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# Collapse of the New York Bay scallop fishery despite sustained larval and juvenile recruitment

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ABSTRACT: Mass mortality events, due to a variety of natural and anthropogenic causes, usually result in population (and associated fishery) crashes. Recovery from such events may not occur for many years, if at all. We have witnessed a mass die-off of adult (1+ yr) bay scallops *Argopecten irradians irradians* in the Peconic Bays, New York, USA, from 2019–2022, with declines in population density from spring to fall of 90–99%. Similar declines in commercial landings have occurred since 2018, with severe economic consequences for fishermen. Observed mortality levels are well above those seen prior to 2019. However, since die-offs of adult scallops have been occurring after the first seasonal spawning cycle, larval and benthic juvenile (0+ yr) recruitment have remained robust through 2021. Nevertheless, with lower numbers of adults surviving to spawn in September–October, resulting in fewer fall recruits, potential buffering of marked annual fluctuations in abundance is now less likely for this short-lived species. Peconic bay scallops are again in a precarious state as these recurring die-offs, likely driven by changing environmental conditions, present further challenges to the persistence of robust populations and the likelihood of successful restoration efforts.

KEY WORDS: Mass mortality · Fishery collapse · Scallop · *Argopecten* · Recruitment · Restoration · Environmental change

## 1. INTRODUCTION

Mass mortality events occur sporadically in wild animal populations due to a variety of natural and anthropogenic factors, including epizootics (Ford & Haskin 1982, Lessios et al. 1984), hypoxia/anoxia (Stachowitsch 1984), marine heatwaves and other extreme climate events (Andrews 1973, Hoegh-Guldberg et al. 2017, Babcock et al. 2019, Fordyce et al. 2019), harmful algal blooms (Cosper et al. 1987) and oil spills (Barron et al. 2020). The long-term impacts of these events and the potential of populations to recover depend on such considerations as whether the cause(s) of the die-off continue to persist, the overall level of mortality, and effective abundance/densities to which affected populations are reduced (Lessios 1988, 2016). Further considerations include spawning stock–recruitment dynamics in the context of the life history of affected species (Stoner & Ray-Culp 2000, Kersting et al. 2020) and potential ecological shifts following mass mortalities (DiCamillo & Cerrano 2015).

Annual or r-selected species are generally considered to be better able to recover from mass mortality events due to their higher reproductive potential. Likewise, metapopulations may be better able to withstand the risk of extinction posed by mass die-offs than individual populations (Marelli & Arnold 2001, Gotelli 2008). Nevertheless, the literature is replete with examples of marine populations that have never rebuilt following mass mortality events:

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e.g. Atlantic cod *Gadus morhua* in the Northwest Atlantic, including off West Greenland (Bonanomi et al. 2015), lobsters *Homarus americanus* in Long Island Sound (Benson et al. 2018), calico scallops in the Gulf of Mexico (*Argopecten gibbus*: FWRI 2020) and Pacific Panama (*Argopecten ventricosus*: Medina et al. 2007) and wedge (*Donax trunculus*: Escrivá et al. 2021) and smooth (*Callista chione*: Baeta et al. 2021) clams in the Mediterranean. These scenarios may reflect shifts to alternate stable states, from which it is often very difficult to return to higher levels of population abundance (Beisner et al. 2003, Knowlton 2004).

Bay scallop *Argopecten irradians* populations are notorious for dramatic natural fluctuations (Belding 1910), which are magnified by the short life history of the species. Although typical lifespans of the northern (*A. i. irradians*) and southern subspecies (*A. i. concentricus*) are given as 18–22 mo (Belding 1910) and 12–18 mo (Gutsell 1930), respectively, they are essentially semelparous, as even in unfished populations the great majority of adults die before they spawn in a second year (Bricelj et al. 1987). Mass mortalities of New York bay scallop populations in the mid-1980s to 1990s were caused by novel brown tide algal blooms (Cosper et al. 1987, Tettelbach & Wenczel 1993). Following the last brown tide in the Peconic Bays of eastern Long Island in 1995, populations remained at very low levels for more than a decade — likely due to recruitment limitation (Tettelbach et al. 2013). Intensive restoration efforts initiated in 2006 to address this constraint led to order of magnitude increases in larval recruitment and benthic densities and, by 2017 and 2018, commercial fishery landings had increased to 32 times that of pre-restoration levels (Tettelbach et al. 2013, 2015, this study).

In 2019, however, the bay scallop populations of the Peconic Bays (hereafter 'Peconic bay scallops') suddenly collapsed. Our population surveys in that spring suggested stocks were robust, but in late summer anecdotal observations of a mass die-off of adult scallops were first reported by baymen making test dredge tows in prospective scalloping areas (P. Winters pers. comm.). Our dive surveys in October 2019 corroborated these observations. We have now witnessed a mass mortality of adult Peconic bay scallops and associated fishery collapse for 4 consecutive years. Other recently published papers (Pales Espinosa et al. 2023, Tomasetti et al. 2023) focus on the drivers of these mass die-offs: a marosporidian parasite whose impacts on adult scallop hosts have been exacerbated by stressful environmental conditions (elevated water temperatures and hypoxia), particularly around the time of spawning. Here, we document the extent of the mass mortality events in 2019–2021 and how their apparent timing, primarily after the first spawning cycle, has still allowed for the high larval/benthic juvenile recruitment which we have observed to date.

## 2. MATERIALS AND METHODS

We attempted to validate anecdotal reports of a scallop die-off in 2019 via continuation of 3 types of scallop population/fishery monitoring that we have been conducting since 2005 in the Peconic Bays as part of our extensive restoration efforts: benthic population surveys (Tettelbach et al. 2015), larval recruitment monitoring (Tettelbach et al. 2013) and compilation of commercial fishery statistics (NYSDEC 2022). Metrics for 2019 were then compared to those obtained in prior, and ensuing, years to evaluate temporal trends.

### 2.1. Benthic population surveys

Our visual dive surveys of wild Peconic bay scallop populations are done to estimate densities of adults in the spring (April to mid-July, but usually May/June) and both adults and juveniles (seed or 0+ yr) in fall (October to early November, but always before the commercial season begins: Tettelbach et al. 2015). While some 2+ yr adults are seen in spring, almost 100 % die before the following fall, so only 1+ yr scallops are considered here. Survey methods, wherein divers count all scallops seen in three 50 × 1 m transects at each of ~20 sites throughout the Peconic Bays (Fig. 1), are detailed in Tettelbach et al. (2015). Here, we focus on survey data from 2008 onwards as earlier years did not cover the full range of sites used later.

Shell heights (SHs) of 25–30 scallops per site per date were recorded during surveys beginning in 2014. For 1+ yr old scallops, SH at the annual growth ring was also measured. For the present study, we were interested in comparing frequencies of adult scallops in fall which possessed a 'small' (≤20 mm) annulus resulting from 'late' (~mid-September to October) spawns (Tettelbach et al. 1999, 2001) in years before and after the die-offs began. This was done as a means of pinpointing when adult scallop mortalities may have occurred in 2019–2021 and also to determine if frequencies of fall-spawned scallops, which likely help buffer fluctuations in bay scallop populations (Tettelbach et al. 2001, Hall et al. 2015), were lower during the years of mass die-offs.

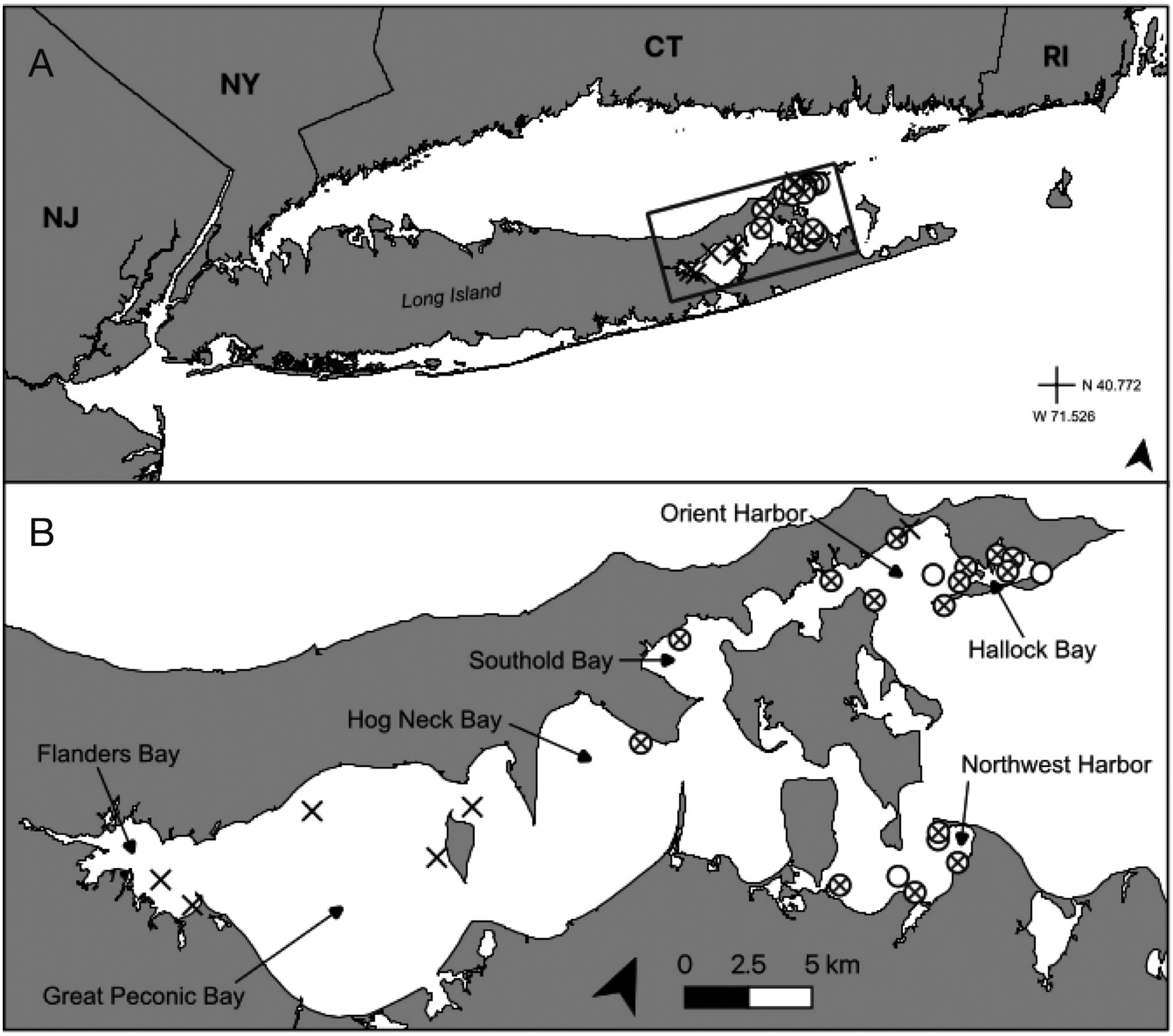

Fig. 1. (A) Southern New England/northern mid-Atlantic and (B) Long Island, NY, USA, showing the Peconic Bay system: NJ: New Jersey; NY: New York; CT: Connecticut; RI: Rhode Island. Embayments noted in the text are shown along with approximate location of most sites where larval recruitment monitoring (○) and benthic population surveys (×) were conducted. To improve legibility, 5 sites in Orient Harbor (n = 1), Hallock Bay (n = 2) and Northwest Harbor (n = 2) are not shown. Modified from Tettelbach et al. (2015)

### 2.2. Commercial fishery landings

Commercial bay scallop landings for the Peconic Bays were obtained from the New York State Department of Environmental Conservation (NYSDEC 2022). For annual (calendar year) landings, we restricted our focus to years beginning in 1996, the year after the last brown tide bloom in the Peconic system (Tettelbach et al. 2013). Scallop harvests and dockside value broken down by season (early November–31 March of the next year), compiled beginning in 2014 (NYSDEC 2022), were also examined. While no data on recreational landings are available, they constitute a very small portion of overall harvest.

### 2.3. Larval recruitment monitoring

Settlement of larval scallops to above-bottom spat collectors was quantified at many of the same sites where we monitored benthic scallop populations

(Tettelbach et al. 2011, 2013). Beginning in early June, successive overlapping sets of 3 replicate collectors were deployed for ~6–7 wk through mid-November to encompass the entire spawning season of Peconic bay scallops (Tettelbach et al. 1999, 2013). As changes in spat bag construction have been necessitated since 2005, comparisons of absolute spat densities for this study were restricted to 2018 vs. 2019 and 2020 vs. 2021, years when the same materials were available for spat bag assembly. Seasonality of larval recruitment was examined for 2018–2021 (n = 11–23 sites: Fig. 1) by grouping numbers of spat settling to collectors across all sites/embayments during 3 periods: spring–summer (early June–late August), late summer (late August–mid-September) and fall (mid-September–mid-November). Because successive spat collector deployments overlapped, in order not to miss any potential spatfall (Tettelbach et al. 2013), scallops settling to collectors initially deployed in the middle of the sampling year (early August or late August) had to be assigned to one of the 3 seasonal periods. This was done on the basis of scallop SH measured at the time of spat bag retrieval/processing, factoring in average shell growth rates for juvenile bay scallops in eastern Long Island, NY, embayments of ~3 mm wk$^{-1}$ (Garcia-Esquivel & Bricelj 1993, Tettelbach & Bonal 2008). For example, for the 6 August to 17 September 2018 spat collector deployment period, spat >9 mm SH were assumed to have settled in the first ~3+ weeks of the ~6 wk deployment period (i.e. by late August) and thus were assigned to the spring–summer seasonal period. Spat ≤9 mm SH would have settled to collectors in the last 3 wk before sampling on 17 September 2018 and thus were assigned to the late summer seasonal period. Although soak times for spat collectors varied in successive deployments and from year to year (although almost all were 41–46 d: see Table 2), all smaller (≤9 mm SH) scallops collected were assumed to have settled in the last 21 d of each of the respective deployment periods.

Four parameters were calculated from our larval recruitment data: (1) mean no. of spat bag$^{-1}$ period$^{-1}$ = total no. of spat / total no. of bags for the period, (2) mean no. of spat bag$^{-1}$ d$^{-1}$ = average of settlement rates for each ~6–7 wk deployment during the given period, (3)% of total spat for period = total no. spat collected in a given period / total no. spat collected for the year, and (4) index of% spat settlement = mean no. spat bag$^{-1}$ for a given period / sum of these settlement rates for the 3 periods. The latter factors in differences in numbers of bags as fewer were often deployed later in the year due to reduced availability of materials. Spawning patterns (via analysis of temporal changes in gonadosomatic index = GSI) of scallops deployed at our primary sanctuary in Orient Harbor (Tettelbach et al. 2013) were monitored in parallel to corroborate larval recruitment monitoring. GSI data will be presented in a forthcoming paper (S. Tettelbach et al. unpubl. data).

### 2.4. Statistical methods

In order to confirm pre-die-off and die-off time periods (yr) for further analyses, we analyzed adult (1+ yr) scallop counts from spring and fall surveys using an intercept-only segmented regression model from the R package 'segmented' (Muggeo 2003, 2008). The model was used to find the threshold where the effect of the covariate (year) on the response variable (fall adult bay scallop counts) changed (i.e. breakpoint or point change analysis: Ulm 1991, Betts et al. 2007).

Temporal differences in adult scallop densities for the pre-die-off and die-off periods were then examined via 2 types of analyses. First, to assess if adult scallop densities differed by season and by time period, adult counts (no. scallops 50 m$^2$ transect$^{-1}$) from spring and fall population surveys were modeled via a zero-inflated, mixed-effect negative binomial generalized linear model (GLMM) from the R package 'GLMMadaptive' (Rizopoulos 2022) with time period (pre-die-off and die-off periods) as a fixed factor and site as a random effect.

Using the fitted values from the GLMM, we then ran a 2-way ANOVA with a Tukey post-hoc test to examine differences between the pre-die-off and die-off time periods and between spring and fall. Second, we used mixed effects linear models to test the hypothesis that the percent change in adult density from spring to fall during the pre-die-off years was not negative (i.e. it remained level or increased through time) but was negative (decreased through time) during the years when die-offs were occurring. Apparent increases in adult scallop densities from spring to fall, which we have regularly observed at many sites, very likely reflect an underestimation of numbers of fall-spawned scallops as many are too small (<15 mm: Tettelbach et al. 2015) to be seen in spring surveys. A decline in observed percent change in adult densities from spring to fall would likely reflect fewer fall-spawned scallops being produced in the prior year. The above analyses were done using the R package 'lme4' (Bates et al. 2022) after performing a log(x + 1) transformation on the percent change in density values, with site as a random factor and year as a fixed factor. Even when site was confirmed as an important (random) factor in models validated with AIC, BIC and LRT, we did not specifically test for significance between sites.

Trends in annual commercial scallop landings for the Peconic Bays were examined via a generalized additive model (GAM), using a Gaussian response variable, in the R package 'mgcv' (Wood 2011). Year was included as a fixed effect and fit with a cubic spline. A GAM was chosen, as opposed to a linear model or GLM, as we expected a highly nonlinear function.

Separate zero-inflated GLMMs, with site as a random factor and year as a fixed factor, were run using the R package 'glmmTMB' (Brooks et al. 2017) to test the hypothesis that spat densities, which were log(x + 1) transformed, were the same in 2018 vs. 2019 and 2020 vs. 2021-years when respective materials used to construct spat collectors were the same.

We also hypothesized that, after the first observed population crash in 2019, there should have been a decrease in the percentage of adult (1+ yr) scallops that were the product of spawns which occurred the previous fall (annulus SH ≤20 mm), relative to offspring resulting from spawns over the entire season. We tested this hypothesis using a zero-inflated, Gaussian GLMM, with site as a random factor and time period (i.e. 2018–2019 vs. 2020–2021) as a fixed factor, with the R package 'glmmTMB' (Brooks et al. 2017). The grouping of 2018 and 2019 together here reflects the fact that annual growth rings are laid down over the winter prior to when scallops reach an age of 1 yr, so 1+ yr adults sampled in fall 2019 represent the 2018 cohort — which were spawned before the first die-off was observed in 2019. Sampling of adult scallops in fall of 2020 and 2021, respectively, were of the 2019 and 2020 cohorts — which would have resulted from scallop spawns during the mass die-off period.

Juvenile (0+ yr) scallops counted in fall population surveys were split into pre-die-off (2008–2018) and die off (2019–2021) periods (per the breakpoint analysis) to assess the relationship between seed count and year for each time period. Regression slopes were modeled using a zero-inflated, mixed effects, negative binomial GLMM from the R package 'glmmTMB' (Brooks et al. 2017) with year as a fixed factor and site as a random factor.

All of the above analyses were performed in R version 4.0.02 (R Core Team 2020). Model validations were assessed using the R package 'DHARMa' (Hartig 2022) and all plots were created using the R package 'ggplot2' (Wickham 2016). Diagnostic plots for each model and brief discussions of model choices are given in Figs. S1–S8 in the Supplement at www.int-res.com/articles/suppl/m714p045_supp.pdf).

## 3. RESULTS

### 3.1. Temporal changes in adult scallop densities

The intercept-only segmented regression model showed 3 distinct breakpoints: 2011.75, 2014.27, and 2018.0 (Fig. 2). Scallop densities generally increased until 2014.27, with a sharp increase occurring between 2011.75 and 2014.27 (Fig. 2). Scallop densities generally decreased after 2014.27, with a sharp decrease occurring after 2018.0 (Fig. 2). Fall scallop densities were significantly lower in 2019–2021 compared

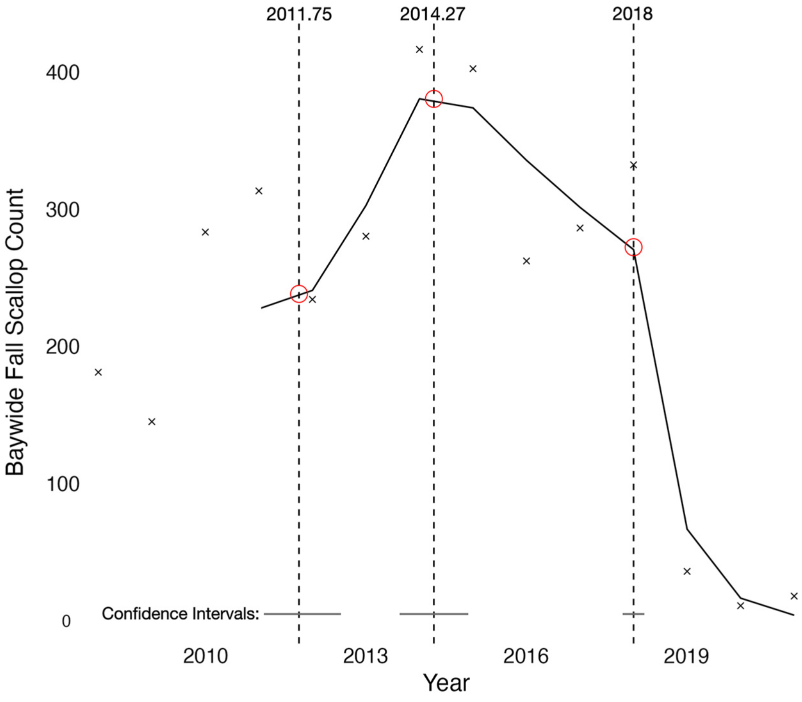

Fig. 2. Intercept-only segmented regression model displaying the threshold where the effect of the covariate (year) on the response variable (fall adult bay scallop counts) changed. Breakpoints are denoted by red circles and their corresponding years are denoted by vertical dashed lines. Lower/upper confidence bounds for the 3 breakpoints (2011.75, 2014.27 and 2018.0) were 2010.97/2012.53, 2013.63/2014.91 and 2017.80/2018.20, respectively

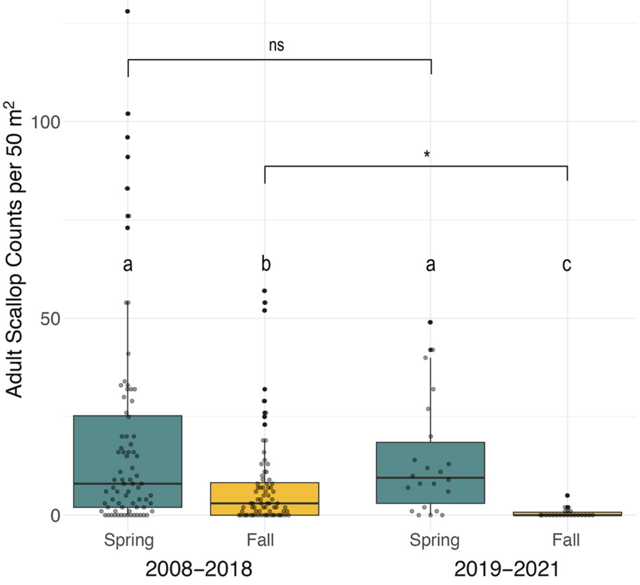

Fig. 3. Median, first quartile and third quartile densities of adult (1+ yr) scallops counted in 50 m$^2$ transects for 2 seasons, spring and fall, and for 2 time periods, 2008–2018 (pre die-off) and 2019–2021 (die-off). Different letters denote significant differences. ns: $p > 0.05$; $^*p < 0.05$

to 2008–2018 (p = 0.045) (Fig. 3). Overall mean ± SE densities in fall for 2016–2018 and 2019–2021 were 0.1310 ± 0.0013 and 0.0082 ± 0.0001, respectively. The highest fall adult mean densities seen at individual sites in these respective 3 yr periods were 1.14 ± 0.19 and 0.09 ± 0.01. Spring scallop densities, however, were not significantly different during the 2019–2021 period relative to 2008–2018 (p = 0.075) (Fig. 3). Adult scallop densities in both periods were significantly lower in the fall relative to the spring (2008–2018: p = 0.004, 2019–2021: p < 0.0001) (Fig. 3), suggesting summer mortality events in both time groups.

For the 2008–2018 time period, the percent change in scallop density from spring to fall showed a sharp increase over time (Fig. 4A); however, during the 2019-2021 period, this percentage showed a slight decrease through time (Fig. 4B). The contrast in slopes highlights the transition in scallop population trends from before 2019 to afterward. Overall mortality of adult scallops, from spring to fall, across all surveyed sites during 2019–2021 was 95, 99 and 90 %, respectively (Fig. 2).

### 3.2. Commercial fishery landings

Annual commercial scallop landings in the Peconic Bays have changed dramatically over the last 25 yr — remaining steady from 1996–2007 (before restoration), increasing from 2008 to 2017–2018 (driven by restoration efforts) and declining sharply during 2019–2021; the GAM (Fig. 5) fit well to these patterns ($F$ = 8.976, edf = 3.759, adjusted R$^2$ = 0.587, deviance explained = 64.9 %, p = 0.0001, n = 25). The breakpoint in adult densities, as determined by the intercept-only segmented regression model, occurred after the landings apex and paralleled the sharp decline in commercial landings (Fig. 5). Peconic landings for the last 3 seasons, 2019/20 to 2021/22, compared to 2018/2019 (before the first die-off), were 6, 0.06 and 8 %, respectively (Table 1). Total dockside value of landings for these last 3 seasons were 9.3, 0.1 and 16.5 %, respectively, of the 2018/2019 value. Commercial harvest

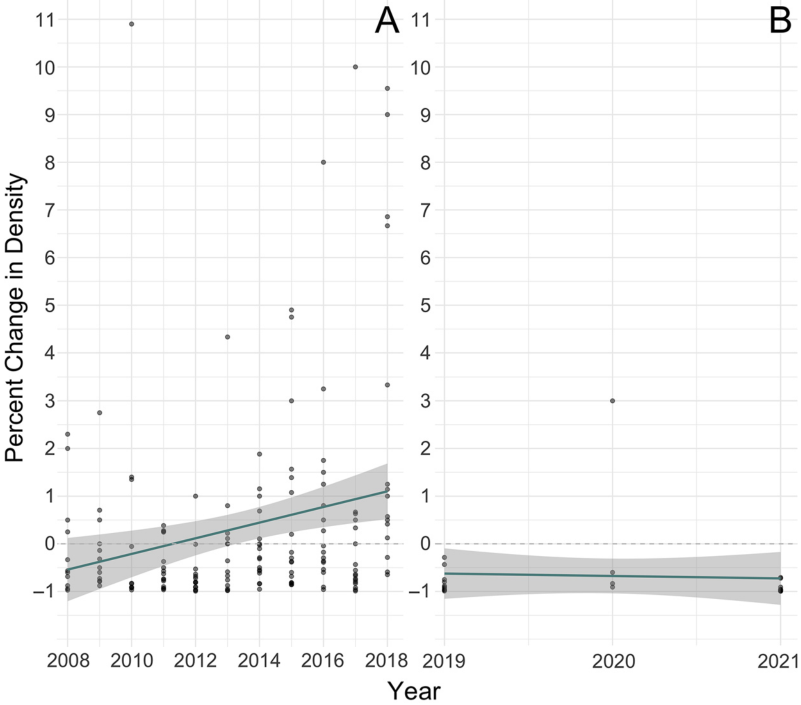

Fig. 4. Models displaying the percent change in density of adult (1+ yr) scallops from spring to fall as linear functions of time during 2 periods: pre die-off (A) (n = 160, p = 0.001, slope = 0.0476) and die-off (B) (n = 23, p = 0.181, slope = −0.1877), as determined by the intercept-only segmented regression model. Statistical analyses for A are separate from B. Raw values are displayed but statistical analyses were performed on log(x + 1) transformed values. Shaded regions represent 95 % confidence intervals

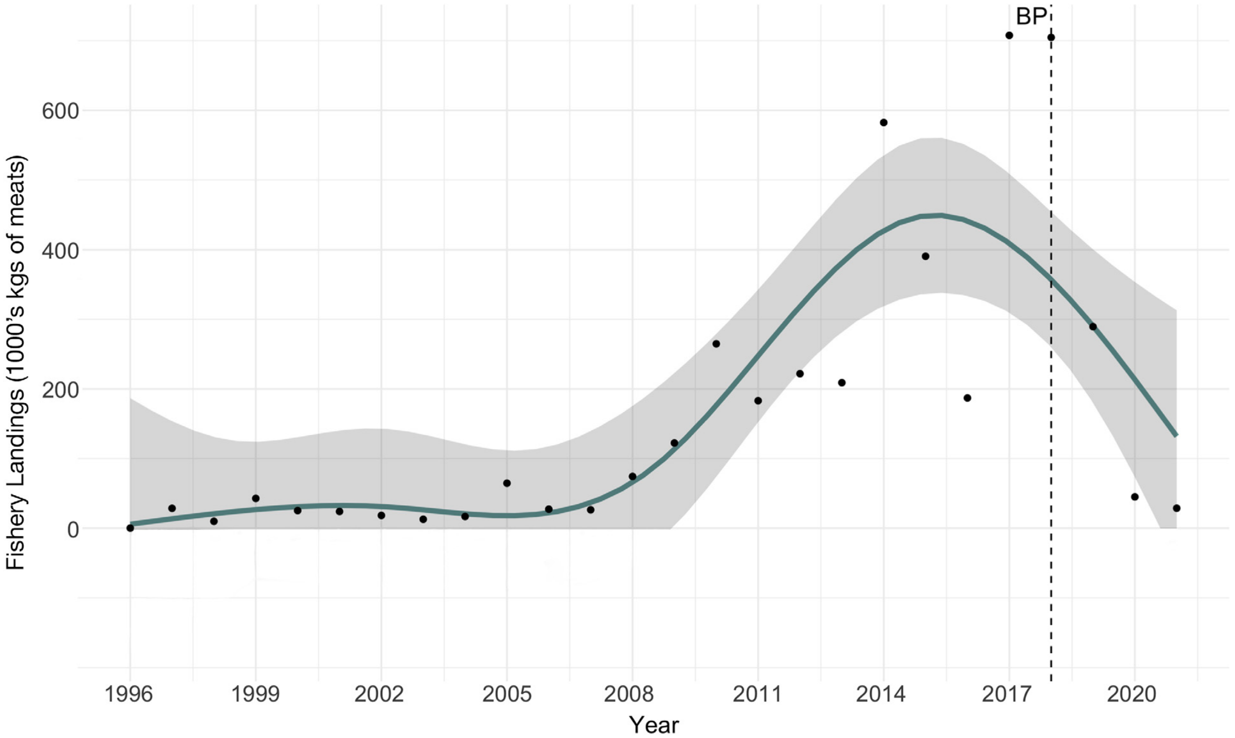

Fig. 5. Generalized additive model (GAM) displaying annual scallop landings (in 1000s of kg of meats) as a function of time from 1996 to 2022 (n = 25, p = 0.0001, $F$ = 8.976, edf = 3.759, adjusted $R^2$ = 0.587, deviance explained = 64.9%). The vertical dashed line denotes the breakpoint that defined our pre-die-off and die-off time periods, as determined by the intercept-only segmented regression model. Shaded regions represent 95% confidence intervals

Table 1. Commercial Peconic Bay scallop landings and dockside values for seasons (early November–late March of the next year) since 2014/15 (NYSDEC 2022)

| Scallop season | Landings (kg meats) | Dockside price ($\$$ kg$^{-1}$) | Total value ($) |
|---|---|---|---|
| 2014/15 | 43964 | 31.97 | 1405412 |
| 2015/16 | 25313 | 31.97 | 809173 |
| 2016/17 | 17860 | 31.97 | 570938 |
| 2017/18 | 51127 | 31.97 | 1634368 |
| 2018/19 | 50279 | 31.97 | 1607282 |
| 2019/20 | 3089 | 48.50 | 149798 |
| 2020/21 | 29 | 55.12 | 1625 |
| 2021/22 | 4015 | 66.14 | 265560 |

for the 2020/21 season was a mere 65 lbs (~29.5 kg), with a dockside value of US$ 1625 (Table 1).

### 3.3. Larval and juvenile recruitment

Although the highest per-site numbers of scallop spat were seen during sampling periods in 2018, compared to 2019, mean spat density did not significantly differ between 2018 and 2019 (Fig. 6A, Table S1). However, spat densities were significantly higher in 2021 compared to 2020 (Fig. 6B, Table S1). Based on our index of% spat settlement the relative rate of larval recruitment to spat collectors in fall was 76.1% in 2018, but declined sharply over the next 3 yr to only 2.7% in 2021 (Table 2). This trend parallels the significantly ($p < 0.01$) lower percentages of adult scallops with small (≤20 mm) annual growth rings which were seen in fall of 2020–2021 compared to fall 2018–2019 (Fig. 7, Table S1).

While seed densities were highly variable from site to site, overall seed densities were higher before 2019 (Fig. 8). Whereas regression models of temporal changes in seed density showed an overall decline from 2008–2018 (Fig. 8A, Table S1), a slight increase in seed densities was evident in 2019–2021 (Fig. 8B, Table S1).

## 4. DISCUSSION

Densities of bay scallops and other marine species vary spatially and temporally based on differential recruitment success, changes in habitat characteristics and overall levels of mortality (Bricelj et al. 1987,

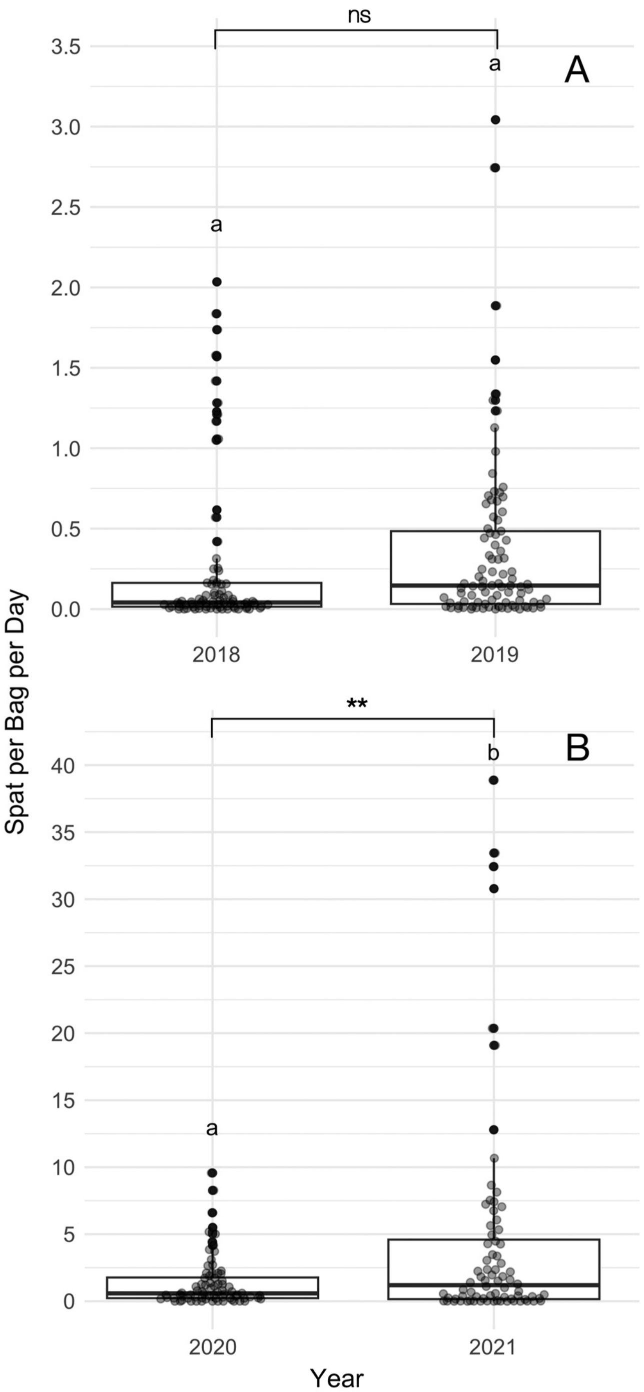

Fig. 6. Median, first quartile, and third quartile densities of spat counted in successive overlapping sets of equivalent replicate collectors deployed for successive ~6–7 wk periods from early June to mid-November for respective periods of 2 yr: (A: 2018–2019, B: 2020–2021). Grey dots are within the confidence intervals; black dots are outside of the confidence intervals. Statistical analyses for A (n = 85 for 2018, n = 89 for 2019) are separate from B (n = 76 for 2020, n = 76 for 2021). Raw values are displayed but statistical analyses were performed on log(x + 1) transformed values. ns: $p > 0.05$; **$p < 0.01$

Table 2. Recruitment to spat collectors deployed for overlapping ~6–7 wk sets at 11–23 sites in the Peconic Bays by period (spring–summer, late summer–early fall, fall) in 2018–2021. Mean no. of spat bag$^{-1}$ period$^{-1}$ = total no. of spat / total no. of bags for the period; mean no. of spat bag$^{-1}$ d$^{-1}$ = average of settlement rates for each ~6–7 wk deployment during the given period; % of total spat for period = total no. spat collected in a given period / total no. spat collected for the year; index of % spat settlement = mean no. spat bag$^{-1}$ period$^{-1}$ / total of these settlement rates for the 3 periods

| Metric of recruitment for period | Early June–late Aug | Late Aug–mid-Sept | Mid-Sept–mid-Nov |
|---|---|---|---|
| **2018** | | | |
| Total no. spat collected | 595 | 1742 | 5958 |
| Total no. bags deployed | 501 | 242 | 223 |
| Mean no. spat bag$^{-1}$ | 1.1876 | 7.1983 | 26.7175 |
| Total no. days deployed | 155 | 52 | 74 |
| Mean no. spat bag$^{-1}$ d$^{-1}$ | 0.0293 | 0.2341 | 1.0051 |
| % of total spat | 7.2 | 21 | 71.8 |
| Index of % spat settlement | 3.4 | 20.5 | 76.1 |
| **2019** | | | |
| Total no. spat collected | 5742 | 701 | 1689 |
| Total no. bags deployed | 357 | 177 | 213 |
| Mean no. spat bag$^{-1}$ | 16.084 | 3.9605 | 7.9296 |
| Total no. days deployed | 149 | 41 | 105 |
| Mean no. spat bag$^{-1}$ d$^{-1}$ | 0.3489 | 0.1943 | 0.2845 |
| % of total spat | 70.6 | 8.6 | 20.8 |
| Index of % spat settlement | 57.5 | 14.2 | 28.3 |
| **2020** | | | |
| Total no. spat collected | 21166 | 994 | 2670 |
| Total no. bags deployed | 242 | 110 | 150 |
| Mean no. spat bag$^{-1}$ | 87.4628 | 9.0364 | 17.8 |
| Total no. days deployed | 150 | 44 | 104 |
| Mean no. spat bag$^{-1}$ d$^{-1}$ | 2.0574 | 0.4112 | 0.5403 |
| % of total spat | 85.2 | 4.0 | 10.8 |
| Index of % spat settlement | 76.5 | 7.9 | 15.6 |
| **2021** | | | |
| Total no. spat collected | 106715 | 3026 | 1828 |
| Total no. bags deployed | 261 | 130 | 150 |
| Mean no. spat bag$^{-1}$ | 408.8697 | 23.2769 | 12.1867 |
| Total no. days deployed | 148 | 44 | 112 |
| Mean no. spat bag$^{-1}$ d$^{-1}$ | 9.8952 | 1.0547 | 0.4275 |
| % of total spat | 95.6 | 2.7 | 1.6 |
| Index of % spat settlement | 92.0 | 5.2 | 2.7 |

Carroll et al. 2010, Tettelbach et al. 2011, 2013, 2015). While bay scallops can swim and be transported 10s of meters by strong tidal currents over periods of several days–weeks (Moore & Marshall 1967, Tettelbach 1986, Sclafani et al. 2022), net changes in adult scallop densities from spring to fall should not be expected to result from immigration or emigration (Tettelbach et al. 2011). From 2008–2018, some individual sites, which represent a range of substrates and depths and experience different current velocities and predator densities (Tettelbach et al. 2015), sustained very high declines in density from spring to fall. However, the overall drop in densities seen in

2019–2021 was much higher than in prior years; hence their characterization as mass die-offs. The crash of the commercial fishery coincided with these mass mortalities of adult scallops.

Mortality of adult bay scallops from spring to fall is thought to be due primarily to predation by crabs, whelks and perhaps finfish (Tettelbach et al. 2011, Sclafani et al. 2022). However, the die-offs described here likely appear to be due to a combination of environmental stressors that are compounding the

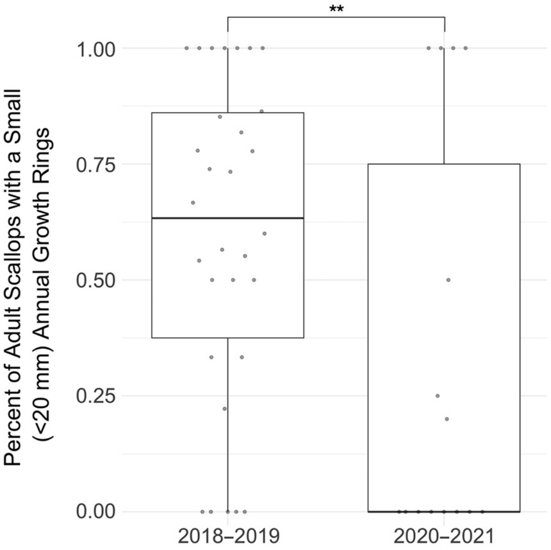

Fig. 7. Decline in the median, first quartile and third quartile percentages of adult (1+ yr) scallops with small annual growth rings (≤20 mm) from 2018–2019 (n = 30) to 2020–2021 (n = 15). **p < 0.01

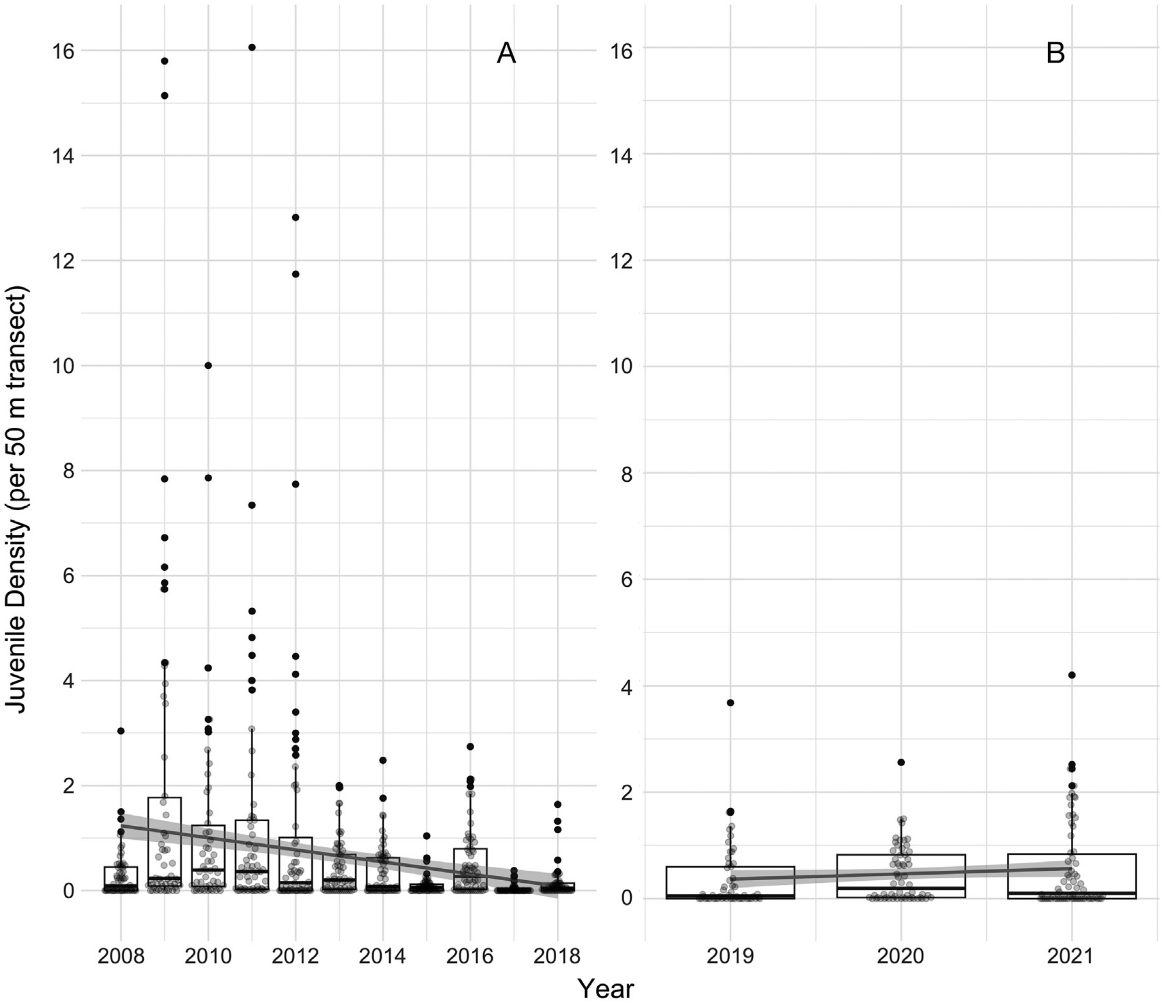

Fig. 8. Models displaying seed (0+ yr) densities in fall during 2 time groups, pre die-off (A) (n = 693, p < 0.0001) and die-off (B) (n = 180, p = 0.056, slope = 0.2757), as determined by the intercept-only segmented regression model. Statistical analyses for A are separate from B. Shaded regions represent 95% confidence intervals. Grey and black dots as in Fig. 6

physiological stress experienced by adult scallops around the time of the first seasonal spawn(s) in late June–late July. The primary driver is likely to be a marosporidian parasite, whose impacts on the health of scallops and contributions to high mortality levels appear to be exacerbated by elevated water temperatures and hypoxia that have become more commonplace in the last few years (Pales Espinosa et al. 2023, Tomasetti et al. 2023).

The die-off of adult bay scallops in the Peconic Bays has been catastrophic for local fishermen and associated industries, prompting the formal federal designation of the New York bay scallop as a fishery disaster. Although dockside price was considerably higher in 2020 and 2021 than in 2018, full-time baymen may have incurred income losses of up to \$50 000 yr$^{-1}$ as a result of the mass mortalities of Peconic bay scallops (P. Wenczel pers. comm.).

Usually, mass mortality events cause population crashes — from which recovery times often vary depending on the life history of the particular species. If population densities and abundance of free-spawning adult invertebrates and fishes are reduced to low levels, due for example to disease outbreaks in sea urchins (Lessios et al. 1984, Lessios 1988), overfishing of queen conch (Stoner & Ray-Culp 2000) or decimation of bay scallop stocks by brown tide algal blooms (Tettelbach & Wenczel 1993), then Allee effects may occur, where at low population abundances and densities fertilization success, larval production and recruitment may be severely impacted (Peterson et al. 1996, Tettelbach et al. 2013, Kersting et al. 2020). In many cases, populations may not recover from mass mortality events for many years, if at all (Bonanomi et al. 2015, Lessios 2016, Benson et al. 2018, FWRI 2020).

However, despite the mass die-off of adult Peconic bay scallops in 2019–2021, larval and juvenile recruitment were still robust and actually increased over this 3 yr period, as evidenced by the lack of differences in spat densities in collectors in 2019 vs. 2018, sustained larval recruitment in 2020–2021 and an increase in benthic 0+ yr scallop densities from 2019 to 2021. This scenario largely reflects the timing of the die-offs. Based on temporal larval recruitment patterns reported here and our reproductive monitoring (S. Tettelbach et al. unpubl. data), it is apparent that successful spawning of adult scallops occurred in June–July of 2019–2021, i.e. before the almost complete die-off of adult bay scallops. Thus, despite low numbers of adults surviving to the start of the harvest season in November, scallop populations have been able to persist during 2019–2021. Furthermore, high rates of larval and benthic juvenile recruitment in 2019–2021 suggest that these life history stages may not have experienced the same levels of extremely high mortality as did adult scallops, probably because larval and juvenile scallops are not undergoing spawning and the severity of parasite infection is lower in juveniles than adults (B. Allam et al. unpubl. data). Thus, these earlier life stages may not have experienced the same level of physiological stresses in the face of adverse environmental conditions.

Besides the overt effects of the mass mortality events on adult Peconic bay scallop populations and the commercial fishery, a more subtle impact is the reduced level of late season spawning, as relatively few adults at our sampling sites survived to September and October. This was reflected in lower proportions of larval settlement in fall of 2019–2021 (compared to 2018), a much lower percentage of sites where an apparent increase occurred in adult scallop density from spring to fall (where such increases very likely reflect an underestimation of numbers of fall-spawned scallops that were too small to be seen in spring surveys) and a lower percentage of adults in fall with small annual growth rings (that very likely were the product of spawns the previous fall). While the timing of Peconic bay scallop spawning and larval settlement may vary from one year to the next (Tettelbach et al. 2013), it is apparent that fall recruitment was much less important in 2019–2021, particularly in the latter 2 yr, compared to 2018. At some other sites (including deeper areas), higher frequencies of adult scallops with small annual growth rings (P. Wenczel pers. comm.) may reflect relatively higher numbers of adults surviving to spawn in fall and/or higher survival of their offspring. Limited data suggest that fall-spawned scallops in New York may survive better than those spawned in spring/summer (Tettelbach et al. 2001). Given that approximately half of fall-spawned bay scallops may not spawn themselves until an age of 1.5–2 yrs (Hall et al. 2015), this portion of the population may serve to extend the lifespan of a given year-class and help buffer populations against drastic annual fluctuations in recruitment that are typical for this species (Belding 1910, Tettelbach et al. 2001, Bishop et al. 2005, Geiger et al. 2010, Hall et al. 2015).

However, the continued occurrence of mass die-offs of adult scallops along with the overall reduction of fall spawning may make stocks less resilient to population crashes in the future. This situation will be even more dire if mass die-offs occur before scallops have had a chance to spawn even once. This exact scenario was observed in North Carolina, USA, where Peterson et al. (2001) determined that a mass mortality of adult southern bay scallops, *A. irradians concentricus*, which was attributed to predation by migrating cownose rays *Rhinoptera bonasus*, occurred before scallops had had a chance to spawn, thus eliminating their contribution to larval production and recruitment. The precarious state of Peconic bay scallops is exacerbated by their short lifespan and reinforces the vital importance of continuing restoration efforts, which were shown to drive the resurgence of scallop populations and fisheries in the Peconic system (Tettelbach et al. 2013, 2015).

Although we have had considerable success in restoring bay scallop populations in the past by boosting larval recruitment following mass mortalities due to brown tide algal blooms (Tettelbach et al. 2013), reasons for the inability of many populations to recover from mass die-offs are not always clear (Lessios 2016). Potential ecological shifts or population crashes to alternate stable states following mass mortality events (Beisner et al. 2003, Knowlton 2004, DiCamillo & Cerrano 2015, Escrivá et al. 2021) present further challenges to the persistence of robust marine populations. These processes, as well as changing environments driven by the global climate crisis (Hoegh-Guldberg et al. 2017, Fordyce et al. 2019, Babcock et al. 2019), also threaten the likelihood of successful restoration efforts.

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