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Implications of extremely high recruitment events into the US sea scallop fishery

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ABSTRACT: Extremely high recruitment events can have profound impacts on marine population dynamics. To demonstrate the complexities surrounding extremely high recruitment and its impact on population assessments, Atlantic sea scallop (*Placopecten magellanicus*) recruitment patterns from 2003 to 2014 were analyzed and the influence of these events on exploitable biomass and harvest numbers was examined. Since 2003, 2 extreme recruitment events have occurred within the scallop stock assessment area on Georges Bank and in the Mid-Atlantic. In 2003, about 12 billion (12×10^9) recruits were present in the Mid-Atlantic, while the total scallop population was about 21 billion scallops. In 2014, about 31 billion recruits were present on Georges Bank, the largest recruit abundance ever recorded, while the total scallop population was about 39 billion scallops. A similar event was also observed outside of the traditional stock assessment area in the Gulf of Maine during 2009. These events dramatically improved the status of the resource. They were not correlated to increases in spawning stock biomass in prior years, suggesting scallop populations do not grow at a constant rate. This growth pattern may be explained based upon scallop fecundity, heterogeneity in scallop distribution, and the importance of early life-history factors. This scenario is not exclusive to scallops and suggests a mismatch between marine population ecology and fisheries management. This mismatch might be rectified through better recognition of ecological and environmental factors, but the complexities surrounding recruitment, exemplified by extremely high recruitment events, suggest a continued need for adaptable management based upon empirical data.

KEY WORDS: *Placopecten magellanicus* · Population dynamics · Benthic imaging

INTRODUCTION

Predicting the number of offspring breeding adults will produce is one of the most uncertain relationships of fish populations and continues to limit our ability to understand and manage fisheries (Zhou 2007, Maunder 2012, Punt et al. 2014). This conundrum may arise from the prescription of models that rely on a direct, static relationship between spawning stock biomass and recruit abundance (Cury et al. 2014, Szuwalski et al. 2015). In reality, after a certain spawning stock biomass, environmental (i.e. member-vagrant hypothesis, Sinclair 1988 or match-mismatch hypothesis, Cushing 1981) factors may more strongly influence patterns of recruitment. This is exacerbated by the high potential fecundity many commercial fisheries species exhibit and by mismatches between the actual and theorized spatial scale of these populations (Rothschild 1986, Hilborn & Walters 1992). The Atlantic sea scallop (*Placopecten magellanicus*) fishery in the eastern USA is an example of a fishery that exhibits this dynamic.

The Atlantic sea scallop fishery in the USA has experienced unprecedented rebuilding over the past 15 years, growing from a low of 5500 t landed in 1998 to an average of over 25 000 t yr^{-1} landed from 2003 to 2014 due primarily to increases in scallop abundance and density (NEFSC 2014). Coupled with a

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sharp increase in demand and price, this growth has transformed the fishery into one of the highest valued US fisheries, with landings worth over $420 million (USD) in 2014 (NMFS 2015). Several factors have led to the successful rebound of US scallop populations, including revised rotational management approaches, investments in improved survey technologies, data-rich stock assessments, and potentially favorable environmental conditions (Hart & Rago 2006, Stokesbury 2012, O'Keefe & Stokesbury 2015). The resource is assessed by size-structured forward projecting models for the 2 large-scale effort areas of the fishery; the Mid-Atlantic and Georges Bank (open areas and closed areas on Georges Bank were separated in the most recent assessment, NEFSC 2014) (see Fig. 2). At this spatial resolution, there is a poor understanding of the stock–recruitment relationship for scallops, which confounds the assessment models and complicates management of the species (NEFSC 2014). This was exemplified by an extremely large, unpredicted recruitment event in 2003 within one small area of the fishery resulting in an overly optimistic harvest projection (Fig. 1). In reality, due to density-dependent factors such as high discard mortality and possibly increased predation, the year class abundance was greatly reduced and the potential was only partially realized (Hart & Shank 2011, Stokesbury et al. 2011a,b).

Here we quantify the largest scallop recruitment event ever observed on Georges Bank. We describe its spatial distribution and magnitude and compare it to previous scallop recruitment patterns within the 2 stock assessment areas and in the Gulf of Maine. We hypothesize that these recruitment events are largely independent of exploitable biomass, which is representative of spawning stock biomass. We test this hypothesis by determining if there were more exploitable scallops (i.e. greater reproductive potential) in the years prior to these extreme spawning events. We discuss how these events impacted the fishery, and examine explanations of why these events were not linked to spawning stock biomass and the implications they have on fisheries management.

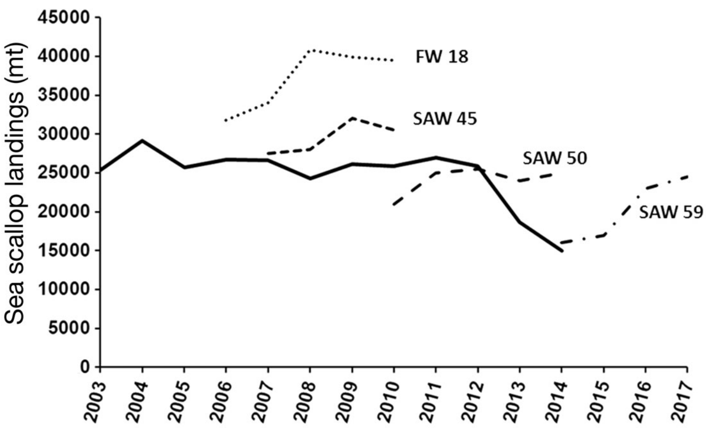

Fig. 1. Scallop landings from 2003 to 2014 (solid line) and the projected landings from Framework 18 of the New England Fisheries Management Council (FW 18) and the Stock Assessment Workshops conducted by the National Marine Fisheries Service (SAW). SAW 45: projected 2007–2010, SAW 50: 2010–2014, SAW 59: 2014–2017

MATERIALS AND METHODS

Observations of scallops were made using a video survey with a centric systematic sampling design. Resource-wide observations of scallops on Georges Bank and the Mid-Atlantic from 2003–2012 and in 2014 were made by stations positioned on a 5.6 by 5.6 km grid (Stokesbury 2002, 2012, Stokesbury et al. 2004), while observations from 2009–2011 and in 2013 and 2014 were made on several banks and ledges in the Gulf of Maine and utilized stations positioned on 1.0 by 1.0 km grids (Stokesbury et al. 2010) (Fig. 2). At each station a sampling pyramid was lowered to the sea floor 4 times. Mounted on the pyramid were 2 downward-facing video cameras, which provided quadrats of 0.60 m^2 and 2.84 m^2, and a camera mounted parallel to the sea floor to aid in the identification of fish and dead scallops. The quadrat sizes were increased based upon the average scallop shell height in the area to adjust for partially visible scallops counted along the edge of the image (O'Keefe et al. 2010). The larger quadrat size was used to calculate exploitable abundance (Stokesbury 2002, Stokesbury et al. 2004, NEFSC 2010). The smaller quadrat size was used to estimate density and recruit abundance, as it gives a better estimate of scallops with shell heights between 30 and 75 mm (Marino et al. 2007, Carey & Stokesbury 2011). The time, depth, number of live and dead scallops, latitude, and longitude were recorded at each station. After each survey, video recordings were reviewed in the laboratory and a still image of each quadrat was captured. The shell height (mm) of each scallop was measured in the still image using Image Pro Plus® software using pixel to mm measurement calibrations for each camera (Carey & Stokesbury 2011).

Mean densities and standard errors of scallops were calculated using equations for a 2-stage sampling design (Cochran 1977). The mean of the total sample is calculated as:

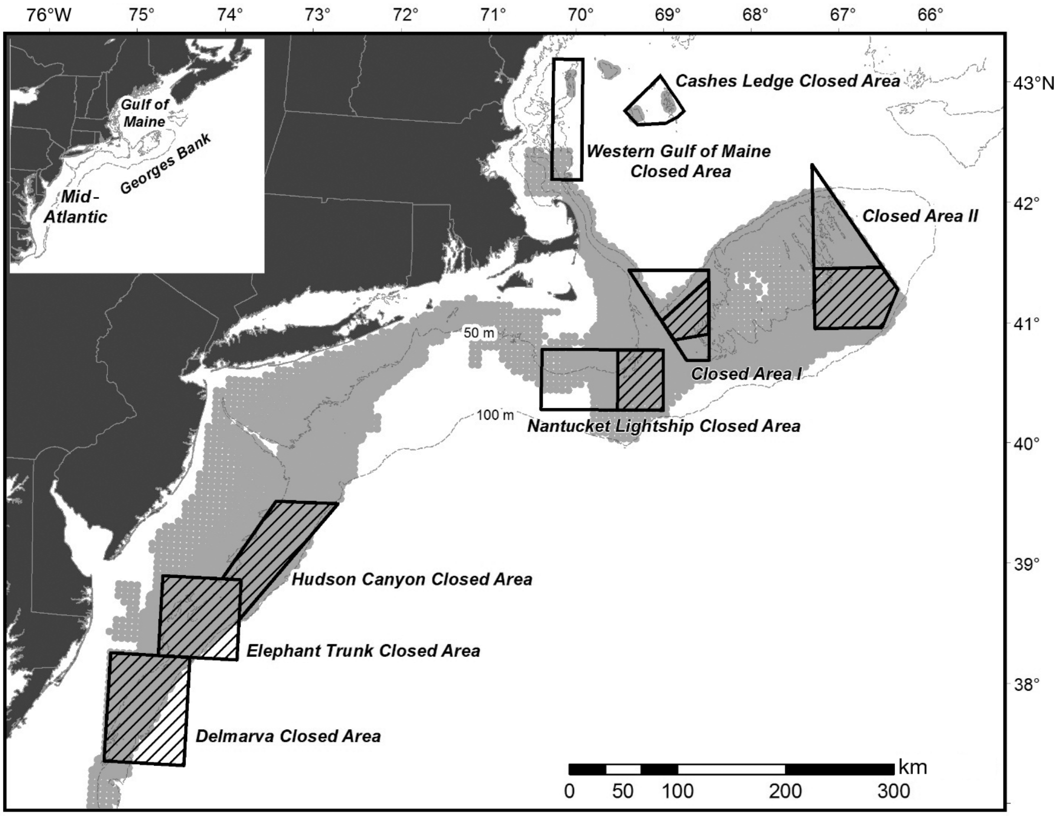

Fig. 2. Spatial extent of the School for Marine Science and Technology, University of Massachusetts Dartmouth (SMAST) scallop video survey on the US continental shelf (shaded areas). Resource-wide surveys were conducted on Georges Bank and in the Mid-Atlantic from 2003–2012 and in 2014 on a 5.6 km grid. Fine-scale surveys on 1 km grids were conducted in 4 areas of the Gulf of Maine from 2009–2014, with the exception of 2012. Hatched marks identify limited access areas, which are periodically opened to scallop fishing

$$\bar{x}_i = \sum_{j=1}^{n}\left(\frac{x_{ij}}{m}\right) \tag{1}$$

$$\bar{\bar{x}} = \sum_{i=1}^{n}\left(\frac{\bar{x}_i}{n}\right) \tag{2}$$

where n = primary sample units (stations), m = elements per primary sample unit (quadrats), x_{ij} = measured value for element j in primary unit i, $\bar{x}_{ij}$ = sample mean per element (quadrat) in primary unit i (stations) and $\bar{\bar{x}}_{ij}$ = the mean over the 2 stages. The standard error of this mean is:

$$\mathrm{SE}(\bar{x}) = \sqrt{\frac{1}{n}(s^2)} \tag{3}$$

where $s^2 = \sum^{n}(\bar{x}_i - \bar{\bar{x}})^2/(n-1)$ is the variance among primary unit (stations) means. According to Cochran (1977), this simplified version of the 2-stage variance is possible when the sampling fraction n/N is small. This is the case for the video survey, where thousands of m^2 are sampled compared to millions of m^2 in the study area. One-way ANOVAs were used to test the significance of shifts in mean individuals m^{-2} over time for each region (Sokal & Rohlf 2012). Shell height frequencies between years with extremely high amounts of recruits and all other years for each region were compared using Kolmogorov-Smirnov tests with the test statistic critical level adjusted to the number of independent samples (survey stations with measurements) taken for each comparison (Siegel & Castellan 1988).

The absolute number of scallops within the survey area was calculated by multiplying scallop density by the total area surveyed (Stokesbury 2002). Exploitable scallop abundance was calculated using a size selectivity curve for a commercial dredge applied to the total number of scallops at each 5 mm interval of shell height (Yochum & DuPaul 2008). Scallops begin to reproduce at about age 2, but make little contribution until age 4 as fecundity significantly increases with size (NEFSC 2014). Thus, exploitable scallop abundance is an approximate proxy for spawning stock biomass because all size classes are included, but the proportion at which they are included follows a logistic curve as size increases (Yochum & DuPaul 2008). A Spearman correlation was used to test for a link between the number of recruits and the number of exploitable scallops 2 or 3 yr prior, as recruit sized scallops are likely 2 or 3 yr old. This correlation removes assumptions about linearity, making it an appropriate test for the Beverton-Holt stock–recruit relationship (Szuwalski et al. 2015), which is prescribed to the Atlantic sea scallop (NEFSC 2014). To include estimates of exploitable scallop abundance in the Mid-Atlantic in 2000 and 2001 (years potentially linked to the production of extremely high recruitment events, but prior to the broadscale survey) exploitable scallop abundance was approximated from the Northeast Fisheries Science Center Stock Assessment Workshop 59 by subtracting the total number of recruits in Fig. B6.39 from total abundance in Table B6.1 estimated by the stock-assessment model (NEFSC 2014).

To estimate the number of scallops harvested in Georges Bank and the Mid-Atlantic, the annual landings reported in the Northeast Fisheries Science Center Stock Assessment Workshop 59 were used (NEFSC 2014). Estimates of scallop meat weight in grams were derived for each year following the National Marine Fisheries Service meat weight regression (NEFSC 2007, Stokesbury 2012, Hart et al. 2013) and the mean exploitable meat weight was calculated by applying the Yochum & DuPaul (2008) selectivity curve. This analysis and Spearman correlation were not done for the Gulf of Maine as the survey occurred largely in areas closed to fishing, (Fig. 2) which are not incorporated into the scallop size-structured forward projecting stock assessment model (NEFSC 2014).

RESULTS

In 2014, approximately 34 billion (34×10^9) scallops were observed on Georges Bank (Table 1). Recruits (scallops with shell heights 30 to 75 mm) totaled about 31 billion and were concentrated in the Nantucket Lightship Closed Area between depths of 70 to 100 m (Fig. 3). Smaller aggregations of juveniles were also observed in the southern portion of Closed Area II and the western portion of Closed Area I (Fig. 3).

The highest density of scallops on Georges Bank occurred in 2014 (ANOVA, df = 10, F = 10.1, $p < 0.001$, Tukey post-hoc test $p < 0.001$; Table 1). The

Table 1. Annual SMAST (see Fig. 1) video survey scallop summary data, including a scallop abundance estimate for each year and area, derived from small quadrat (0.60 m^2) observations for the Gulf of Maine, Georges Bank and Mid-Atlantic. MW: meat weight

Year	No. of stations	Scallops m^{-2}	SE	Shell height (mm) n	Shell height (mm) Mean	Shell height (mm) SD	Mean MW (g)	Abundance (scallops × 10^9)
Gulf of Maine								
2009	298	1.19	0.185	736	47.9	15.2	2.37	0.35
2010	290	0.97	0.156	661	50.7	14.2	2.63	0.28
2011	300	0.46	0.084	338	68.5	20.8	6.36	0.14
2013	286	1.11	0.136	735	57.1	26.2	4.62	0.32
2014	291	0.62	0.083	426	79.9	32.3	10.88	0.19
Georges Bank								
2003	904	0.17	0.017	281	88.3	28.9	14.07	4.74
2004	921	0.13	0.014	196	101.4	32.0	20.85	3.57
2005	902	0.10	0.013	154	111.2	33.6	27.95	2.79
2006	916	0.14	0.014	191	109.1	36.3	27.24	3.99
2007	901	0.20	0.022	337	80.0	39.0	14.16	5.49
2008	882	0.15	0.019	354	99.4	43.0	24.75	4.15
2009	942	0.16	0.019	308	96.1	37.5	20.78	4.53
2010	905	0.13	0.012	188	103.4	33.7	23.69	3.57
2011	920	0.15	0.018	272	92.8	35.4	19.99	4.13
2012	713	0.13	0.020	231	118.4	38.9	34.33	2.77
2014	999	1.11	0.286	2009	50.8	21.2	4.14	34.35
Mid-Atlantic								
2003	799	0.71	0.143	1040	58.6	23.7	4.67	17.42
2004	829	0.23	0.026	330	84.7	23.3	11.67	5.94
2005	860	0.22	0.027	274	87.2	30.2	14.12	5.79
2006	872	0.20	0.022	343	93.4	26.0	16.01	5.52
2007	931	0.22	0.021	401	90.4	24.3	14.04	6.33
2008	913	0.22	0.021	451	90.7	31.6	16.95	6.09
2009	928	0.13	0.009	211	98.1	28.5	19.93	3.61
2010	903	0.10	0.010	168	104.6	32.9	24.49	2.69
2011	966	0.08	0.007	150	95.1	31.4	19.07	2.25
2012	1168	0.14	0.021	341	61.3	34.6	9.14	5.00
2014	1170	0.14	0.010	342	77.9	38.9	14.55	4.88

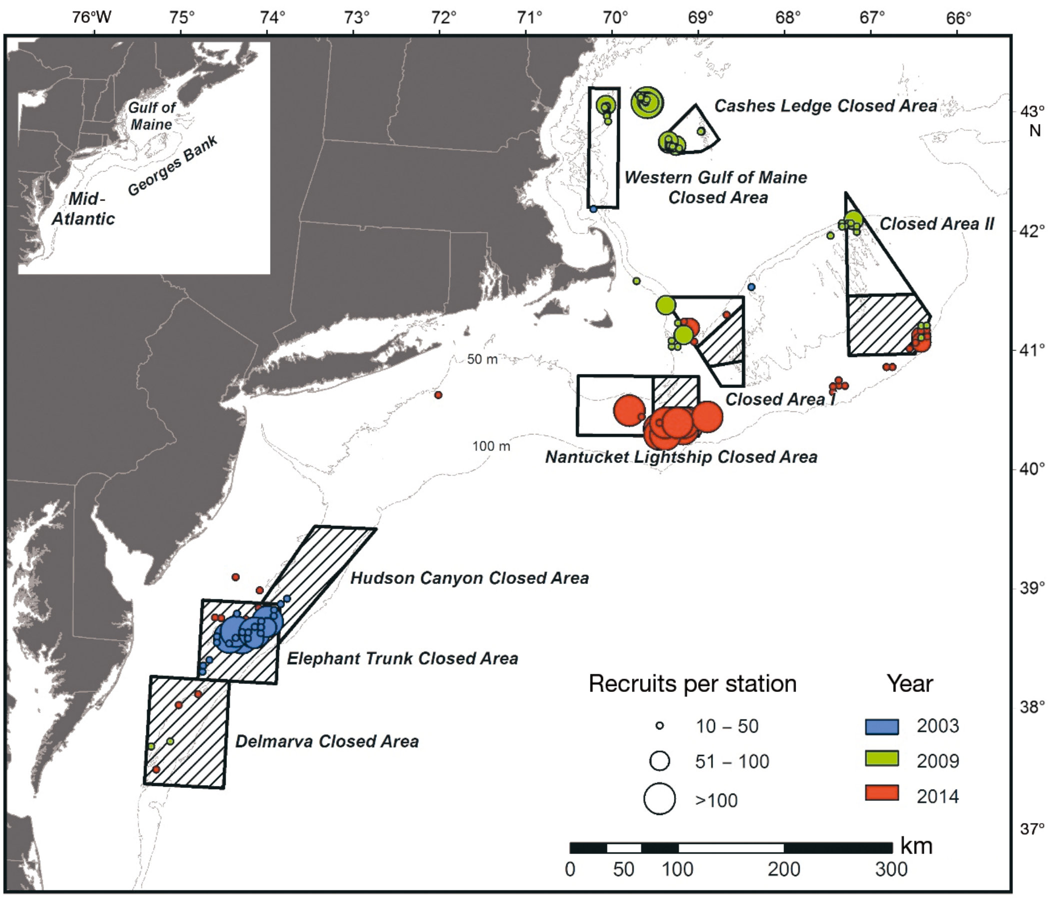

Fig. 3. Number of recruits (<75 mm shell height) observed by the SMAST (see Fig. 1) scallop video survey in 2003, 2009, and 2014. One station represents approximately 12 m^2 observed. Hatched marks identify limited access areas, which are periodically opened to scallop fishing

density of scallops in the Mid-Atlantic during 2003 was also significantly higher than any other density in the region (ANOVA, df = 10, $F = 15.8$, $p < 0.001$, Tukey post-hoc test $p < 0.001$; Table 1). The density of scallops in the Gulf of Maine was significantly higher in 2009, 2010, and 2013 compared to 2011 and 2014 (ANOVA, df = 4, $F = 5.6$, $p < 0.001$, Tukey post-hoc test $p < 0.050$; Table 1).

On average there were approximately 6.2 billion (SD = 1.05) sexually mature scallops and 6.7 billion (SD = 9.58) recruits in the scallop stock between 2003 and 2012 and in 2014 (Fig. 4). The variation between the numbers of sexually mature scallops each year was much smaller than the variation of recruits between each year, particularly in 2003 and 2014 (Fig. 4). Removing these years drops the average number of recruits to approximately 3 billion (SD = 1.14) and substantially reduces the variation between years. Within each region, the shell height frequency during the years of extremely high recruitment was significantly different from the shell height frequency of other years (Georges Bank $D_{172,1529} = 0.57$, $p < 0.001$, Mid-Atlantic $D_{284,2023} = 0.20$, $p < 0.001$ Gulf of Maine $D_{96,377} = 0.26$, $p < 0.001$) (Fig. 5).

The number of exploitable scallops in Georges Bank decreased significantly between 2003 and 2014 ($r^2 = 0.41$, $p < 0.02$, $n = 11$; Fig. 6). The average shell height and meat weight varied significantly annually on Georges Bank (ANOVA, df = 10, $F = 296.1$, $p < 0.001$), but dramatically decreased in 2014 (Table 1). The number of harvested scallops increased slightly on Georges Bank from 2003 to 2014 ($r^2 = 0.30$, $p < 0.05$, $n = 11$), despite the decrease in the number of exploitable scallops (Fig. 6).

The number of exploitable scallops in the Mid-Atlantic also decreased between 2003 and 2014 ($r^2 = 0.71$, $p < 0.001$, $n = 11$; Fig. 6). However, the average shell height and meat weight generally increased until 2011 and varied significantly between years (ANOVA, df = 10, $F = 118.2$, $p < 0.001$; Table 1). The number of harvested scallops decreased in the Mid-Atlantic ($r^2 = 0.45$, $p < 0.05$, $n = 11$; Fig. 6).

There was no correlation between the abundance of recruits and exploitable scallops 2 ($r_S(9) = -0.18$, $p = 0.64$) or 3 ($r_S(8) = 0.26$, $p = 0.53$) years prior on Georges Bank. Similarly, there was no correlation between the abundance of recruits and exploitable scallops 2 ($r_S(10) = -0.12$, $p = 0.75$) or 3 ($r_S(10) = -0.49$, $p = 0.15$) years prior in the Mid-Atlantic.

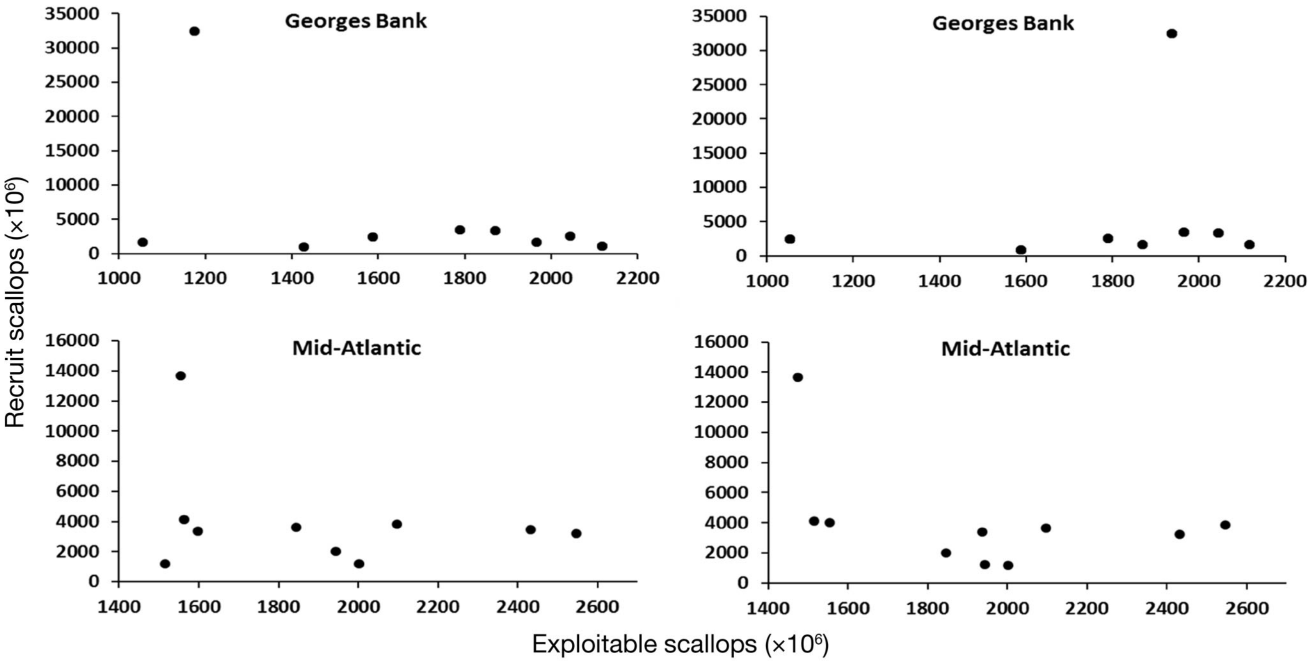

Fig. 4. Estimated number of recruit scallops and number of exploitable scallops 2 (left) or 3 (right) years prior to recruitment in Georges Bank and the Mid-Atlantic

DISCUSSION

Since 2003, 2 extreme recruitment events have occurred within the scallop stock assessment area (Fig. 3). In 2003, about 12 billion recruits were observed in the Mid-Atlantic, while the total scallop population on Georges Bank and in the Mid-Atlantic was about 21 billion scallops (Stokesbury et al. 2004). In 2014, about 31 billion recruits were present on Georges Bank, the largest recruit abundance ever recorded, while the total scallop population was about 39 billion scallops. The number of recruit scallops in these years was equal to or greater than the number of exploitable scallops and much larger than the annual harvested stocks. Neither of these events were predictable based upon a direct relationship between spawning stock biomass and recruitment.

These extremely large recruitments shifted the size structure of the stocks, resulting in different patterns in exploitable biomass and harvest numbers on Georges Bank and in the Mid-Atlantic. The average shell height and meat weight varied annually on Georges Bank, but dramatically decreased in 2014, when the stock was dominated by the extreme recruitment of small scallops. Preceding this event, a greater proportion of adult scallops needed to be taken to maintain landings, due to declining recruitment into the fishery. This is shown by the increase in the number of harvested scallops, despite the decrease in exploitable biomass. In 2003, 7% of the exploitable scallops on Georges Bank were harvested, steadily increasing to 42% in 2014. Clearly, the 2014 recruitment event was not preceded by a growing spawning stock biomass on Georges Bank.

In the Mid-Atlantic, a different pattern was apparent. The average shell height and meat weight generally increased until 2011, reflecting the growth and harvest of the scallops from the 2003 extreme recruitment event (Stokesbury 2012; our Table 1). The number of harvested scallops decreased in the Mid-Atlantic as the 2003 recruitment grew into the fishery, reducing the number of scallops that were needed to maintain the landings. For example in 2003, 36% of the exploitable scallops in the Mid-Atlantic were harvested, but this decreased to 20% by 2006. By 2009, fishery effort had been shifted to the Mid-Atlantic and without a large recruitment pulse similar to 2003, exploitable biomass and landings began to decrease by 2012 (Fig. 6). The influence of the Georges Bank and Mid-Atlantic extreme recruitment events on projected landings was also apparent as dramatic increases in landings were expected after the scallops produced in these events reached harvestable size (Fig. 1).

A lack of spawning stock to recruitment relationship can be seen outside of the traditional stock assessment area. In 2009, close to 0.5 billion recruit-sized scallops were observed on several banks and ledges in the Gulf of Maine and northern Georges

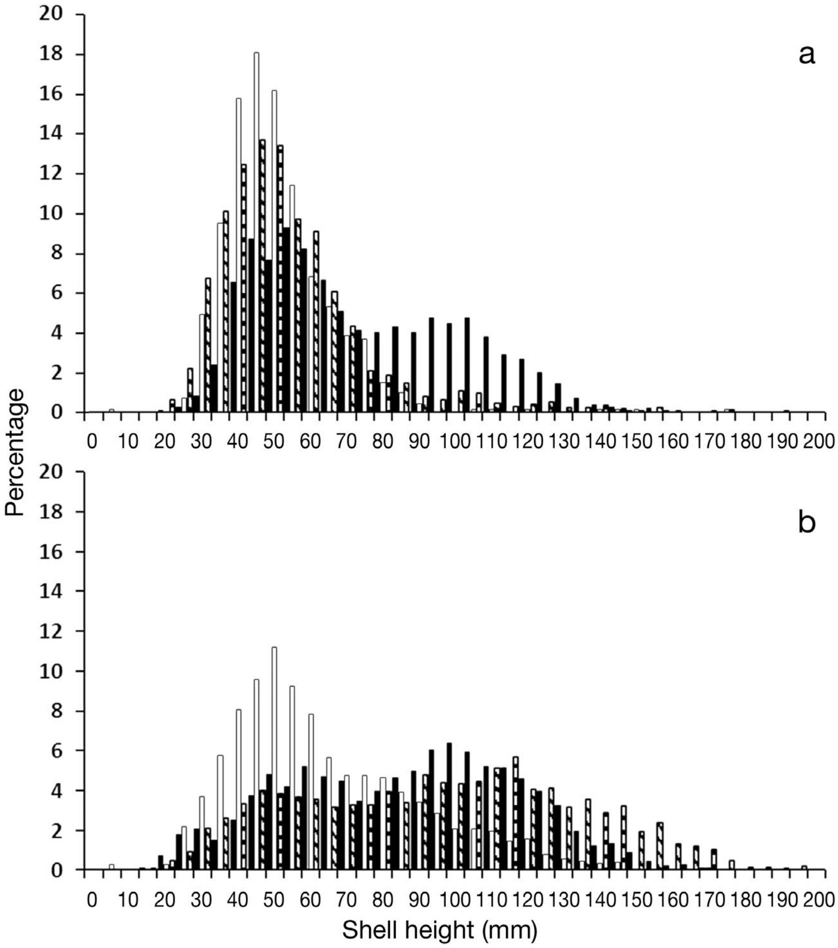

Fig. 5. (a) Atlantic sea scallop shell height frequencies on Georges Bank in 2014 (black), in the Mid-Atlantic in 2003 (white), and in the Gulf of Maine in 2009 (hatched) and (b) shell height frequencies for all other years. The 2 panels reflect years (a) with and (b) without extremely high recruitment events

Bank (Fig. 3). Scallop densities on the banks and ledges of the Gulf of Maine, totaling approximately 300 km^2, ranged from 2.6 to 18.8 times higher than in high density areas on Georges Bank (Stokesbury et al. 2010). Less than 1% of the scallops had shell heights greater than 100 mm, suggesting a small adult biomass in these areas prior to 2009 (Stokesbury et al. 2010). Similar scallop densities in 2009, 2010 and 2013, were due to the persistence of the 2009 recruits rather than continued extremely large recruitment events. By 2011, the density was significantly lower, suggesting a rapid, natural die-off of many of the recruits, perhaps related to the carrying capacity of the habitat, as the areas are mostly closed to fishing. Another large recruitment event appears to have occurred in 2013, but the density of scallops in this year is inflated by the 2009 event because almost 10% of the scallops had shell heights over 100 mm.

None of these recruitment events were predictable based upon a direct relationship between spawning stock biomass and recruitment, a disconnect also seen in the past. Rapid increases in the scallop population due to exceptional recruitment events were observed in the early 1960s and in 1972. In both these cases, the events were preceded and followed by periods of low recruitment and subsequent decreases in spawning stock biomass (Serchuk et al. 1979). Recruitment indices did not increase on Georges Bank after area closures led to increases in spawning stock biomass, although extremely large year classes were observed both before and after the implementation of closed areas (Hart & Rago 2006, Hart et al. 2013). Caddy's (1989) conclusion that this resource is sporadic rather than constant or cyclic appears to hold true even with the addition of long-term closed areas into management plans.

This recruitment pattern suggests that scallop populations do not grow at a constant rate, a dynamic that could be explained based upon scallop fecundity and the importance of settlement factors over spawning stock biomass. Atlantic sea scallops are extremely fecund; a healthy 10 yr old female scallop may release over 9.0×10^7 eggs during a single spawning season (MacDonald 1986, Davies et al. 2015). Over the 10 yr reproductive span of one year class, the scallop resource could theoretically produce 3.6×10^{18} eggs. Of these eggs, only 2.2×10^{-7} need to be fertilized, survive and settle on suitable habitat to replenish the generation. This demonstrates how a minute change in fertilization success or early survival rate could result in huge differences in recruit abundance and how difficult it is to determine a stock–recruitment relationship without accounting for these early life-history factors.

Heterogeneity in scallop size and density within the 2 stock areas influences fertilization success and distorts estimates of recruitment based upon spawning stock biomass. Scallop fecundity increases with size (Davies et al. 2015), and free-spawner fertilization success increases with adult proximity (Pennington 1985, Claereboudt 1999). The creation of closed areas

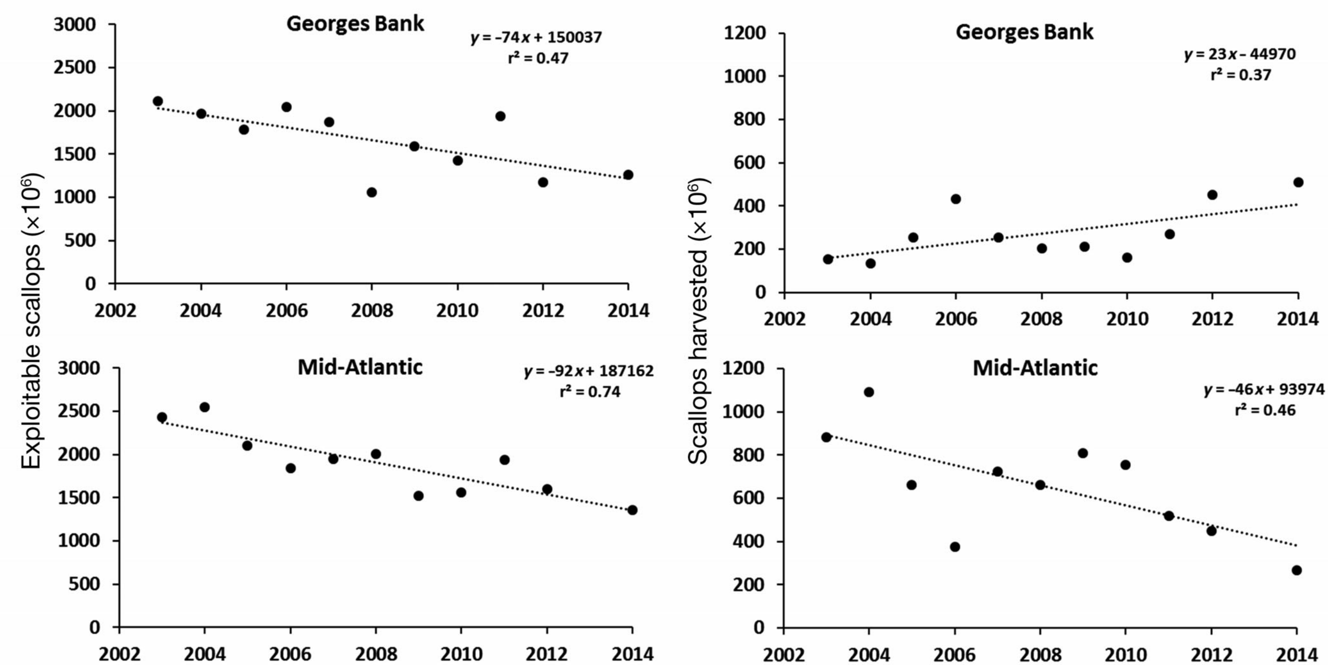

Fig. 6. Number of exploitable and harvested scallops regressed from 2003–2014 for Georges Bank and the Mid-Atlantic stocks

on Georges Bank and the adoption of a rotational harvest system have created sub-areas of large scallops in high densities. On Georges Bank, these closed areas increased larval supply and settlement within the region (Davies et al. 2015). Within these closures, 11 persistent high-concentration aggregations of highly fecund scallops have been identified (Harris 2011). On any given year, these scallops have the potential to produce the extremely high recruitment event observed in 2014. However, extremely high recruitment events are erratic and were observed prior to the creation of closed areas, suggesting that factors extrinsic to scallops play a central role.

The factors effecting the early survival rate of scallops are numerous, but larval dispersal and post-settlement predation substantially influence recruitment in this region. Overall, inter-annual variation of larval retention on Georges Bank and survival due to the physical environment are enough to offset the increase in larval supply and settlement from the closed areas (Davies et al. 2015). Though the majority of scallop larvae produced on Georges Bank are usually retained, substantial amounts of larvae are dispersed towards the Mid-Atlantic and the Gulf of Maine. The magnitude of this dispersal is highly variable, but can exceed the amount of larvae retained on Georges Bank in some years (Tian et al. 2009). Within the Mid-Atlantic, the addition of physical processes and larval behavior improved the link between sea scallop biomass within the Hudson Canyon limited access area and recruitment in an adjacent, downstream area (Munroe et al. 2015). This creates a complicated ecological scenario; depending on the prevailing oceanographic conditions of the year, extremely large settlement events could be derived from highly productive sub-areas of the stock or from areas outside of the stock.

Post-settlement predation is another ecological factor that can determine the magnitude of scallop recruitment. Crabs (*Cancer* spp.) and sea stars (*Asterias* spp.) are the primary predators of scallops on Georges Bank and the Mid-Atlantic, with predation-related mortality focused within the first 8 wk of settlement (Barbeau et al. 1996). Sea star abundance is associated with areas of low recruitment in the Mid-Atlantic (Hart 2006) and Georges Bank (Marino et al. 2009). Crabs can consume more than 3 times as many recruit-sized scallops per day than sea stars (Nadeau et al. 2009) and may have been the primary factor in the loss of 10 billion scallops in the Elephant Trunk limited access area between 2003 and 2004 (Fig. 3, Hart & Shank 2011, Stokesbury et al. 2011b). In controlled experiments, crabs and sea stars decreased the density of recruit-sized scallops from 69 to 1 per m^2 within 24 d (Wong et al. 2005). Thus, these predators have the ability to rapidly decrease post-settlement survival rates and prevent extremely large recruitment events from occurring.

Accounting for spatial heterogeneity and incorporation of environmental variables could improve predictions of extremely large scallop recruitment events. High recruitment variability due to environmental factors is a recognized attribute of scallop populations around the world (Joll & Caputi 1995, Gutiérrez & Defeo 2005, Slater 2005, ICES 2015). However, our current knowledge of Atlantic sea scallop life history and ecology and our ability to model the numerous factors influencing recruitment magnitude and survival are insufficient to predict the population dynamics of the sea scallop resource. We detailed how larval dispersal and post-settlement predation could define the magnitude of recruitment, but food abundance, competition, disease, water temperature, incidental fishing mortality, and settlement substrate could also play important roles. Further, many of these attributes are highly variable from year to year and affect not only larval and pre-recruit survival, but also alter growth (Truesdell et al. 2015) and fecundity (Shephard et al. 2010). Improvements to the link between spawning stock biomass and recruitment for the Atlantic sea scallop have been made by reducing spatial scales and incorporating larval dispersal (Munroe et al. 2015), accounting for heterogeneity in growth and mortality (Truesdell et al. 2015), and phytoplankton concentration (Friedland et al. 2014), but substantial error and unexplained variance persist in projecting recruitment (NEFSC 2014). As advancements in understanding and modelling these factors are made and incorporated into stock assessments, intensive monitoring of juvenile scallops and projecting their growth, coupled with flexible management schemes, have been shown as effective mechanisms to fully utilize recruitment into scallop fisheries (Beukers-Stewart et al. 2003, Hart et al. 2013, Caputi et al. 2014).

Large, unexpected recruitment pulses that drive overall abundance are not unique to scallops and have significant implications for fisheries managers. The haddock (*Melanogrammus aeglefinus*) stock of Georges Bank had an extremely large year class in 2003 (800 million age-1 fish, about 700 million more than the decade average), leading to high total catch in subsequent years (Brodziak et al. 2006). The sockeye salmon *Oncorhynchus nerka* run in the Frasier River reached 34 million fish in 2010 after 20 years of decline and a run size of 1.5 million in 2009 (Larkin 2010). In Western Australia, a pre-recruit abundance of the pearl oyster *Pinctada maxima*, 5 times larger than the previous 15 yr average, led to a significantly higher population and catch limits from 2009 to 2011 (Caputi et al. 2014). Meta-analysis of global stock–recruitment relationships show poor or no correlations and indicate that the environment more strongly influences recruitment (Curry et al. 2014, Szuwalski et al. 2015). Similar to our results with the Atlantic sea scallop, these events and results suggest no direct relationship between spawning stock biomass and recruitment. This mismatch between marine population ecology and fisheries management might be rectified through better recognition of heterogeneity and integration of environmental conditions and species interactions into stock assessments. However, the complexities surrounding recruitment, exemplified by extremely high recruitment events, suggest adaptable management based upon empirical data will likely be needed.

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