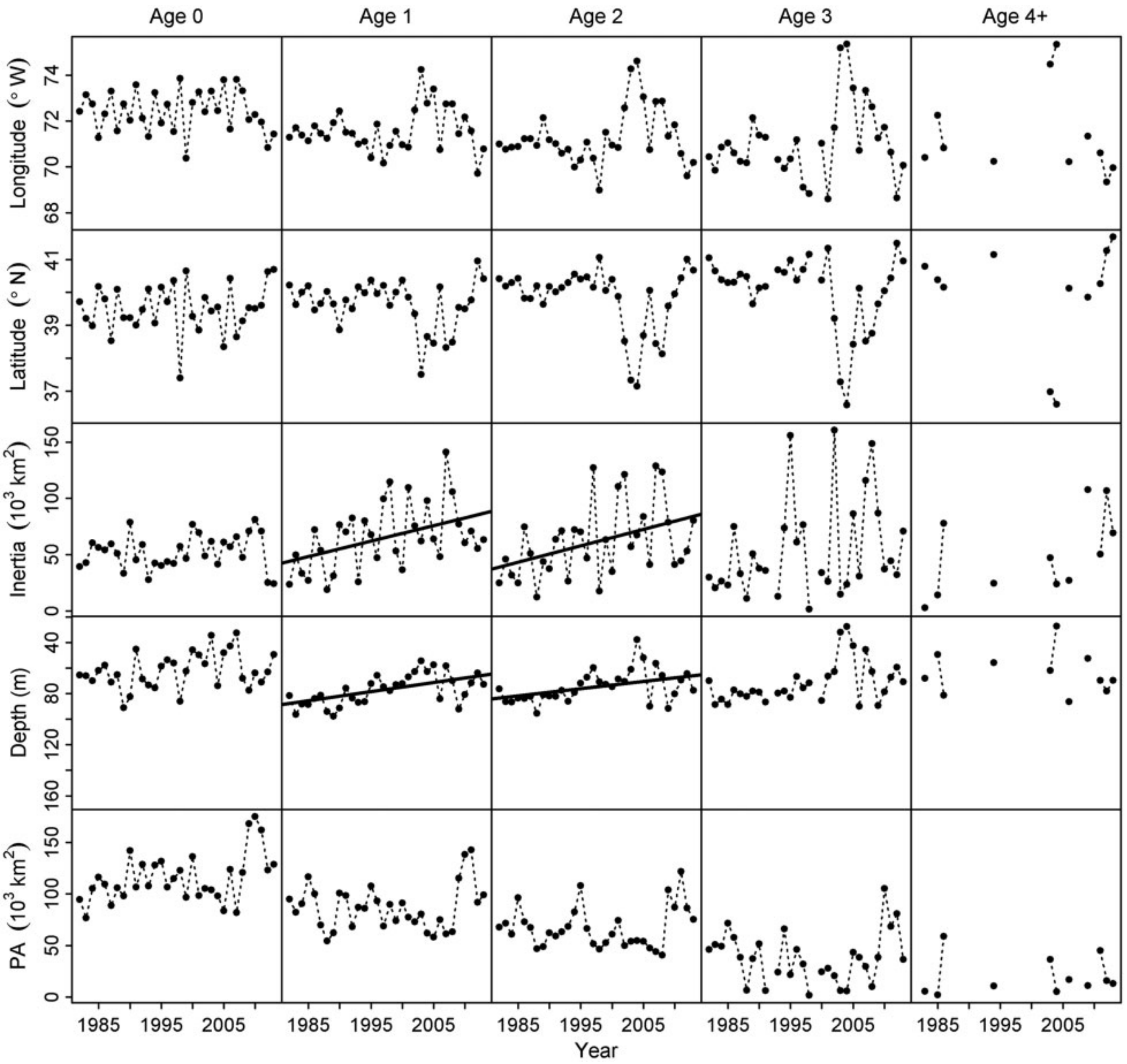

Figure 4. Fall time series of spatial indicators for butterfish ages 0 to 4+. Solid lines indicate a significant linear fit at the level of $\alpha = 0.05$. Note that linear models were tested on XCG and YCG, not the back-transformed longitude and latitude, which are shown here to aid interpretation.

Environmental and density-dependent effects

The highly significant relationship between surface temperature and area occupancy was the primary environmental effect in the spring. Given the lack of northward movement during this time, this suggests that, in the spring, the response of butterfish to shelf warming will be a range expansion, with the CG remaining in the Southern New England/Mid-Atlantic Bight region. Murawski and Mountain (1990) hypothesized that, if shelf warming results primarily in warmer fall and winter conditions, then species such as butterfish should be found north and shoalward of their present winter and early spring distributions, with perhaps some northward extension of their summer range. The present analysis supports their hypothesis. Positive area maps comparing warm vs. cold years help to visualize what such a range expansion might look like (Figure 5). The stratified mean surface temperature (for the strata used in this analysis) was 4.3 and 8.2 °C in 2004 and 2012, respectively. PA tiles for 2004 illustrate the typical spring distribution of butterfish along the shelf edge; whereas in 2012 the north and shoalward distribution predicted by Murawski and Mountain (1990) is observed. Although average sea surface temperatures on the northeastern continental shelf of the USA in 2012 were the highest in the 160-year record (Fratantoni *et al.*, 2013), this example illustrates a possible range expansion for butterfish under a shelf warming scenario.

The only other significant effect was that surface temperature had a positive correlation with the YCG for age 1 butterfish. Previous analyses found no relationship between surface temperature and the weighted mean latitude of total number of butterfish (Murawski and Mountain, 1990; Mountain and Murawski, 1992). These conflicting results may be because of the use of more recent data and/or because an age-specific effect was revealed in the present analysis. Future studies with a longer time-series of environmental data may resolve this issue.

Table 1. Slope (β), standard error, *t*-value, degrees of freedom and *p*-value for multiple linear regressions of butterfish spatial indicators as a function of abundance and hydrographic parameters.

Spring							**Fall**						
Indicator	**Predictor**	β	**s.e.**	***t*-value**	**d.f.**	***p*-value**	**Indicator**	**Predictor**	β	**s.e.**	***t*-value**	**d.f.**	***p*-value**
							Age 0						
							XCG	bottemp	85.92	18.06	4.76	14	<0.001
							YCG	surfsalin	190.61	45.41	4.20	14	0.001
							Depth						
							PA	bottemp	18365.54	7181.13	2.56	13	0.024
								surftemp	−15863.07	6687.19	−2.37	13	0.034
Age 1							**Age 1**						
XCG							XCG						
YCG	surftemp	73.49	25.90	2.84	12	0.015	YCG	bottemp	65.96	27.16	2.43	14	0.029
Depth							Depth	bottemp	6.52	2.30	2.84	13	0.014
								surftemp	−7.19	2.14	−3.36	13	0.005
PA	surftemp	21883.31	3899.04	5.61	12	<0.001	PA						
Age 2							**Age 2**						
XCG							XCG						
YCG							YCG						
Depth	surfsalin	−34.07	15.43	−2.21	12	0.047	Depth	bottemp	9.75	3.54	2.76	14	0.015
PA	surftemp	17382.32	2572.99	6.76	12	<0.001	PA						
Age 3							**Age 3**						
XCG							XCG						
YCG							YCG						
Depth							Depth	bottemp	15.52	5.02	3.09	11	0.010
PA	surftemp	15526.80	2207.73	7.03	12	<0.001	PA	logage3	21999.00	5391.00	4.08	11	0.002
Age 4+							**Age 4+**						
XCG							XCG						
YCG							YCG	logage4	−109.93	42.02	−2.62	5	0.047
Depth							Depth						
PA	surftemp	12853.10	2867.98	4.48	8	0.002	PA						

Spatial indicators and associated units are: geographically referenced longitude and latitude of the centre of gravity (XCG and YCG, respectively; km), depth (m) and positive area (PA; km^2). Predictor variables are: stratified mean bottom temperature (bottemp), surface temperature (surftemp), and surface salinity (surfsalin); as well as log transformed stratified mean number of butterfish per tow for ages 3 and 4+ (logage3 and logage4, respectively). Predictors were selected using a backward elimination procedure with significance level set at $\alpha = 0.05$. Only significant predictors are shown.

The spatial distribution of age 0 recruits appears to be driven by environmental conditions. There was a positive correlation between hydrographic parameters and the CG. The seemingly conflicting correlations of bottom and surface temperature with area occupancy can be explained as follows. Bottom temperature used in the multiple linear regression analysis ranged from 10.1 to 12.9 °C, whereas surface temperatures ranged from 15.3 to 18.3 °C. A previous analysis showed that a histogram of the proportion of positive tows for butterfish using NEFSC fall survey data, 1963–1997, peaked at 12 °C (Cross *et al.*, 1999). Thus, the negative relationship with surface temperature in the present analysis would correspond to the right tail of the histogram in the previous analysis. This interpretation is consistent with Colton (1972), who reported a contraction of the northern and eastern limits of butterfish during a downward trend in temperatures during the period 1953–1967.

Environmental effects on older age classes in the fall appear to be restricted to bottom temperature. There was a positive correlation between bottom temperature and the YCG for age 1 butterfish; and an increasingly strong relationship between bottom temperature and depth for age 1–3 butterfish. Conflicting trends between bottom and surface temperature and the depth of age 1 butterfish are less readily resolved. This serves as a reminder that biological factors, such as predators and prey, can affect the vertical distribution of fish (e.g. Murawski and Finn, 1988).

The only clear density-dependent effect was between the abundance of fall age 3 butterfish and area occupancy. Lange and Waring (1992) reported a negative relationship between the proportion of zero tows and abundance of large (>12 cm) butterfish in the fall NEFSC survey data, 1976–1985. Frisk *et al.* (2011) found a positive relationship between abundance and area occupancy of butterfish on Georges Bank, using fall NEFSC survey data, 1963–2006. Further research is needed to determine whether the findings in these previous studies are driven by age 3 butterfish.

Ideally some measure of fishing pressure would have been included in the multiple linear regressions as a predictor variable. Landings were not used in this analysis because butterfish have been caught primarily as bycatch in the directed longfin squid fishery over the last decade (Adams *et al.*, 2015). Given the

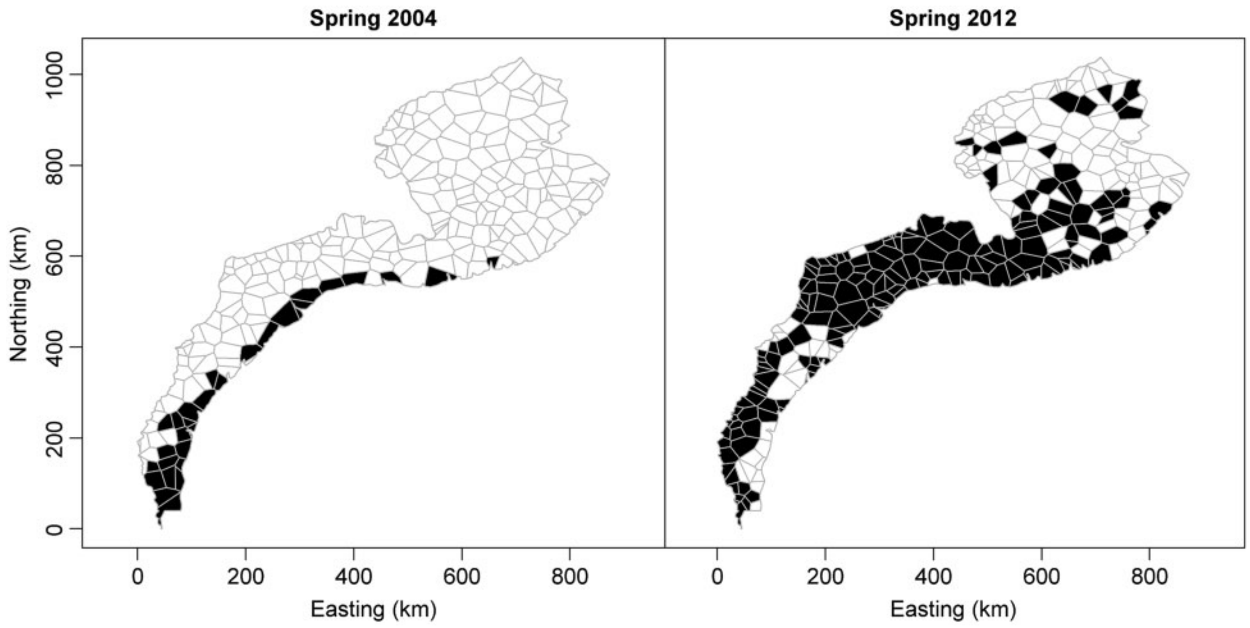

Figure 5. Positive area maps for age 1 butterfish in spring 2004 and spring 2012, when stratified mean surface temperatures were 4.3 and 8.2 °C, respectively. Black polygons indicate positive tows.

resumption of a directed fishery in 2013, future analysis could include an exploitation index.

Conclusions

This study can inform future butterfish assessments in several ways. With respect to the fall NEFSC survey index (which was used in the most recent assessment), there has been no change in the CG or PA through 2013. This indicates that the assumption of constant habitat suitable for production is being met within the boundaries of the strata used in this analysis. This conclusion should be verified using the assessment strata. In terms of the diverging spring and fall indices, increased area occupancy in the spring suggests that availability to the spring survey is increasing. Decreasing coefficients of variation for the NEFSC spring survey in recent years (Adams *et al.*, 2015) support this interpretation. In the spring NEFSC survey index (which was not used in the most recent assessment), increased area occupancy suggests that butterfish should be more broadly distributed over the shelf as shelf warming continues. Under this scenario, the spring index would be a candidate to be included in the assessment model. Finally, potential range expansion into the Gulf of Maine (Figure 5) illustrates that the inclusion of these strata should be re-examined.

This study has demonstrated the importance of an age-based and seasonal spatial distribution analysis. Increased area occupancy was observed only in the spring, whereas changes in depth and dispersion in the fall were restricted to specific age classes. Increased area occupancy in the spring was correlated with surface temperature, demonstrating that responses to climate change may be manifested as range expansions, rather than poleward movement of the CG. Spatial distribution analyses can inform stock assessments by providing insights into diverging survey indices and availability to surveys in general. Furthermore, spatial distribution analyses can be used to verify the spatial equilibrium assumption for the calculation of biological reference points.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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