

ARTICLE

Winter Flounder Navigate the Postsettlement Gauntlet with a Bet-Hedging Strategy

Tara E. Dolan,*  Anne E. McElroy, and Robert Cerrato

School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794-5000, USA

Lyndie A. Hice-Dunton

Responsible Offshore Science Alliance, Washington, D.C. 20035, USA

Catherine Fede

New York State Department of Environmental Conservation, Marine Resources Division, 205 North Belle Mead Road, East Setauket, New York 11733, USA

Michael G. Frisk

School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794-5000, USA

Abstract

Winter Flounder *Pseudopleuronectes americanus*, a coastal flatfish species of historically economic and cultural importance, have declined throughout the past few decades within the southern New England and mid-Atlantic region of the United States, reaching a low point of less than 9% of their historic biomass in 2009. Unusually high postsettlement mortality is thought to impose a critical recruitment bottleneck on the population, potentially stalling recovery of Winter Flounder populations despite management measures. Survival and growth during early life history play a key role in the recruitment dynamics of marine fishes. Spatiotemporal differences in these vital rates from young-of-the-year (i.e., age-0) Winter Flounder have been variously linked to environmental gradients, anthropogenic stressors, differences in the timing of settlement, and location. To better understand local declines in recruitment productivity, we assessed vital rates of age-0 Winter Flounder in five different bays in Long Island, New York. A weekly or biweekly beam-trawl survey targeting age-0 Winter Flounder was implemented over five summers. We compared survey-based estimates of age-0 mortality and growth, finding significant differences between locations in growth but not mortality. A consistently high abundance of age-0 Winter Flounder in Shinnecock Bay and Mattituck Creek was prolonged by a secondary settlement pulse later in the season. Hypothesizing that multiple settlement pulses are a bet-hedging strategy against temporally varying environmental conditions, we compared mortality, growth, and occupied habitat conditions between settlement pulses (cohorts), finding differences in growth and habitat occupancy that varied across years.

*Corresponding author: dolan.tara.e@gmail.com

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The first year of life is an influential time period for determining year-class strength in many fish species. Mortality can be highly variable during the egg and larval phase, translating to volatility in recruitment productivity (Wilber et al. 2013a; Garrido et al. 2015; Oeberst et al. 2018). This variability is later constrained by regulating mechanisms affecting mortality and growth during the postsettlement juvenile stage (Gulland 1965; Sissenwine 1984; Van der Veer et al. 2000; Houde 2008). Flatfish in particular show low recruitment variability relative to other taxa (Gibson 1994; Van der Veer et al. 1994, 2000). Variability in flatfish recruitment is thought to be constrained during and after their transition to a demersal life stage and concentration in nursery habitats (Beverton 1995; Van der Veer et al. 2000; Le Pape et al. 2003; Archambault et al. 2014). Fine-scale variation in mortality and growth during this time act as a gauntlet, dampening variability in year-class strength (Bailey 1994; Van der Veer et al. 1994; Leggett and Frank 1997; Archambault et al. 2014; Amorim et al. 2016). Growth conditions encountered by settling larvae will mediate their vulnerability to starvation, predation, and environmental change (Sogard and Able 1992; Van der Veer et al. 1994; Kamermans et al. 1995; Rose et al. 1996; Manderson et al. 2006).

Many flatfish species spend their first year of life in shallow estuarine or coastal habitats, where they are subjected to strong environmental stressors and anthropogenic disturbance (Rijnsdorp et al. 1992; Leggett and Frank 1997; Camp et al. 2011; Wilber et al. 2016; Amorim et al. 2018). Fine-scale spatial variability in juvenile densities and growth rates in nursery habitats can be high (Modin and Pihl 1994; Berghahn et al. 1995; Leggett and Frank 1997; Sogard et al. 2001; Wilber et al. 2016). Certain settlement areas may disproportionately contribute to productivity during most years, while other areas supplement that productivity and provide insurance in case the major habitat is unable to function (Secor 2007; Schindler et al. 2010, 2015). Termed the “rescue effect,” this diversity in patterns of juvenile habitat productivity serve to reduce risk to year-class strength overall. The use of alternate habitats is considered a form of bet-hedging against spatial variability. Pulsed recruitment is another form of bet-hedging, in this case against temporal variability. The production of more than one cohort within a season is an outcome of pulsed recruitment through episodic larval delivery or multiple spawning modes (Conover et al. 2003; Secor 2007). Each settlement pulse encounters different conditions for transport and growth and potentially a different arena of predators that shifts with the arrival of the cohort relative to the phenology of the system (Chant et al. 2000; Manderson et al. 2006; Frisk et al. 2018). The partitioning of risk between cohorts is an example of the “portfolio effect” and may promote long-term population resilience (Secor 2007; Schindler et al. 2010, 2015). Distinct maturation schedules associated with multiple

cohorts within a population have been documented in a number of species (e.g., Atlantic Cod *Gadus morhua*, Fogarty et al. 2001; Bluefish *Pomatomus saltatrix*, Conover et al. 2003; Wilber et al. 2003; generally, Secor 2007). Despite the “insurance policy” of producing more than one cohort, persistent stressors, including overfishing, anthropogenic stressors, and climate-related ecosystem changes, can still impact recruitment (Bell et al. 2014; Frisk et al. 2018).

Winter Flounder *Pseudopleuronectes americanus* is an example of a flatfish species with remarkable intraspecific diversity in both life history and response to stressors (Percy 1962; Sagarese and Frisk 2011; Frisk et al. 2014; Gallagher et al. 2015; Ziegler et al. 2019). Historically a commercially and recreationally important food species, Winter Flounder populations have declined since the late 1980s throughout their range in North America from Labrador to Georgia (Pereira 1999; Colette and Klein-MacPhee 2002). In the United States, Winter Flounder are managed as three stocks: Gulf of Maine, Georges Bank, and southern New England and mid-Atlantic region (SNE/MA). The SNE/MA stock underwent a severe reduction in biomass, declining to <9% of target biomass levels in 2009. The stock increased to 23% in 2014, following the institution of commercial restrictions in state waters and a moratorium in federal waters. In 2014, the federal rebuilding plan for SNE/MA Winter Flounder was extended to 2023, and the stock was last estimated at 30% of the target levels (NEFSC 2011, 2015, 2017, 2020). Despite this recent improvement, Winter Flounder is no longer a viable fishery in New York, where commercial catch is currently <3% and recreational catch is <0.3% of peak levels observed in the early 1980s (NEFSC 2017). The prolonged overfished state has altered the age structure of the fishery. Maximum age for the SNE/MA stock declined from 15 to 6 years between the 1980s and 1990s, portending lasting productivity depletion (Rouyer et al. 2011; Siskey 2020). Recruitment indices for the SNE/MA stock in 2013 fell to a recent historic low point of 4% of maximum estimated levels. Maximum recruitment was estimated at 68,685 (thousands of recruits) in 1981, the earliest year of the time series (NEFSC 2017). Recruitment had a small peak in 2018 (6.4 million); however, it has again dropped below the 10-year average (4.7 million) in 2019 (3.4 million; NEFSC 2020). Poor recruitment of young-of-the-year (age-0) fish has limited expectations for the species’ recovery, though causes of weak recruitment are poorly understood (Manderson 2008; Able et al. 2014; Gallagher et al. 2015).

Mortality during the postsettlement phase might impose a bottleneck on recruitment. The first summer after transitioning to demersal life is a particularly vulnerable time for Winter Flounder, not only due to predation but because of their stage-specific physiological requirements and the

variety of abiotic stressors they face during their postsettlement estuarine residence (Sogard et al. 2001; Bell et al. 2014; Frisk et al. 2018). Abundance of newly settled Winter Flounder peaks in late spring and early summer in coastal estuaries (Sogard et al. 2001; Manderson 2008), where they serve as an important prey source for transient marine predators arriving in coastal bays following overwintering offshore (Polis et al. 1997; Taylor et al. 2019). High interannual variability in juvenile densities and growth indicate a potentially important interplay between local environmental factors, predation mortality, and fine-scale genetic differences in controlling recruitment dynamics (Sogard et al. 2001; Manderson et al. 2003). For example, relationships between bottom temperature and age-0 productivity are temporally variable (Manderson et al. 2003; Wilber et al. 2013a). Warm winters seem to benefit early season recruitment, while negatively impacting late season recruitment and summer survival (Frisk et al. 2018).

Growth rates are also expected to be temporally and spatially dynamic: hierarchical linear modeling by Gallagher et al. (2015) found that the relationship between extrinsic environmental factors and growth rate in wild age-0 Winter Flounder depended on the date of settlement and individual condition and that the relationships differed between bays. The persistence of variable growth conditions among estuaries favors a spatial bet-hedging approach with juveniles occupying different systems and some achieving greater production than others in any given year. Recent evidence for spawning in nearshore oceanic habitats (Wuenschel et al. 2009; DeCelles and Cadrin 2010; Fairchild et al. 2013; Fairchild 2017; Siskey 2020) could indicate that these alternate habitats provide a refuge for age-0 Winter Flounder from deteriorating estuarine conditions (Secor 2007).

Winter Flounder are obligate batch spawners, producing pulses of larvae throughout the season (Murua and Saborido-Rey 2003). Spawning occurs annually, though a small percentage of females captured in the New York Bight were found to halt gonadal development (skip spawning) when stored energy reserves were low (Wuenschel et al. 2009). Heightened periods of spawning activity produce distinct pulses and can occur over a period of several months between December and March (Ziegler et al. 2019). The production of more than one cohort has been proposed as a bet-hedging strategy to avoid total year-class loss due to adverse environmental conditions (Juanes and Conover 1995; Conover et al. 2003; Secor 2007). Thus, when conditions are favorable for both cohorts, the estuary will remain productive throughout the season. In some years, spawning earlier will improve chances of off-spring survival, whereas in other years spawning later improves survival. A population that exhibits both strategies would theoretically be more stable over time (Secor 2007; Schindler et al. 2010, 2015).

Inshore populations in Long Island, New York, have not experienced the recent (since 2010) positive trend in number of recruits per spawner exhibited in Connecticut bays (Frisk et al. 2018). These subpopulations were found to exhibit genetic inbreeding and a low number of effective breeders, potentially indicating their vulnerability to local depletion (O'Leary et al. 2013). Winter Flounder have life history characteristics that may limit connectivity between nursery areas, impeding the rescue effect, with important implications for population persistence in the SNE/MA region. These include natal philopatry (Phelan 1992; DeCelles and Cadrin 2011), demersal estuarine spawning (McCracken 1963; Able and Fahay 1998; Wilber et al. 2013a), bottom-oriented larvae (Chambers and Leggett 1987), high rates of larval retention (Crawford and Carey 1985; Chant et al. 2000; Wilber et al. 2013a), and limited juvenile movement (Saucerman and Deegan 1991). Winter Flounder age-0 abundance tracks settlement in some habitats but is decoupled from larval supply in others (Manderson et al. 2003). Thus, our ability to assess the vulnerability of inshore populations to external forcing depends on thorough sampling of young of the year from multiple locations throughout the postsettlement period. The goal of this study was to quantify postsettlement mortality and growth in Winter Flounder from six different Long Island bays, spanning a period of 10 years, to better understand local-scale declines in recruitment productivity.

METHODS

Study area.—Winter Flounder were collected from six different bays in Long Island, New York: Jamaica Bay, Moriches Bay, Shinnecock Bay, Cold Spring Pond, and Napeague Harbor on the south shore of Long Island and Mattituck Creek on the north shore (Figure 1). Separated by less than 200 km, these sites represent a gradient of human population density that decreases from west to east (LIRPC 2010). Mattituck Creek is a shallow tidal system connecting with the Long Island Sound via Mattituck Inlet (NOAA 2013). The south shore bays of Jamaica, Moriches, and Shinnecock are part of the Long Island barrier beach-lagoon system characterized by extensive salt marshes and tidal flats. Jamaica Bay connects with lower New York Bay to the west through Rockaway Inlet. Napeague Harbor and Cold Spring Pond are located on the northern coast of the south shore of Long Island and connect to the greater Peconic Bays Estuary, situated between Long Island's north and south forks.

Fish collection and environmental data.—Age-0 Winter Flounder were collected from a beam trawl survey using a stratified random design. The survey was conducted from June through October in 2010 and 2011 and from May through August in 2015, 2016, and 2017. Shinnecock Bay was surveyed in 2010, 2011, 2016, and 2017. Jamaica and

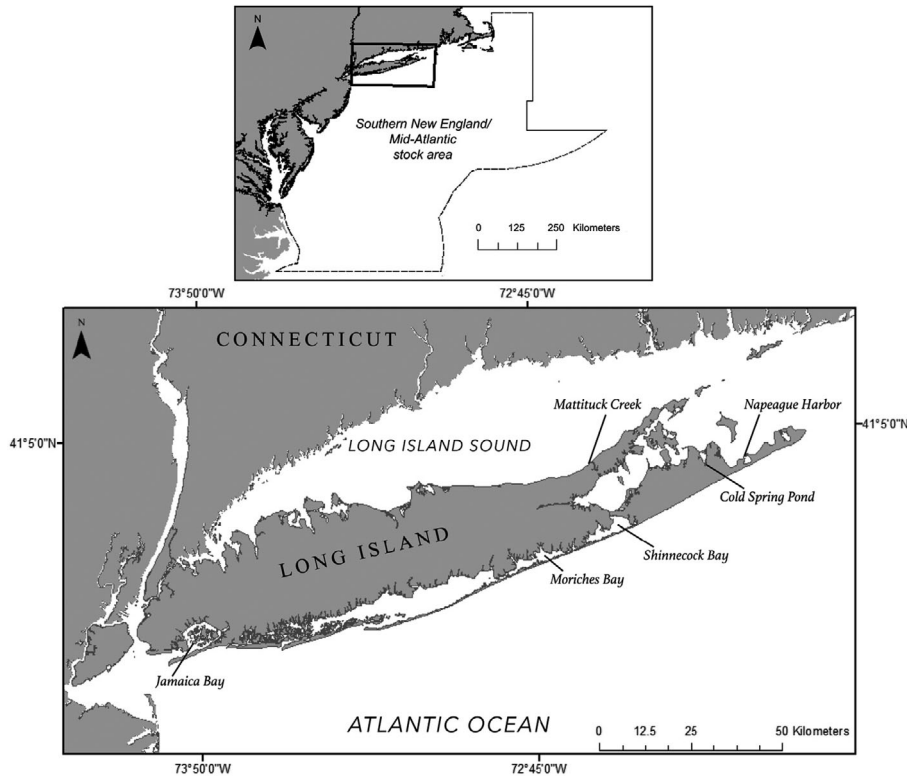


FIGURE 1. Maps showing the southern New England and mid-Atlantic region Winter Flounder stock area, with Long Island, New York, shown in the inset (top panel), and showing the location of the surveyed bays in Long Island, New York (bottom panel).

Moriches bays were surveyed in 2010, 2011, and 2016, Napeague Harbor in 2010 and 2016, and Cold Spring Pond in 2010 only. Trawling was conducted every other week in 2010 and 2011 and weekly in 2016 and 2017, with sampling continuing until two consecutive surveys failed to yield a single fish in that location. Young of the year were collected from the Mattituck Creek system every other week from May to September in 2015 and 2016. Ten 5-min tows were conducted using a 1-m beam trawl equipped with 0.635-cm mesh. Captured age-0 fish were measured and immediately released. Water quality measurements of temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/L), and salinity (‰) were taken at the end of each tow using a YSI multiprobe. Depth, longitude, and latitude were recorded for the start and endpoint of the transect covered in each tow in 2016 and 2017.

Cohort assignment.—To determine summer survival, age-0 fish were further classified as belonging to either the early season or late season cohort. We determined whether year-classes could be split in this way by fitting a normal distribution to length frequencies within each bay and each week using the package *fitdistrplus* (Delignette-Muller and Dutang 2015) in the R environment for statistical computing (R Core Team 2017) and comparing the model fit to a multinomial distribution using Akaike information criterion (Burnham and

Anderson 2002). Cohort analysis was conducted only for bays where a multinomial distribution had a better fit to the length frequency data than a normal distribution during a consecutive period of weeks that represented the majority of weeks surveyed in that bay and year. This limited the cohort analysis to Shinnecock Bay in 2016 and 2017 and Mattituck Creek in 2016. Age-0 fish were assigned to a cohort by fitting length frequencies for each week to a multinomial distribution using the package *mixtools* (Benaglia et al. 2009). The fitted multinomial distribution produced a threshold length for each week that was visually verified. Individuals measuring greater than the threshold at that given week were assigned to the early cohort. We validated this approach on a subset of individuals previously aged by Ziegler et al. (2019) using otolith increment analysis.

Estimating mortality.—Catch per unit effort (CPUE) was standardized to area swept (m^2), obtained from vessel tracks. We corrected relative abundance data for selectivity using the following equation:

$$s_x = \frac{1}{1 + \exp^{-g(l-l_h)}}, \quad (1)$$

where s_x is selectivity at length x , g is the shape parameter, l is the fish length, and l_h is the length at 50%

selectivity (Quinn and Deriso 1999). Gear selectivity parameters were estimated for beam trawling ($lh = 51.4$ mm; $g = 0.092$) using data collected from the trawl survey in Shinnecock Bay in 2016 and were used to correct abundance estimates.

We estimated daily natural mortality in each bay using catch curve analysis (Quinn and Deriso 1999), facilitated by the package *FSA* in R (Ogle et al. 2018). We plotted values of relative abundance (\log_e CPUE) against time, resulting in a piecewise linear relationship with two segments: an ascending segment preceding peak selectivity to the gear and a descending segment representing losses from natural mortality. The slope of the descending segment represents the instantaneous mortality rate (M), related to the natural log numbers of individuals caught (C) at each time (t):

$$M = \ln(C_t) - \ln(C_{t+1}). \quad (2)$$

The mortality rate at each time step (A) is then $A = 1 - e^{-M}$.

To quantify differences between mortality rates of fish collected from different bays, cohorts, or years, we fit a linear regression to the descending limb of each catch curve, standardizing the time to days elapsed since peak abundance. For cases where multiple peaks in abundance were present, we fit separate curves for each cohort (see cohort analysis), or when comparing across cohorts, we used the larger of the two maxima. We extracted coefficients, confidence intervals, and P -values for the effect each factor had on mortality using an ANCOVA implemented in the R package *car* (Fox et al. 2007). If it was determined that there were significant differences between bays, years, or cohorts, we then made post hoc pairwise comparisons based on the t -test for slope using the R package *lsmeans* (Lenth 2016) and using a Bonferroni correction for multiple comparisons. Tests for significant differences between cohorts within a year were conducted separately from tests between bays and years.

Growth.—We estimated growth (G ; mm/d) as the change in average length (L ; mm) at each time step (t ; days), following Yenchou et al. (2015):

$$G = \frac{L_2 - L_1}{t_2 - t_1}. \quad (3)$$

Where two cohorts were present, we additionally separately estimated growth for each cohort. We used a linear regression, ANCOVA, and post hoc pairwise comparisons to compare growth rates between groups, following the analysis for mortality as described above.

Comparison of occupied physicochemical habitat.—To determine if early and late cohorts, present at the same time, occurred in different physicochemical environments,

we compared abiotic habitat characteristics of temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/L), salinity (‰), and depth (m) between early and late cohorts within the same bay and year. This cohort comparison was limited to Shinnecock Bay in 2016 and 2017, where cohorts could be detected reliably and environmental data were available. The analysis was further constrained to include only weeks where both cohorts were captured, totaling 5 weeks in 2016 and 6 weeks in 2017 (Table S1 in the Supplement available separately online). Abiotic characteristics of occupied habitat conditions between cohorts were compared using a method developed by Perry and Smith (1994), following Sagarese et al. (2014). The cumulative distribution function of occupied habitat conditions $g(t)$ was estimated as the catch-weighted distribution of the habitat variable:

$$g(t) = \sum_h \sum_i \frac{W_h y_{hi}}{n_h \bar{y}_{st}} I(x_{hi}) \quad (4)$$

where $I(x_{hi}) = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases}$,

where y_{hi} is the number of age-0 fish caught in trawl i and stratum h , \bar{y}_{st} is the stratified mean catch, W_h is the proportion of the survey in stratum h , n_h is the number of trawls in stratum h , x_{hi} is the measurement for the habitat variable (e.g., temperature) in trawl i of stratum h , and I is an indicator function where t represents an index ranging from the lowest to the highest value of the habitat variable. The strength of association between catch and habitat was calculated as the maximum difference between the cumulative distribution functions for each cohort:

$$\max |g(t)_{\text{cohort1}} - g(t)_{\text{cohort2}}| = \max \left| \sum_h \sum_i \frac{W_h}{n_h} \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{hi}) \right|. \quad (5)$$

This test statistic (TS) was then compared with a pseudopopulation (PT) created from generating 10,000 randomized pairings of the catch and the stratified habitat variable across the dataset, and significance was determined as $P = \frac{PT \geq TS}{1,000}$.

RESULTS

Mortality

A total of 1,340 tows were conducted in Long Island bays between 2010 and 2017 (Table 1). Ten to twelve tows were completed in each bay per week, with an average swept area of 292 m² per tow. Peak abundance of age-0 Winter Flounder occurred between mid-May and mid-July (Table 1). The slopes of catch curves, representing instantaneous daily mortality (M), were not significantly

TABLE 1. Catch and effort summarized over bay and year for Winter Flounder caught in Long Island bays. Catch per unit effort (CPUE) is measured as fish captured per square meter of area swept. Mean CPUE is the grand mean across the summer of weekly CPUEs. The peak refers to the week of the survey that year for which CPUE was highest.

Bay	Year	Total catch	Area swept (m ²)	Number of tows	Mean CPUE	Start date	End date	Date of peak	CPUE at peak
Cold Spring Pond	2010	28	16,067	66	0.0027	Jun 10, 2010	Sep 9, 2010	Jul 14	0.0073
Jamaica Bay	2010	10	13,110	58	0.0016	Jun 21, 2010	Sep 1, 2010	Jun 21	0.0037
	2011	25	13,893	70	0.0052	May 27, 2011	Sep 14, 2011	Jun 24	0.0206
	2016	89	26,283	86	0.0055	May 17, 2016	Jul 5, 2016	May 17	0.0180
Mattituck Creek	2015	1,885	22,799	65	0.0825	Jun 24, 2015	Sep 1, 2015	Jul 7	0.2588
	2016	137	29,094	82	0.0052	May 16, 2016	Aug 23, 2016	Jun 30	0.0097
Moriches Bay	2010	131	19,961	82	0.0089	Jun 9, 2010	Oct 13, 2010	Jun 25	0.0282
	2011	93	12,733	68	0.0111	Jun 7, 2011	Sep 16, 2011	Jul 12	0.0347
	2016	38	46,259	129	0.0013	May 18, 2016	Aug 18, 2016	Jun 17	0.0031
Napeague Harbor	2010	390	16,624	77	0.0403	Jun 18, 2010	Oct 8, 2010	Jun 18	0.1866
	2016	49	37,077	107	0.0023	May 19, 2016	Aug 2, 2016	Jun 15	0.0101
Shinnecock Bay	2010	253	21,029	87	0.0184	Jun 10, 2010	Oct 13, 2010	Jun 28	0.0556
	2011	245	16,275	90	0.0202	Jun 6, 2011	Oct 28, 2011	Aug 24	0.0303
	2016	674	50,972	144	0.0206	May 18, 2016	Aug 31, 2016	Jul 13	0.0498
	2017	827	48,572	129	0.0286	Jun 2, 2017	Aug 24, 2017	Jun 22	0.1197

different between bays, but differences were found between years ($P > 0.05$; Table 2). The instantaneous daily mortality ranged from 0.019 ± 0.016 (mean \pm SE) in Napeague Harbor in 2010 to 0.077 ± 0.017 in Shinnecock Bay in 2017, translating to 1.85% and 7.39% daily, respectively (Figure 2).

Growth

Shinnecock Bay showed a broad length distribution across the summer in all years studied due to the presence of an additional recruitment pulse that occurred later in the season (Figure 3). The other bays, particularly Jamaica Bay and Cold Spring Pond, peaked earlier and did not show the same broad distribution in length found in Shinnecock Bay. There were significant differences in growth rate between bays and years ($P < 0.001$) but no significant bay \times year interaction (Table 2). Growth rate ranged from 0.082 ± 0.071 mm/d (mean \pm SE) in Cold Spring Pond in 2010 to 0.73 ± 0.070 mm/d in Jamaica Bay in 2011 (Figure 2). Pairwise comparisons between bays yielded seven significant (corrected for multiple comparisons) contrasts out of a possible 105 ($P < 0.0001$; Figure S1 in the Supplement available separately online). Five out of seven significant contrasts included Napeague Harbor in 2010. No contrasts between years within the same bay were significant; however, there was one significant contrast between bays within the same year: Moriches Bay and Napeague Harbor in 2010 ($P < 0.0001$).

Cohort Comparisons

Multiple peaks in abundance were detected consistently across seasons in Shinnecock Bay in 2016 and 2017 and in Mattituck Creek in 2016, allowing for the assignment of individuals to cohorts (Table S1). Length frequency data in Mattituck Creek in 2015 had a better fit to a unimodal normal distribution compared with the fit of a bimodal normal distribution. Thus, it was necessary to exclude these data because cohorts could not be reliably detected during a consecutive period of time representing the majority of weeks surveyed. Validation of the cohort assignment approach was conducted by checking against cohorts that had been previously aged by otolith increments (Figure S2). This method resulted in complete separation by length on the Mattituck Creek 2015 data. However, during certain weeks in Mattituck Creek in 2016, there was some overlap where individuals born within a few days of each other could be assigned by length to separate cohorts.

Mortality rates differed between early and late cohorts in Mattituck Creek but not in Shinnecock Bay (Figure 4A). Mortality was significantly lower in the early cohort ($M = 0.0292 \pm 0.003$) compared with the late cohort ($M = 0.0688 \pm 0.002$) in Mattituck Creek in 2016 ($P > 0.001$; Table 2). Growth in Shinnecock Bay in 2016 and 2017 was significantly different between years and also between cohorts ($P < 0.001$; Figure 4B) but lacked a significant cohort \times year interaction (Table 2). There were no

TABLE 2. Results of ANCOVA comparing the slope of catch curves (abundance versus days elapsed since peak abundance) and growth curves (length in millimeters versus time in days) between bays and years, between cohorts and years in Shinnecock Bay, or between cohorts in Mattituck Creek 2016. The slope of the catch curve corresponds to instantaneous daily mortality (M). Modifications of the slope by the factors bay and year and the bay \times year interaction or by cohort and year and the year \times cohort interaction are given. Intercepts have no ecological meaning in this context and are not reported. Significance values on the F -tests are given, where one asterisk represents $P < 0.001$ and two asterisks represents $P < 0.05$.

Analysis	Factors	Sum of squares	df	F	Pr(> F)
Mortality between bays	Bay	2.88	5	0.73	6.04×10^{-1}
	Year	8.50	4	2.69	3.76×10^{-2} **
	Bay \times year	3.64	5	0.92	4.72×10^{-1}
	Residuals	55.99	71		
Growth between bays	Bay	8,268	5	12.30	7.21×10^{-12} *
	Year	2,407	4	4.48	1.31×10^{-3} **
	Bay \times year	854	5	1.27	2.73×10^{-1}
	Residuals	581,915	4,329		
Mortality between cohorts in Shinnecock Bay	Year	0.95	1	1.693	2.06×10^{-1}
	Cohort	0.28	1	0.498	4.87×10^{-1}
	Year \times cohort	1.74	1	3.080	9.20×10^{-2}
	Residuals	13.53	24		
Mortality between cohorts in Mattituck Creek 2016	Cohort	1.21	1	46.698	4.82×10^{-4} *
	Residuals	0.16	6		
Growth between cohorts in Shinnecock Bay	Year	1,268	1	20.9122	5.18×10^{-6} *
	Cohort	7,376	1	121.685	2.20×10^{-16} *
	Year \times cohort	11	1	0.1843	0.6678
	Residuals	96,987	1,600		
Mortality between cohorts in Mattituck Creek 2016	Cohort	57.2	1	0.4971	0.4826
	Residuals	10,234.5	89		

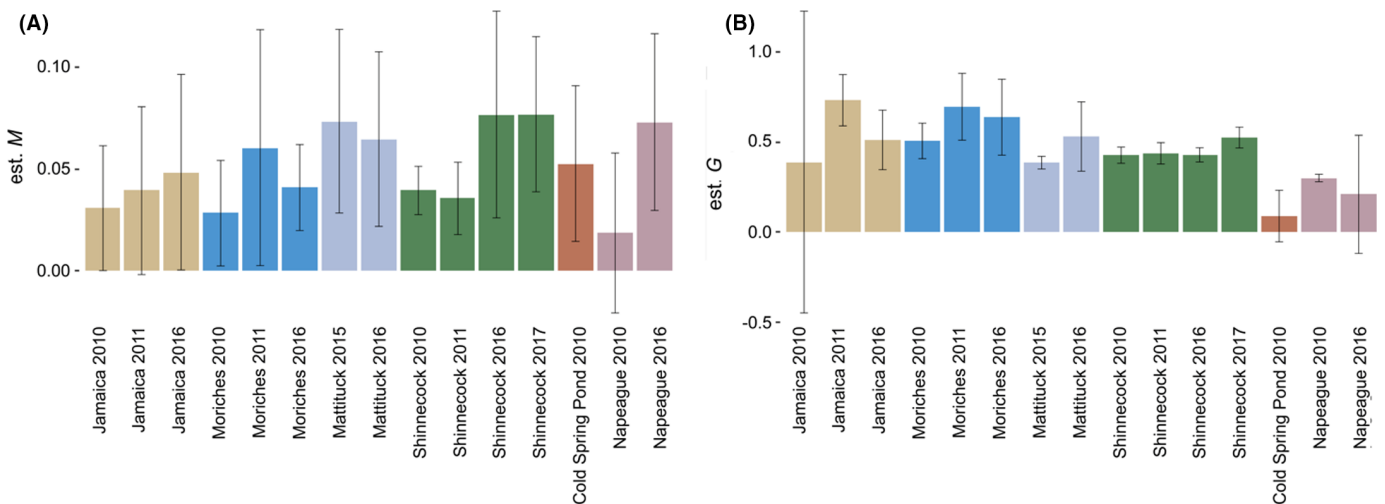


FIGURE 2. Panel (A) shows mortality estimates for age-0 Winter Flounder caught in six Long Island bays. The instantaneous daily mortality (M) is shown on the y -axis, and 95% confidence intervals for each estimate are indicated with error bars. Panel (B) shows growth estimates (mm/d) by bay and year for age-0 Winter Flounder caught in six Long Island Bays. The instantaneous rate of growth (G) is given on the y -axis, and 95% confidence intervals for each estimate are represented by error bars.

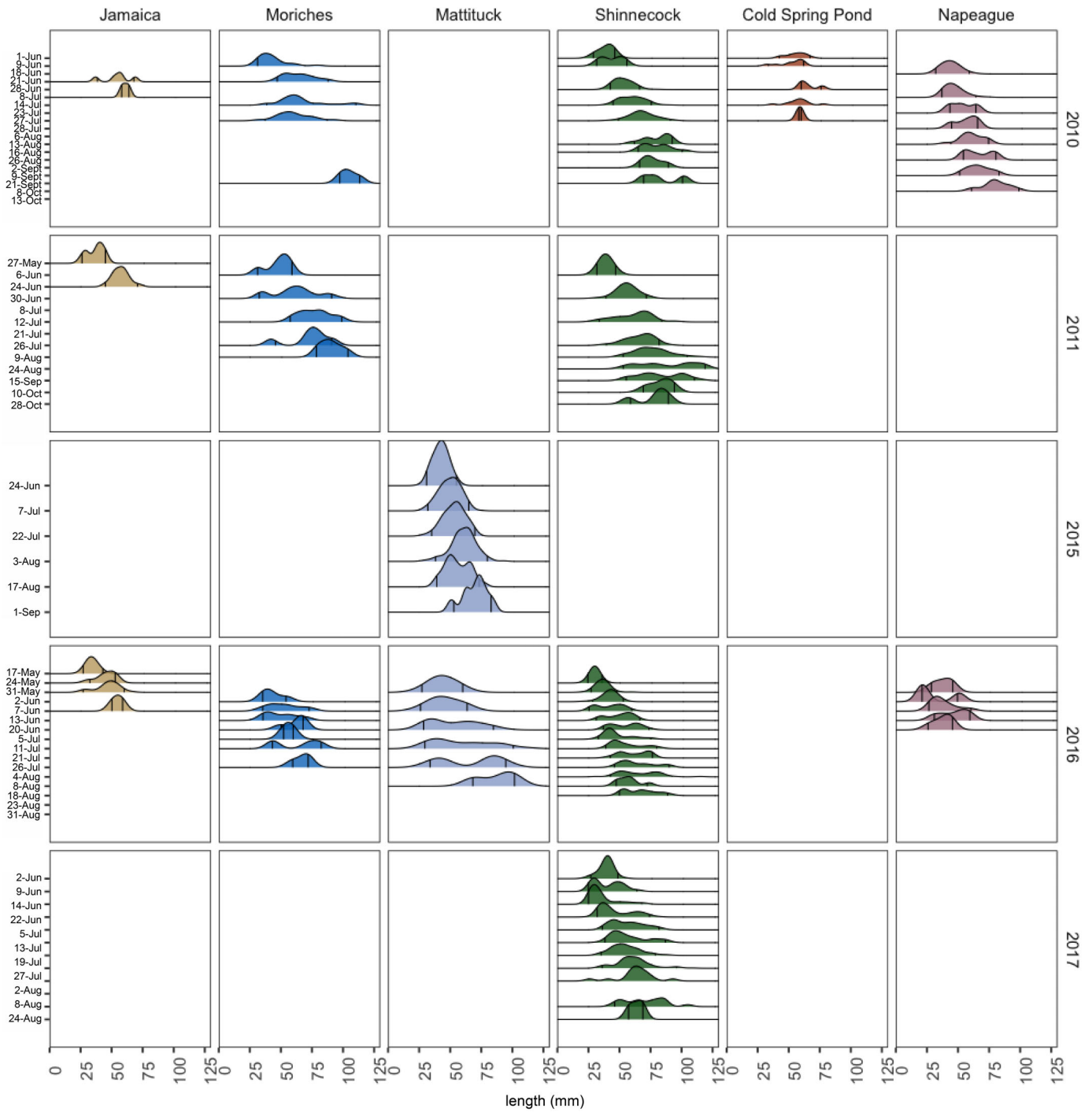


FIGURE 3. Smoothed density plots showing the relative distribution of length (mm) at date for age-0 Winter Flounder caught in Long Island bays. The date represents the first date surveyed that week. Estimates of density (height of distribution) are scaled relative to the total for each bay, not to the total for all bays. The 95% confidence intervals of each length distribution are represented by vertical black bars.

significant differences between growth of cohorts in Mattituck Creek in 2016. Pairwise comparisons between cohorts of each year in Shinnecock Bay were significant, corrected

for multiple comparisons (Table S2; $P > 0.01$), except the contrast between late cohort 2016 and late cohort in 2017 ($P = 0.024$). Separately estimating growth of individual

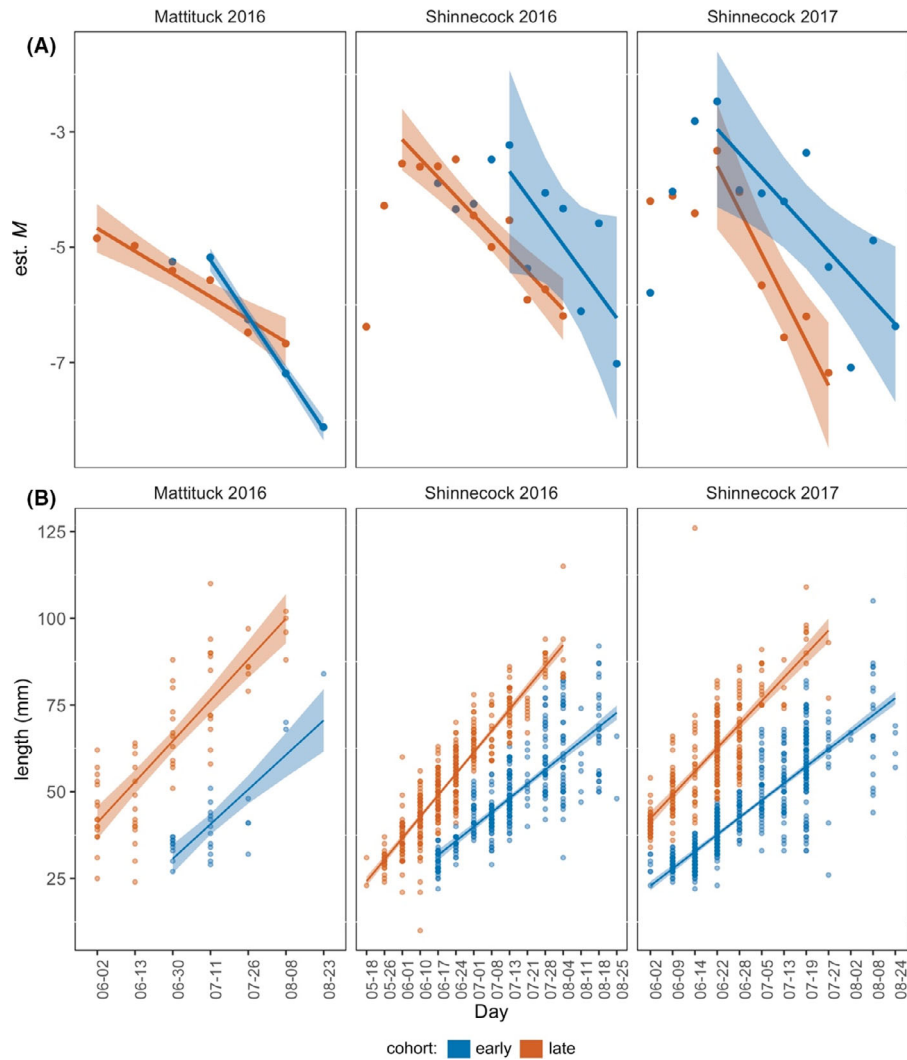


FIGURE 4. Vital rates for early and late cohorts in Mattituck Creek (2016) and Shinnecock Bay (2016, 2017), showing (A) estimates of mortality (est. M) versus date and (B) estimated growth in length (mm) versus date. In (A), points represent the natural log of catch per unit effort (CPUE), the line represents the linear trend in CPUE since peak abundance, and the shaded area represents the 95% confidence intervals on the linear regression. In (B), points represent length measurements of young-of-the-year Winter Flounder captured that day, the line and shaded area are a linear regression through length with 95% confidence intervals.

cohorts within a bay and year generally resulted in higher estimates of growth compared with estimates generated from data on both cohorts combined.

Habitat Occupancy

Individuals that were caught contemporaneously, but that belonged to different cohorts, occupied different physicochemical habitat. Late season cohorts were caught at higher temperatures, lower dissolved oxygen, and higher salinity in 2016 than early cohorts (Figure 5). We found that late season cohorts were caught at shallower depths than early season cohorts present during the same period. Only the comparison of dissolved oxygen habitat occupancy between early versus late cohorts in Shinnecock

Bay 2016 was significant when corrected for multiple comparisons ($P < 0.0001$; Table S3).

DISCUSSION

Understanding postsettlement dynamics of Winter Flounder is critical for determining the prospects for persistence and recovery of the species in the region. Our results highlight the life history diversity of age-0 Winter Flounder resulting from the timing of spawning and temporally varying environmental conditions. Estimates of mortality and growth and comparisons of physicochemical habitat preferences indicate that reliance on multiple inshore bays with differing growth potential, and mortality

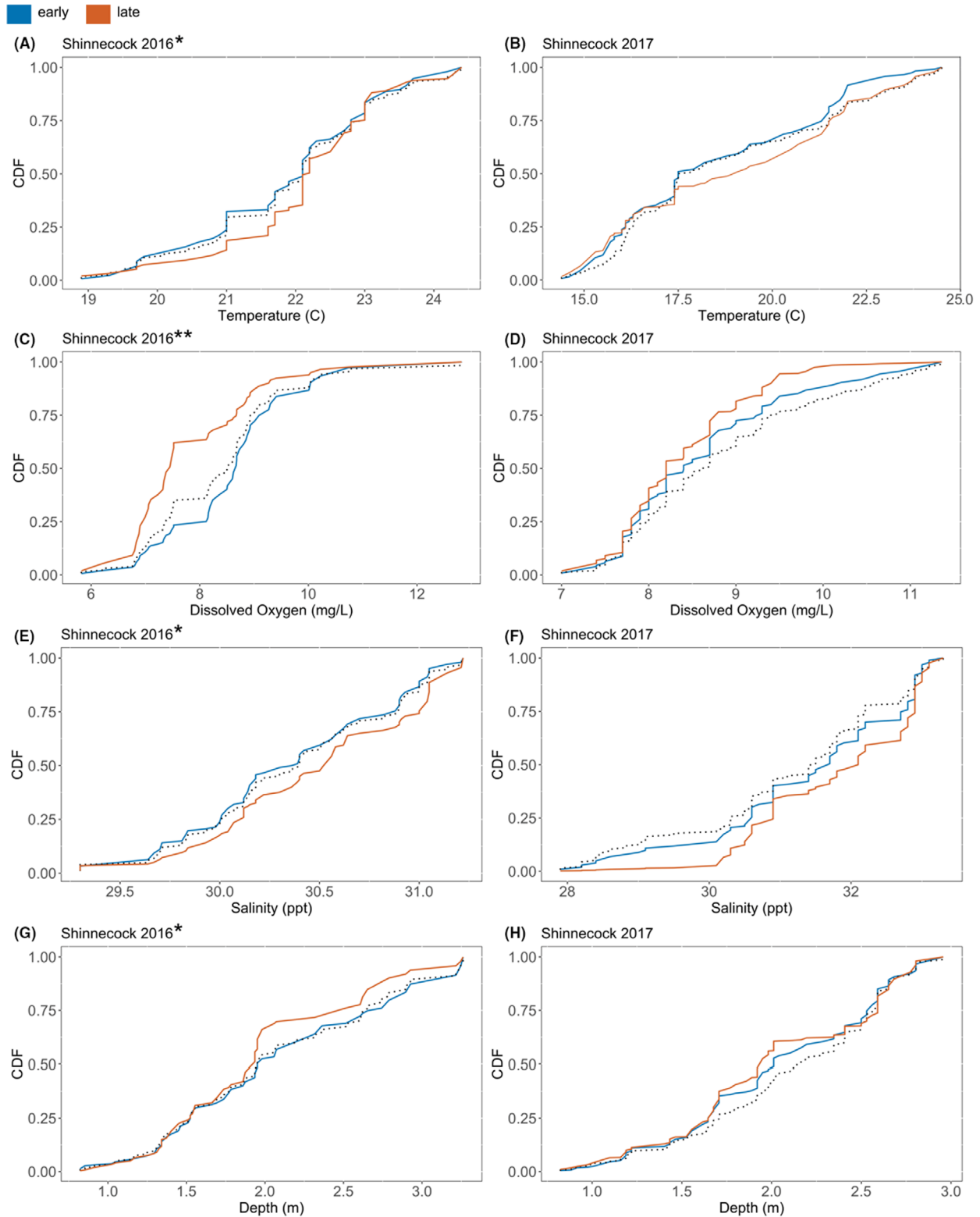


FIGURE 5. Cumulative distribution functions of occupied (solid line) and available (dotted line) habitat conditions for early and late cohorts within 2016 and 2017 in Shinnecock Bay. Different habitat conditions are depicted in each panel: (A) temperature ($^{\circ}\text{C}$) in 2016, (B) temperature ($^{\circ}\text{C}$) in 2017, (C) dissolved oxygen (mg/L) in 2016, (D) dissolved oxygen (mg/L) in 2017, (E) salinity (‰ [ppt]) in 2016, (F) salinity (‰) in 2017, (G) mean depth per tow (m) in 2016, and (H) mean depth per tow (m) in 2017. A single asterisk denotes significant differences between cohorts ($P < 0.05$); double asterisks denote significant differences between cohorts corrected for multiple comparisons (Bonferroni corrected; $P < 0.00625$).

risks, contributes to the dynamics of Winter Flounder stocks in the region. Survival and growth were mediated by characteristics of postsettlement habitat that vary over small spatial and temporal scales. Even though mortality rates were relatively consistent across bays, those sites that produced a second settlement pulse were able to maintain high abundances for a longer duration. A protracted spawning season that produces more than one cohort may serve to reduce recruitment variability by improving the odds that at least one cohort will overlap with conditions favorable for survival and growth.

We found evidence of cohort-specific growth and mortality rates in Shinnecock and Mattituck bays, respectively. The switch in mortality risk and growth conditions for early versus late cohorts suggests that adult spawning behavior that results in more than one cohort likely increases the probability of successful postsettlement survival in temporally varying environments. One possible explanation for the intracohort patterns in mortality is that early cohorts experience more variable mortality from year to year, while later cohorts experience slightly higher, but more temporally stable, mortality. The production of a second cohort thus can rescue the year-class from high early season mortality. In our study the early cohort of the 2017 year-class in Shinnecock Bay experienced very high mortality relative to the later cohort. In contrast, in 2016 the early cohort was likely responsible for most of the cohort production in both bay systems. This may arise because of the differences in growth patterns that we observed between cohorts. Early cohorts experience faster growth compared with slower and more variable growth in the late cohort.

Optimal growth conditions are created by a complex interplay of factors that may at times serve to moderate the effects of other drivers. For example, early cohorts may have advantages in terms of outcompeting smaller conspecifics for space and energetic resources (Bailey 1994; Van der Veer et al. 1994; Gibson et al. 2002). Further, the relative advantage in survival and growth potential gained by settling before the arrival of major predators into the estuary may be dampened if early season temperatures are too cool for optimum growth (Roff 1991; Sogard 1997; Wilber et al. 2013b, 2016; Garrido et al. 2015). Similarly, in a cool summer the later cohort can take advantage of maximal growth conditions to converge on the first cohort (Sogard 1997), but in a warm summer thermal maxima may be reached, reducing growth, even as age-0 fish become more thermally tolerant with age (Sogard and Able 1992; Manderson et al. 2002).

Winter Flounder in Long Island bays frequently experience thermal conditions exceeding the range that is physiologically optimal (consistently $>27^{\circ}\text{C}$; McCracken 1963), whereas individuals that were spawned offshore may be relatively protected from extreme thermal conditions (Phelan 1992; Wuenschel et al. 2009; Wilber et al. 2013a; Fairchild

2017; Siskey 2020). Winter Flounder settling in estuaries earlier in the spring may be able to maintain optimal growth rates for a longer period of time before water temperatures increase to detrimental levels. The production of multiple cohorts may ensure that productivity is sustained despite interannual variability in the phenology of the system. Our results suggest that early and late cohorts partitioned physicochemical habitat, occupying different depths and ranges of dissolved oxygen during the same time period. We found that smaller individuals from late cohorts in 2016 occupied areas with significantly lower dissolved oxygen than their larger counterparts, which may account for the lower growth rates in late season cohorts. Exposure to dissolved oxygen of 5.0 mg/L at 20°C , similar to conditions encountered in the field during the present study, reduced growth by 50% in laboratory trials (Stierhoff et al. 2006). Smaller fish may also make use of habitat with relatively low dissolved oxygen to avoid competition with larger conspecifics (Taylor et al. 2016), to take refuge from predators (Froeschke and Stunz 2012), or because it is associated with high organic matter sediments, which juveniles and newly settled age-0 prefer (Stoner et al. 2001; Wilber et al. 2013b). Finally, late season cohorts were associated with shallower areas than their early season counterparts, in agreement with previous findings that smaller flatfish tend to occupy shallower areas (Sogard and Able 1992; Gibson et al. 2002; Ryer et al. 2010; Amorim et al. 2018).

Winter Flounder demonstrate a high plasticity in growth rates during their early life history that could impact our ability to identify and track cohorts throughout the season (Sogard and Able 1992; Bertram et al. 1993; Yencho et al. 2015). Annual variation in environmental conditions influences the growth of age-0 fish settled at different periods of a given year (Gallagher et al. 2015). This may influence the relative growth rates of cohorts, leading to overlapping size distributions late in the season (Yencho et al. 2015). Exceptionally cool winters may delay metamorphosis for early cohorts, shortening the gap in the timing of settlement between early and late season pulses, which could obscure the ability to detect cohorts (Laurence 1975; Sogard 1992; Sogard et al. 2001; Wilber et al. 2016). Therefore, we limited our cohort designation to weeks when both cohorts were clearly delineated. Additionally, the earlier cohort recruited to the gear at a larger size than latter cohorts in all cases except Shinnecock Bay in 2016, possibly indicating that we did not start sampling early enough in 2017 or in Mattituck Creek in 2016 to initially identify cohorts. Gallagher et al. (2015) found a switch from a negative to a positive relationship between settlement date of age-0 Winter Flounder and growth that varied between years. These factors make it difficult to identify cohorts and ultimately isolate cohort-specific growth and mortality rates. However, evidence provided in this research suggests that cohorts can

be identified and that significant differences in rates of growth and mortality were detected.

High rates of postsettlement mortality have been proposed as a critical recruitment bottleneck factor suppressing recovery of Winter Flounder in Long Island bays (Gallagher et al. 2015; Yenko et al. 2015; Frisk et al. 2018). Natural mortality rates for age-0 Winter Flounder ranged from 0.019 ± 0.016 (mean \pm SE) in Napeague Harbor in 2010 to 0.077 ± 0.017 in Shinnecock Bay in 2017. Estimates of mortality fell within the range of published estimates for the SNE/MA region (Meise et al. 1999; Yenko et al. 2015); the lower bound is 0.01–0.03 in the Connecticut River and New Haven, Connecticut, and the highest is 0.083 ± 0.02 in Shinnecock Bay, New York. During the years of our study, we did not find unusually high mortality during the first summer season following settlement. Natural mortality rates were not significantly different between sites. Comparisons between bays were hindered by low statistical power, likely due to uncertainty associated with estimating mortality utilizing survey-based abundance approaches. However, consistent mortality estimates across bays could also be a symptom of climate-driven synchronization of nursery production (Manderson 2008) and/or trophic interactions with other species that are more directly impacted by climate (Liebhold et al. 2004; Able et al. 2014; Taylor et al. 2019). To the latter point, predation mortality on age-0 Winter Flounder in Long Island bays can be up to six times greater than other causes of natural mortality (Dolan 2020). Summer Flounder *Paralichthys dentatus* may consume up to ~60% of the age-0 Winter Flounder within the immediate area during peak settlement (Taylor et al. 2019).

We posit that the fine-scale spatiotemporal variation in growth and survival regimes shown in this study could potentially translate to recruitment variation across Long Island bays. Basic forms of the stock–recruitment relationship assume that external drivers (e.g., temperature, dissolved oxygen, predation, fishing) act uniformly across the range of the stock. However, this assumption is contravened by evidence from multiple species of flatfish, including Winter Flounder, showing growth and mortality that is habitat specific and/or temporally varying (for Winter Flounder specifically: Sogard and Able 1992; Phelan et al. 2000; Sogard et al. 2001; Wilber et al. 2013b; Gallagher et al. 2015; for flatfish generally: Miller et al. 1991; Van der Veer et al. 2000; Archambault et al. 2014). Variability in growth rate, as we found between bays, mediates recruitment through size-selective mortality (during early life) and/or by means of size-dependent onset of maturation (Van der Veer et al. 1994). Differences in growth and survival across space are another potential manifestation of bet-hedging. The use of alternate habitats provides a buffer from perturbations (e.g., natural disasters or storms) or years of environmental conditions that are unfavorable for recruitment success (Schindler et al. 2015). Recruitment trends and overall productivity in

SNE/MA Winter Flounder has differed between inshore coastal bay (age-0) and ocean (age-1) surveys, with recruitment increasing in estuaries but decreasing in ocean surveys during the 2000s (Frisk et al. 2018). Furthermore, warmer thermal regimes are associated with decreased interannual variation and increased spatial synchrony of Winter Flounder recruitment (Manderson 2008; Able et al. 2014; Siskey 2020). The study of intraspecific heterogeneity in growth and mortality rates therefore has implications for predicting how populations will respond to environmental change.

Future research focusing on connecting growth and mortality to seasonal productivity could advance the understanding of bet-hedging strategies and regional stock resilience. Specifically, a study might simulate the effects of spatiotemporally varying growth at different scales to understand the influence of the scale of variation of recruitment drivers when parameterizing the stock–recruitment function. The present study focused on bays in Long Island, New York. Data from additional locations throughout the range of Winter Flounder, spanning multiple years, would facilitate evaluation of how the phenomena of bet-hedging contributes to short-term and longer-term regional stock productivity and resilience. Growth, mortality, and environmental metrics could be evaluated as drivers of productivity, measured as recruits per spawner and each location's contribution to regional stock dynamics.

We were able to estimate age-0 mortality and growth across six systems and for separate cohorts in two study systems. Together, the results suggest that vital rates differ between study locations and over the course of a season. These differences are driven by locally variable growth rates and the presence or absence of secondary settlement pulses. Bays that produced multiple cohorts had extended periods of high age-0 abundance, even when mortality rates were the same. Early and late cohorts may partition habitat to reduce competition and improve growth and survival outcomes. Each system, to some degree, may have a differing likelihood of recovering stocks. Given the current understanding of population complexes in Long Island bays, managers might seek to implement precautionary “weakest link” conservation approaches to restoring inshore populations (Kerr et al. 2017). Effort should be made to understand what factors allow certain nursery areas to produce a secondary cohort and the relative contribution of each location to the productivity of inshore stocks. Experimental manipulations could be used to understand the time-varying nature of environmental drivers of survival and growth. Further research on connectivity between Long Island bays and offshore (ocean-spawned) stocks, and vital rates of the latter, are needed to understand the ability of these offshore habitats to provide a rescue effect. Our finding of spatially and temporally variable vital rates must be connected to a more thorough understanding of metapopulation structure in the region to reveal their role in mediating recruitment dynamics.

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ORCID

Tara E. Dolan,  <https://orcid.org/0000-0003-0937-0342>

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.