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ARTICLE

# Growth and Mortality in Coastal Populations of Winter Flounder: Implications for Recovery of a Depleted Population

**Melissa A. Yencho**

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

**Adrian Jordaan**

*Department of Environmental Conservation, University of Massachusetts Amherst, Holdsworth Hall, Amherst, Massachusetts 01003, USA*

**Robert M. Cerrato**

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

**Hannes Baumann**

*Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, Connecticut 06340-6048, USA*

**Michael G. Frisk\***

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

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## Abstract

We studied growth, mortality, and settlement distributions of juvenile Winter Flounder *Pseudopleuronectes americanus* in two bays of Long Island, New York, to better understand localized population dynamics of a species experiencing a protracted population decline. Juvenile mortality in Long Island bays ranged between 0.02 and 0.04 per day and was as high as or higher than values reported for other systems. Settlement distributions had multiple peaks (cohorts) occurring between March and late July in 2007 and between February and May in 2008. The presence of multiple cohorts limited the usefulness of field-derived, length-based estimates of growth, resulting in unrealistic values compared with otolith-based measures (field based:  $-0.05$  to  $0.25$  cm/d; otolith based:  $0.05$ – $0.06$  cm/d). Thus, we recommend the use of otolith methods or the repeated measurement of individuals to estimate growth of juvenile Winter Flounder. Otolith-based growth rate was significantly higher for Port Jefferson Harbor during 2007 than for all other year  $\times$  location combinations. Together with previous research showing genetic differentiation and migratory diversity, our finding of multiple spawning cohorts in Long Island Winter Flounder suggests a degree of isolation, and local management will be needed to support healthy populations. Future research

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\*Corresponding author: [mfrisk@notes.cc.sunysb.edu](mailto:mfrisk@notes.cc.sunysb.edu)

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to determine adult spawning, migratory behavior, stock structure, duration of the larval period, and settlement timing is required to unravel the complex behavior of Winter Flounder.

The Winter Flounder *Pseudopleuronectes americanus* is a right-eyed flounder that is found in coastal waters from Labrador, Canada, to Georgia, USA, but it is most common between Nova Scotia, Canada, and Delaware, USA (Klein-MacPhee 2002). Winter Flounder populations in the northeastern USA have a history of supporting recreational and commercial fisheries in federal waters (Brown and Gabriel 1998) and in non-federal waters (e.g., Long Island, New York, bays) since the early 1900s (Lobell 1939). However, a 2008 stock assessment placed the southern New England–Mid-Atlantic Bight population at 9% of the management target, and a closure was enacted in federal waters south of Cape Cod to support rebuilding of the stock (NEFSC 2008). Coincidentally, fishery catches and abundance indices of Long Island bay populations have declined by more than an order of magnitude since the 1980s (Figure 1), and Winter Flounder are nearly absent from areas that once supported active fisheries (Socrates and Colvin 2006; Sagarese 2009; O’Leary et al. 2013).

In addition to the documented overfishing, other causes of Winter Flounder population declines have been hypothesized, including targeted fishing of spawning adults, environmental change, and increased predation by crustaceans and finfishes (Fairchild and Howell 2000; Keller and Klein-MacPhee 2000; Manderson et al. 2000; Taylor 2004; Scharf et al. 2006). Despite declines in the adult populations targeted by fisheries, abundance and length frequency data from a seining survey conducted by the New York State Department of Environmental Conservation indicated that production of newly settled young-of-the-year (age-0) Winter Flounder in Long Island estuaries remained relatively stable during the initial population decline in the 1990s (Socrates and Colvin 2006; Yencho

2009). It appears that postsettlement mortality constrained recruitment to the adult stock to near zero and produced a bottleneck during the first year of life. Therefore, high postsettlement mortality within Long Island bays may be an important factor limiting population recovery.

According to the traditional life history model of Winter Flounder, adults migrate from deeper offshore waters into inshore estuarine habitats for spawning in winter and then move back offshore during the spring (Lobell 1939; Perlmutter 1947; Van Guelpen and Davis 1979; Collette and Klein-MacPhee 2002). However, historical evidence suggests a more complex population structure in Long Island bays, consisting of distinct behavioral groups termed resident “bay fish” and migratory “ocean fish” (Lobell 1939; Perlmutter 1947). Homing and fine-scale population structuring in Winter Flounder have been observed before (Saila 1961; Buckley et al. 2008; O’Leary et al. 2013), and recent tagging evidence suggests that some fish exhibit persistent residency in inshore estuarine habitats (DeCelles and Cadrin 2010; Sagarese and Frisk 2011).

Our overall goal was to better understand the growth, mortality, and settlement behavior of Winter Flounder in Long Island bays. Specifically, we used relative abundance and otolith microstructure in age-0 Winter Flounder to estimate (1) growth and mortality and (2) settlement date distributions. We discuss our results in the context of recovering depleted populations, and we explore the implications of population structuring and field-based approaches for estimating growth.

## METHODS

**Study locations.**—Age-0 Winter Flounder were obtained from two Long Island bays: Port Jefferson Harbor (PJ) and Shinnecock Bay (SB; Figure 2). The two areas differ in habitat type, temperature regime, and depth profile. Port Jefferson Harbor is connected to Long Island Sound and is a deep, well-stratified bay with a coolwater refuge during the summer months. The PJ coastline is primarily rocky and gravelly, with patches of soft bottom and vegetation. In contrast, SB is directly connected to the Atlantic Ocean and is a shallow, vertically mixed bay with little temperature refuge during the warm summer months.

**Sampling regime.**—Field sampling was conducted between March and November 2007 and between May and November 2008 (Figure 2). In 2007, a beach seine (61 × 3 m; 6-mm mesh) was used in PJ and SB. In addition, a smaller beach seine (30 × 3 m; 6 mm mesh) was occasionally used and was assumed to sample half the area relative to the larger net. The small net was not used to describe

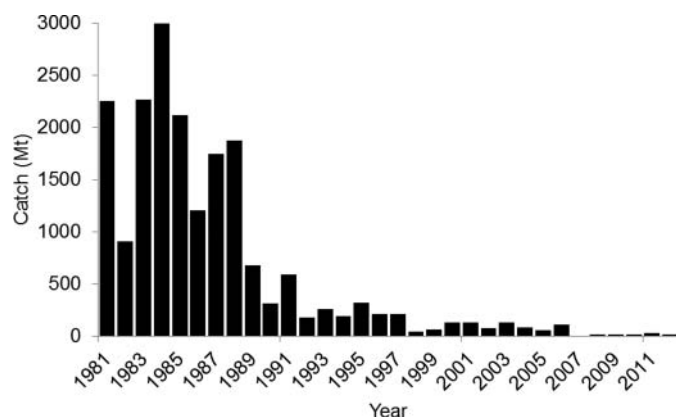


FIGURE 1. Estimates of Winter Flounder recreational catch (metric tons [mt]) in New York's inland waters (NOAA 2012).

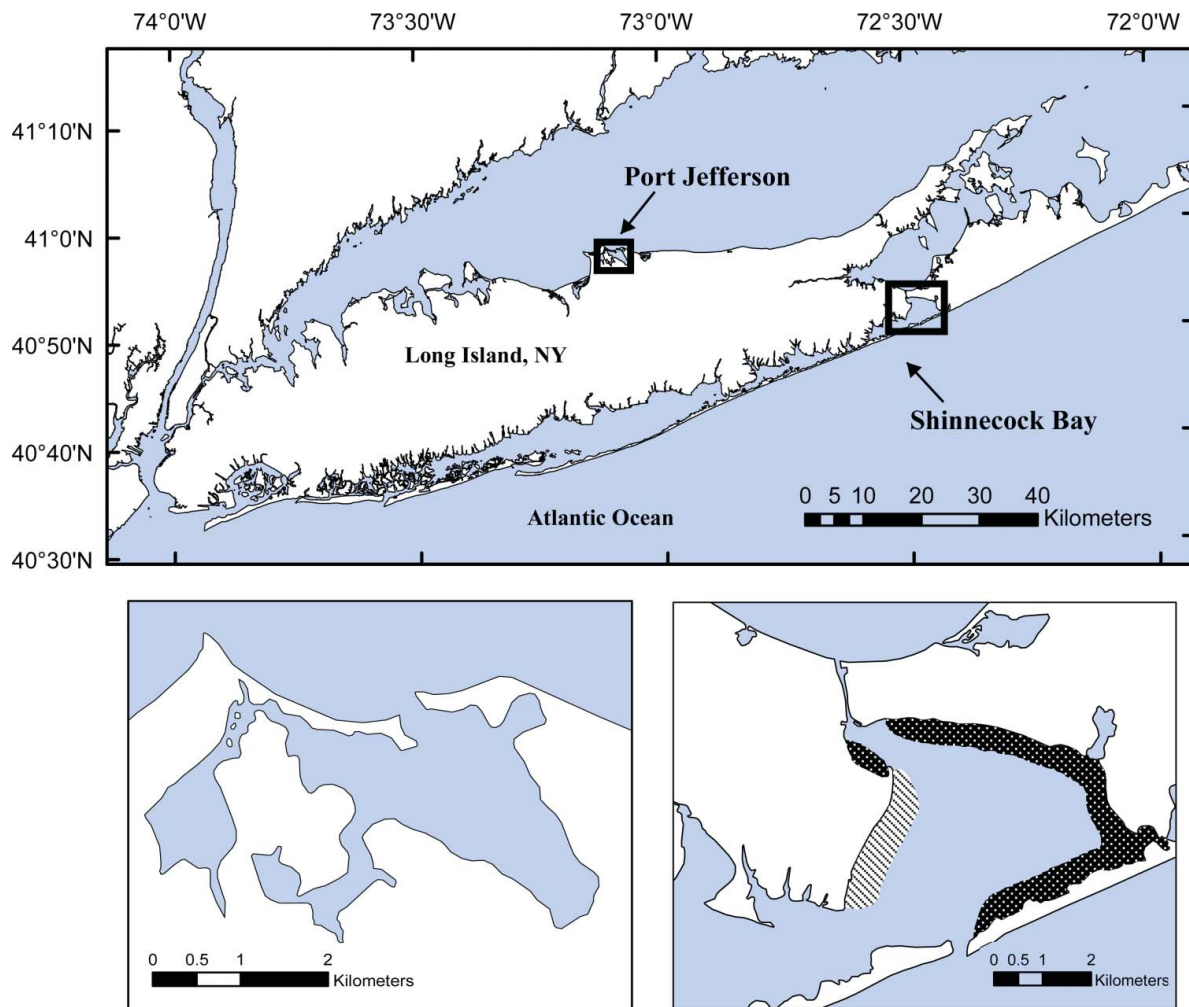


FIGURE 2. Winter Flounder sampling locations in Port Jefferson Harbor (bottom left panel) and Shinnecock Bay (bottom right panel), Long Island, New York. Beam-trawl sampling covered the entire area of Port Jefferson Harbor. For Shinnecock Bay, the gray hatched portion represents the sampling area used in both 2007 and 2008; the dark stippled area indicates the additional area sampled in 2008.

the “descending segment” of relative abundance used in mortality estimation (see description of catch-curve analysis below). However, it was used for results pertaining to beach seining conducted in SB on April 26, May 22, June 5, and June 19, 2007. The smaller seine had a design identical to that of the large net and was assumed to have similar selectivity. It is possible that the shorter offshore reach of the smaller net resulted in the sampling of a smaller proportion of the population; however, results were very similar for the two nets. Beach seining in PJ and SB was conducted every other week during 2007 and monthly during 2008. A single pull of the net was completed at each sampling station; the stations were randomly selected based on 500-m intervals along the perimeter of each bay. All captured Winter Flounder were enumerated, and the TL of each fish was measured to the nearest millimeter.

In 2007, a 1-m beam trawl (6-mm mesh) was utilized to sample known Winter Flounder habitat within SB (Figure 2).

Three-minute tows were conducted at stations that were randomly selected from a grid of equal-sized cells. Preliminary analysis of the 2007 SB beam-trawling data suggested that this method provided better survey estimates than beach seining; thus, beam trawling was expanded in 2008 to cover the entire area of PJ and to include nearshore habitat throughout SB (Figure 2). Consequently, seining was reduced to once per month for both bays in 2008. The CPUE was calculated to estimate relative abundance. Effort was defined as one pull of the large seine and as minutes towed for beam trawling. The objective was to successfully sample 7–12 stations/d via seine or beam trawl, but weather and other issues sometimes prevented completion of sampling at the desired number of stations.

Catch-curve analysis was employed to estimate mortality (Quinn and Deriso 1999) of Winter Flounder for each year, bay, and gear type. Values of relative abundance ( $\log_e \text{CPUE}$ ) were plotted over time, resulting in a piece-wise linear

relationship with two segments. The ascending segment represents increasing selectivity to the gear until full selectivity is reached at the peak. The descending segment beyond the peak represents losses resulting from natural mortality (Quinn and Deriso 1999). Relative abundance data were corrected for selectivity by using

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

where  $s_x$  is selectivity for length interval  $x$ ;  $g$  is the shape parameter;  $l$  is fish length; and  $l_h$  is the length at 50% selectivity. The descending segment of relative abundance (corrected for selectivity) was regressed against time to estimate the slope (instantaneous mortality  $M$ ). The parameters were estimated by minimizing the sum of squares for all catch data using Solver in Microsoft Excel 2007 (Microsoft Corporation). The selectivity correction was applied to the number of fish in each length-class and was used to estimate relative abundance. Several steps were taken to ensure that spawning and settlement had ended at the time indicated by the peak of the catch-curve (i.e., that no newly recruited age-0 fish were entering the sampling areas after selectivity was reached). First, length frequency data obtained on dates before and after the peak were compared to determine when settlement had ended. Second, fish larger than 10 cm were excluded from early dates (since that size indicates an age greater than 1 year for fish in the Long Island region).

Two growth rate estimates were calculated: one derived from length data and another derived from otolith-based age-length relationships. Growth rates from length data were calculated by taking the difference between average lengths obtained from sampling dates over time,

$$G = \frac{L_2 - L_1}{t_2 - t_1},$$

where  $L_2$  is the average length at time  $t_2$ ; and  $L_1$  is the average length at time  $t_1$ . Growth rates were estimated for intervals between sampling events and were expressed in centimeters per day. Otolith-derived growth rate estimates were obtained from linear regressions of TL against the daily age (days post-settlement) estimated from daily increment counts (Sogard and Able 1992). Slope estimates yielded the growth rate in centimeters per day.

**Otolith preparation.**—The total numbers of sagittal otoliths processed for aging were 87 and 88 from SB Winter Flounder (2007 and 2008 samples, respectively) and 76 and 82 from PJ fish. Otoliths were dissected and the remaining tissue was removed by using a Nikon Eclipse 80i dissection microscope; the otoliths were then dried for 24 h on glass slides. After drying, cyanoacrylate glue was used to affix each otolith to a clean slide. Otoliths were polished in the sagittal plane with

30- and 3-micron lapping film (3M) until the micro-increments between the secondary primordia (a proxy for settlement; Sogard 1991) and the otolith edge were sufficiently discernible. Postsettlement ages were determined from calibrated photographs of the polished otoliths (Nikon Model DX1200C digital camera attached to a compound microscope) by marking and counting the micro-increments that had formed outward of the secondary primordia (Image Pro-Plus version 6.0; Media Cybernetics). Micro-increments were assumed to form daily (Sogard 1991). Each otolith was read three times, and each reading was given a qualitative measure of reliability ranging from 1 (least confidence in reading) to 5 (most confidence in reading). Within- and between-reader aging precision was estimated using average percent error (APE; Campana and Jones 1992),

$$\text{APE}_j = 100 \cdot \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - \bar{X}_j|}{\bar{X}_j},$$

where  $X_{ij}$  is the  $i$ th reading for the  $j$ th fish;  $R$  is the number of readings; and  $\bar{X}_j$  is the mean of readings for the  $j$ th fish (Campana 2001). Within-reader APE was calculated based on all otoliths read, and a random subsample of 17 otoliths was examined by an independent reader to estimate between-reader APE (Frisk and Miller 2006).

**Statistical analysis of growth and mortality.**—Likelihood ratio tests were used to examine the coincidence of linear regressions for mortality and growth models. The tests compared an overall relationship (i.e., with a common slope, intercept, and variance) to a relationship based on individual models for each location and year. The procedure tested the null hypothesis that linear relationships were derived from a common data population, and the test statistic was compared with a chi-square distribution. Significant differences were further evaluated by using Tukey's honestly significant difference (HSD) test. Additionally, mortality and growth rate estimates were compared with previously published values for Winter Flounder.

**Settlement date analysis.**—Estimates of individual age and daily instantaneous mortality were used to evaluate the strength of settlement throughout the season. The analysis assumes that mortality is constant from the date of settlement until the date of capture; the approximate timing and magnitude of settlement are determined. Abundance at settlement ( $N_s$ ) was calculated as

$$N_s = N_c \cdot \exp^M,$$

where  $N_c$  is the relative abundance at capture; and  $M$  is the cumulative instantaneous mortality from settlement to capture. Relative abundance at settlement was estimated by using selectivity-corrected catch values. A modal analysis was performed to determine the modes of cohorts or spawning cycles. The analysis utilized maximum likelihood to fit a multinomial

distribution of expected frequencies to the observed settlement frequencies by fitting the mean ordinal date ( $x$ ), variance ( $\sigma^2$ ), and height ( $h$ ) of the distributions (Hastings and Peacock 1975; Haddon 2001). Modal analysis assumes that each detected mode is normally distributed and corresponds to a separate discrete cohort or settlement group. Both statistical interpretation (Akaike's information criterion [AIC]) and biological interpretation of trends were used as criteria to identify cohorts.

## RESULTS

### Sampling

During 2007, seining was conducted on a total of 7 d in PJ and on 10 d in SB (Table 1); the number of seining stations per sampling day ranged between 5 and 12 (mean = 8 stations) for PJ and ranged between 2 and 12 (mean = 7 stations) for SB. During 2008, seining was conducted on 5 d in PJ and on 4 d in SB. The number of stations seined per sampling day ranged between 8 and 11 (mean = 10 stations) for PJ and ranged between 6 and 10 (mean = 8 stations) for SB. Length frequencies showed one or more cohorts that were first captured by beach seining at approximately 2–3 cm TL and that reached 7–9 cm TL by autumn (Figure 3).

Beam trawling was conducted in SB during 2007 and in both PJ and SB during 2008. In SB during 2007, beam-trawl samples were collected on 12 d (Table 1); the number of locations per sampling day ranged between 7 and 19 (mean = 16 trawl locations). In 2008, beam trawling was conducted on 9 d in PJ and 10 d in SB. The number of locations per sampling day ranged between 7 and 19 (mean = 16 trawl locations) for PJ and ranged between 6 and 21 (mean = 16 trawl locations) for SB. Length frequencies showed one or more cohorts that were first captured by beam trawling at approximately 2.5–4.5 cm TL and that reached 7–9 cm TL by autumn (Figure 4).

### Mortality

Gear selectivity parameters were estimated for beach seining ( $lh = 4.97$ ;  $g = 0.95$ ) and beam trawling ( $lh = 5.05$ ;  $g = 1.30$ ) and were used to correct abundance estimates. In 2007, new settlement of age-0 fish had stopped and full selectivity had occurred on July 5 and July 3 for seining in PJ and SB, respectively, and on July 2 for beam trawling in SB. In 2008, new settlement of age-0 individuals had ended and full selection to the gear took place on July 8 and July 21 for beam trawling in PJ and SB, respectively. Relative abundance declined at all locations after selection to the gear (Figure 5). Values of  $M$  ranged from 0.02 to 0.04 per day (Table 2). Calculation of  $M$  was not possible for 2008, as too few age-0 Winter Flounder were caught by beach seines in either PJ or SB. A likelihood ratio test for coincident regressions indicated that mortality was not statistically different between locations and years ( $P > 0.459$ ). Raw and selectivity-corrected relative abundance data are provided in the Supplement (available online).

### Growth

The APE for within-reader precision in estimating daily increments was 5.6% ( $n = 163$ ) for 2007 and 4.7% ( $n = 170$ ) for 2008. Between-reader precision was 5.1% ( $n = 17$ ). Significant length–age relationships were found for both locations in both years, and otolith-derived growth rates ranged from 0.05 to 0.06 cm/d (Figure 6; Table 3). A likelihood ratio test of coincident regressions was significant ( $P < 0.001$ ), and multiple comparisons indicated that the otolith-derived growth rate for PJ during 2007 was significantly higher than those for all other year  $\times$  location combinations (Tukey's HSD test:  $P < 0.001$ ; Table 4). No other differences in otolith growth rate were observed between years or between locations (however, the difference between PJ and SB in 2008 was nearly

TABLE 1. Summary of catch and sampling effort for age-0 Winter Flounder collected from Port Jefferson Harbor (PJ) and Shinnecock Bay (SB), Long Island, New York. The CPUE is expressed as number of individuals per seine haul for beach seine data and number of individuals per minute towed for beam-trawl data; CPUE estimates are based on days when age-0 fish were captured (not on the total number of sampling days).

Gear type	Location	Year	Number of sampling days	Number of tows	Time towed (min)	Total number of age-0 fish	CPUE
Beach seine	PJ	2007	7	89		679	17.42
	PJ	2008	5	48		48	1.92
	SB	2007	10	52.5		202	7.7
	SB	2008	4	32		114	5.88
Beam trawl	PJ	2008	9	163	494	63	0.23
	SB	2007	12	98	352	358	1.53
	SB	2008	10	174	527	68	2.13
Total						1,532	

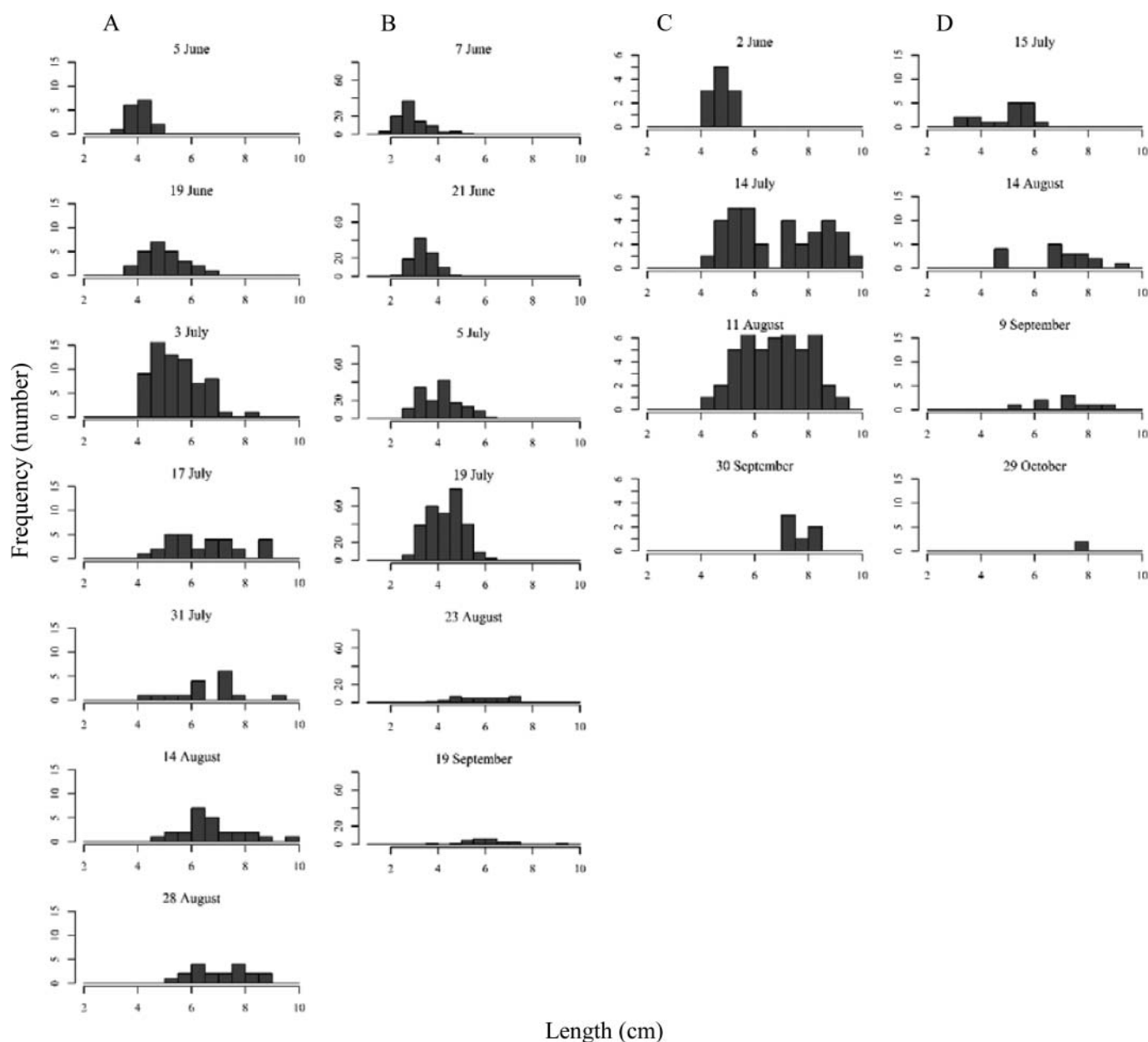


FIGURE 3. Length frequency histograms (cm TL) for age-0 Winter Flounder sampled by beach seining in (A) Shinnecock Bay during 2007, (B) Port Jefferson Harbor during 2007, (C) Shinnecock Bay during 2008, and (D) Port Jefferson Harbor during 2008. Note that individuals greater than 10 cm were excluded, as were dates when no Winter Flounder were captured (Port Jefferson Harbor: May 10, 2007, and July 3, 2008; Shinnecock Bay: April 24, April 26, and May 22, 2007).

significant:  $P = 0.054$ ). Field-derived growth rates were highly variable and in some cases unrealistic, ranging from  $-0.25$  to  $0.12$  cm/d throughout the season (Table 5). As a result, no statistical comparisons were made using field-derived growth estimates.

### Settlement Date

Modal analyses of PJ data indicated that mean peak settlement occurred during late April and early May in 2007, with

smaller peaks occurring at the end of May and at the end of July (Figure 7A). The three-mode model had the lowest AIC value (i.e., best performance) and matched observed trends more consistently than the two-mode and one-mode models. For PJ in 2008, only a single-mode model was fitted after visual inspection, and settlement was estimated to occur between March and May (Table 6; Figure 8A).

Modal analyses for SB in 2007 indicated that mean peak settlement occurred in late March and April, a smaller peak was present during May, and settlement also took place during

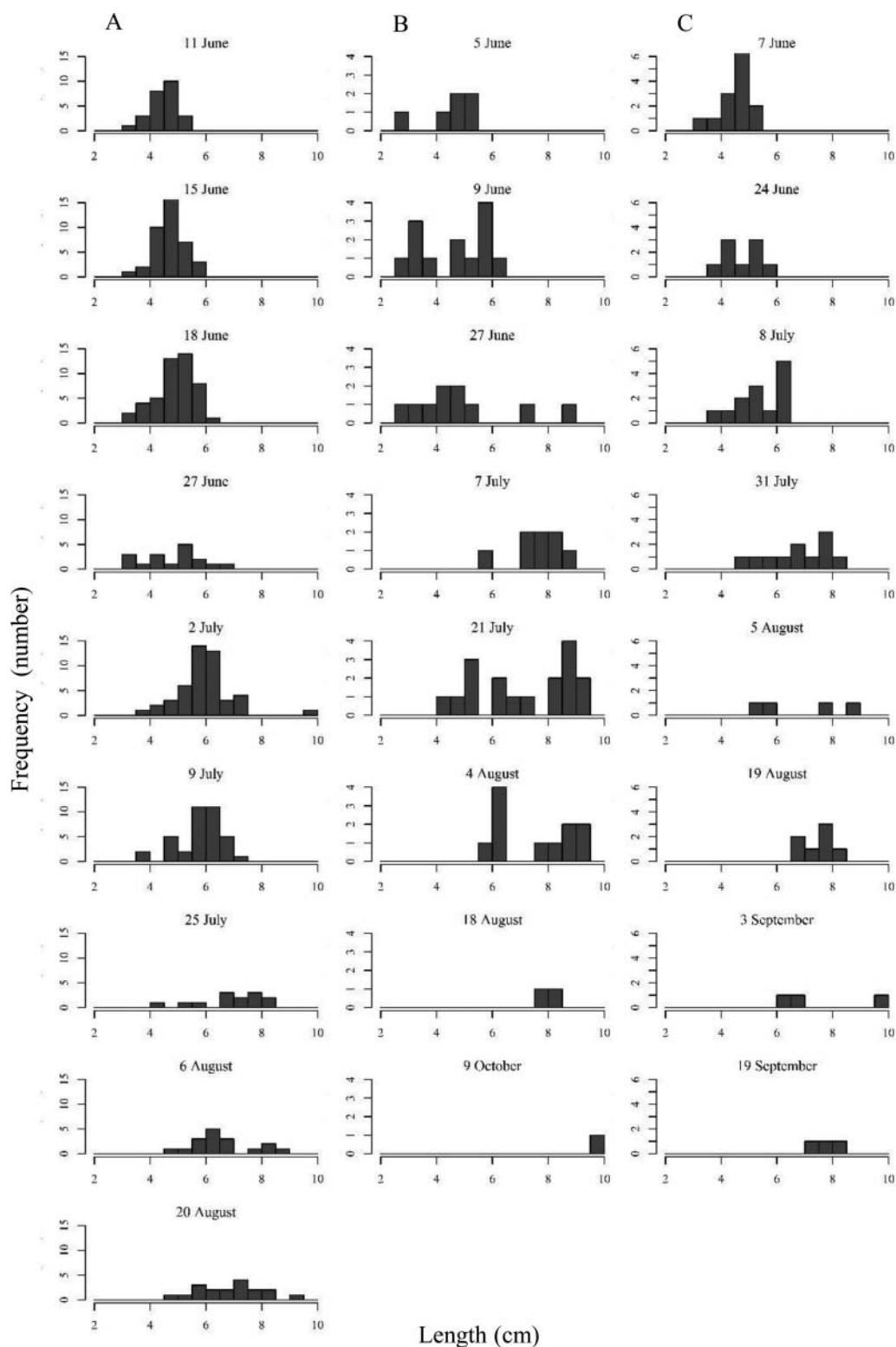


FIGURE 4. Length frequency histograms (cm TL) for age-0 Winter Flounder sampled by beam trawling in (A) Shinnecock Bay during 2007, (B) Shinnecock Bay during 2008, and (C) Port Jefferson Harbor during 2008. Note that individuals greater than 10 cm were excluded, as were dates when no Winter Flounder were captured (Port Jefferson Harbor: May 24, 2008; Shinnecock Bay: June 6, 2007; September 28 and October 25, 2007 [when only two fish were captured]; and April 29 and May 13, 2008).



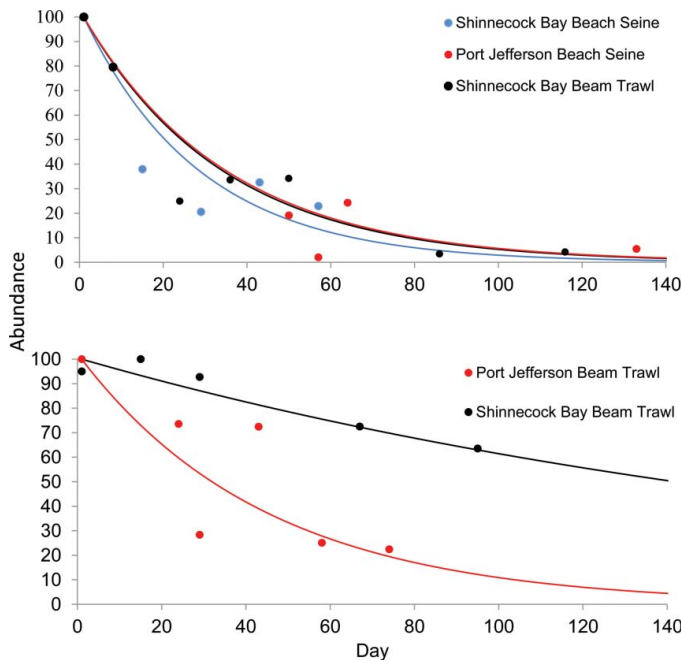


FIGURE 5. Changes in estimated relative abundance during the first 140 d postsettlement for age-0 Winter Flounder in Long Island bays: (upper panel) 2007 and (lower panel) 2008. Using the projection equation  $N_t = N_0 e^{-Mt}$ , the number of fish on day  $t$  ( $N_t$ ) was estimated relative to an initial abundance of 100 individuals ( $N_0$  = day of settlement;  $M$  = mortality rate estimated from catch-curves).

July and August (Figure 7B; Table 6). The three-mode model had the lowest AIC in comparison with the two-mode and one-mode models (Table 6). For SB data from 2008, visual inspection suggested that only one mode was likely, so the two- and three-mode models were not attempted. Settlement in 2008 occurred between late February and early May (Table 6; Figure 8B).

### Comparison with Published Growth and Mortality Rates

Estimates of Winter Flounder mortality were similar to or within the higher range of estimates from research previously conducted in Connecticut and Rhode Island (Table 5). Growth rate estimates in the present study were within the range of or lower than field- and otolith-derived measures from other studies (Table 5).

### DISCUSSION

The population dynamics of age-0 Winter Flounder were investigated in response to the species' dramatic decline in abundance along the coast of Long Island. Mortality rates in the present study were within the range estimated for Winter Flounder in the Connecticut River and New Haven Harbor during the late 1990s (Meise et al. 1999) and also coincided with the upper range of estimated  $M$  for Rhode Island

TABLE 2. Statistical analysis of catch-curve results for Winter Flounder sampled from Shinnecock Bay and Port Jefferson Harbor, Long Island ( $n$  = number of sampling days;  $M$  = daily instantaneous mortality rate; L95% = lower 95% confidence limit of  $M$ ; U95% = upper 95% confidence limit of  $M$ ;  $y$  = y-intercept).

Gear type	Year	$n$	$M$	L95%	U95%	$y$	$r^2$	$F$	$P$
<b>Shinnecock Bay</b>									
Beam trawl	2007	7	-0.03	-0.04	-0.02	1,169.95	0.89	36.06	0.002
Beach seine	2007	5	-0.04	-0.06	-0.01	1,406.57	0.90	21.92	0.018
Beam trawl	2008	4	-0.03	-0.07	0.01	1,372.15	0.90	17.19	0.053
<b>Port Jefferson Harbor</b>									
Beach seine	2007	6	-0.03	-0.07	0.01	1,141.09	0.52	4.26	0.108
Beam trawl	2008	6	-0.02	-0.04	-0.01	884.98	0.68	8.77	0.041

TABLE 3. Otolith-derived growth rates ( $G$ , cm/d; i.e., slope value) for Winter Flounder sampled from Shinnecock Bay and Port Jefferson Harbor, Long Island ( $n$  = number of observations; L95% = lower 95% confidence limit of  $G$ ; U95% = upper 95% confidence limit of  $G$ ;  $y$  = y-intercept).

Year	$n$	$G$	L95%	U95%	$y$	$r^2$	$F$	$P$
<b>Shinnecock Bay</b>								
2007	87	0.05	0.05	0.06	1.2	0.64	152.33	<0.001
2008	88	0.05	0.046	0.06	1.1	0.65	162.64	<0.001
<b>Port Jefferson Harbor</b>								
2007	76	0.06	0.05	0.07	-0.03	0.67	149.57	<0.001
2008	82	0.05	0.04	0.06	1.6	0.69	178.81	<0.001

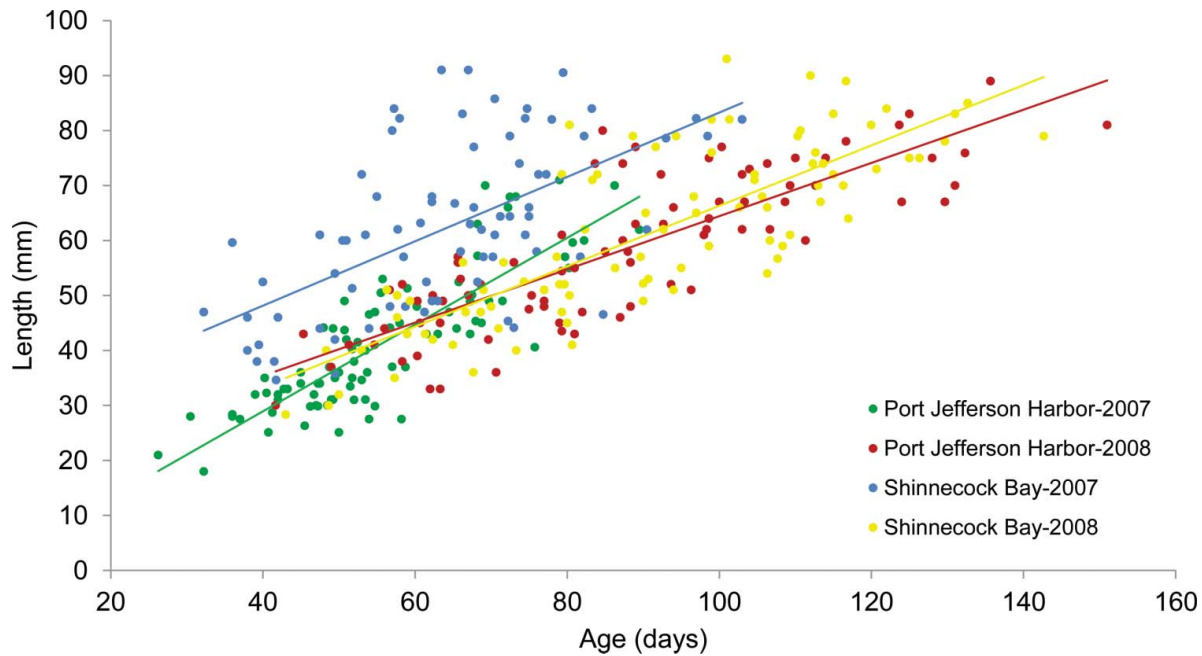


FIGURE 6. Otolith-derived growth rates of age-0 Winter Flounder sampled from Port Jefferson Harbor and Shinnecock Bay, Long Island, during 2007 and 2008. The only significant difference in growth rates was a higher value for Port Jefferson Harbor in 2007 than for all other year  $\times$  location combinations ( $P < 0.001$ ; see Table 4).

(DeLong et al. 2001) but were much higher than estimates for the Niantic River, Connecticut, and the Mystic River estuary, Connecticut (Pearcy 1962; Rose et al. 1996). In contrast, growth rates of Long Island Winter Flounder were within the range of or lower than estimates reported for other populations. Although our estimates of vital rates were within the range of previous estimates, it is difficult to gauge population health without the availability of historical baselines for Long Island Winter Flounder. Productivity of the Long Island coastal populations may not be high enough to promote recovery; therefore, research addressing a wider range of life history stages is needed.

There is little doubt that Winter Flounder inhabiting Long Island bays are in a depleted state, and a recent genetic analysis has detected inbreeding (O'Leary et al. 2013). For depleted populations, it is particularly pressing to understand which

factors might suppress recruitment and therefore which management options are potentially most conducive to stock recovery. Mortality of age-0 Winter Flounder is affected by a suite of environmental variables, including prey availability, density of intraspecific and interspecific competitors, temperature, salinity, dissolved oxygen, pollution, and the presence of physical structures in nursery grounds (Sogard 1991; Bejda et al. 1992; Able et al. 1999; DeLong et al. 2001; Meise et al. 2003). Although many potential impediments to recovery exist, predation on age-0 Winter Flounder is a likely cause of the higher  $M$  observed in our study relative to studies in the Niantic River and the Mystic River estuary. Migratory predators originating from other systems can act as subsidized consumers in that population productivity is decoupled from local drivers (*sensu* Polis et al. 1997). For example, the Striped Bass *Morone saxatilis* is a migratory generalist predator with consumption rates that can exceed local prey resources (Hartman and Margraf 2003). Even low individual predation rates by predators at high abundance can lead to substantial mortality of depleted Winter Flounder populations. Summer Flounder *Paralichthys dentatus* and Bluefish *Pomatomus saltatrix* have been shown to consume age-0 Winter Flounder (Manderson et al. 2000, 2004; Sagarese et al. 2011) and may represent a substantial source of mortality for age-0 fish (Nuttall et al. 2011). Thus, recovered populations of piscivorous predators are potentially impeding the recovery of resident Winter Flounder populations in the Long Island region. Additional research is needed to estimate age-0 Winter Flounder consumption by finfish species

TABLE 4. Results ( $P$ -values) from Tukey's honestly significant difference tests comparing otolith-derived growth rates of age-0 Winter Flounder sampled from Port Jefferson Harbor (PJ) and Shinnecock Bay (SB), Long Island, during 2007 and 2008.

Location and year	PJ 2007	SB 2007	PJ 2008
PJ 2007			
SB 2007	<0.001		
PJ 2008	<0.001	0.054	
SB 2008	<0.001	0.963	0.145

TABLE 5. Comparison of daily mortality ( $M$ ) and growth rate ( $G$ ) estimates for age-0 Winter Flounder. To facilitate comparison across studies, values of  $M$  were converted to daily rates, and values of  $G$  were converted to centimeters per day.

Study	Location	$M$ ( $d^{-1}$ )	Field $G$ (cm/d)	Otolith $G$ (cm/d)
Present study, 2007	Shinnecock Bay, New York	0.03–0.04	–0.2	0.05
Present study, 2007	Port Jefferson Harbor, New York	0.03	–0.06	0.06
Present study, 2008	Shinnecock Bay	0.04	–0.25	0.05
Present study, 2008	Port Jefferson Harbor	0.02	0.01–0.12	0.05
Pearcy 1962	Mystic River estuary, Connecticut	0.01		
Meise et al. 1999	Connecticut River and New Haven, Connecticut	0.01–0.03	0.02–0.05	
Meise et al. 2003	Navesink River–Sandy Hook Bay, New Jersey		0.02–0.03	0.1
Rose et al. 1996	Niantic River, Connecticut	0.01		
DeLong et al. 2001	Rhode Island	0.01–0.02		
Sogard and Able 1992	New Jersey			0.06–0.12
Sogard et al. 2001	New Jersey			0.03–0.14

in order to confirm or refute predation as the mechanism behind the species' decline and to identify the predators with the greatest impact.

In addition to predation by piscivorous fishes, crustaceans have been documented to prey on age-0 Winter Flounder.

Crustacean predators include the sand shrimp *Crangon septemspinosa*, green crab *Carcinus maenas*, and blue crab *Callinectes sapidus* (Taylor 2004, 2005; Collier et al. 2014), the latter of which have experienced an increase in abundance throughout the region (Nuttall et al. 2011). Winter Flounder eggs and small juveniles were detected in the stomachs of sand shrimp sampled from May to early June (Taylor 2004). Taylor (2005) found evidence that green crabs begin to prey on age-0 Winter Flounder in late spring and early summer, possibly accounting for 0.4–7.7% of daily mortality in some systems. Taylor's (2005) results also indicated that 1.1–32.3% of the Winter Flounder year-class could potentially be consumed and that variation in the abundance and size of green crabs coincided with variability in age-0 survival. Thus, any future work should examine predation from both vertebrates and invertebrates.

Growth rates previously estimated based on length frequency analysis or otolith increment analysis of juvenile Winter Flounder have shown high variation, making it difficult to decipher the relative influence of causal factors, such as habitat quality and temperature (Phelan et al. 2000). Calculations based on length frequency, the pooling of individuals, or both may introduce bias to estimates because they (1) ignore small fluctuations that occur over time or (2) obscure individual variations that may prove important (Miller et al. 1988; Pepin 1993). Periods of starvation or high metabolic costs can lead to losses in length and weight, and increased size-based mortality could generate bias in length-based estimators (Jordaan and Brown 2003). In the case of Winter Flounder, our results indicate a bias due to multiple cohorts of newly settled individuals of a smaller size and younger age, which likely explains the high variability in length-based growth estimates. If discrete cohorts are not easily identifiable or separable in the analyses, otolith approaches and/or repeated measurements of individuals should be used when estimating growth in age-0 Winter Flounder so as to avoid unrealistic results.

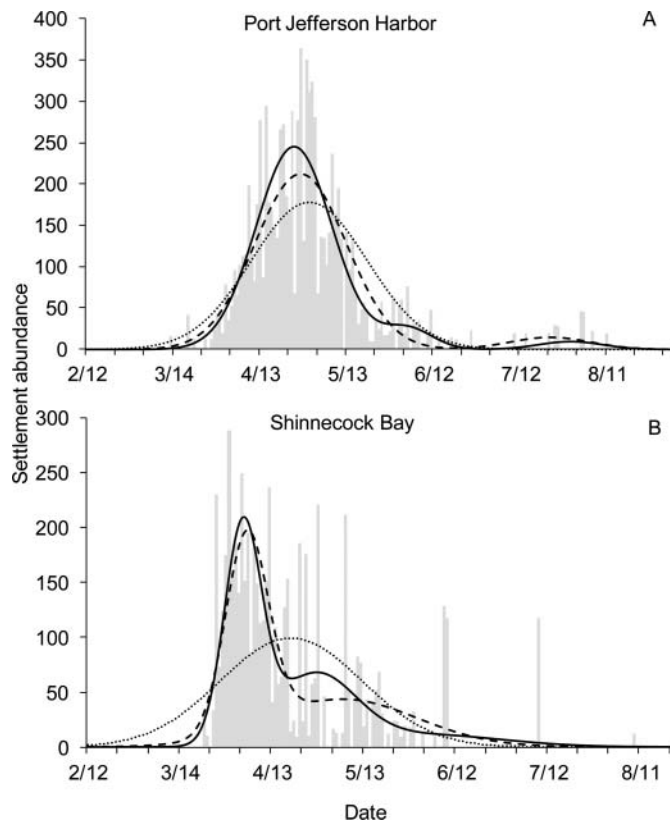


FIGURE 7. Frequency of abundance at settlement for Winter Flounder captured throughout spring and summer 2007 at (A) Port Jefferson Harbor and (B) Shinnecock Bay. Data are based on the daily instantaneous mortality rate and age-length relationship estimated for each region (solid line = three-mode fit; dashed line = two-mode fit; dotted line = single-mode fit).

TABLE 6. Modal analyses for age-0 Winter Flounder collected from Port Jefferson Harbor and Shinnecock Bay, Long Island, in 2007 and 2008. The mean ordinal date ( $x$ ), variance ( $\sigma^2$ ), and height parameter ( $h$ ) of the normal distribution are provided along with Akaike's information criterion (AIC) values. Note that two-mode and three-mode models were not fitted for 2008 data.

Model	AIC	Parameter	Mode		
			1	2	3
Port Jefferson Harbor, 2007					
Three-mode	76,175	$x$	114.74	153.88	210.45
		$\sigma^2$	13.16	8.70	11.10
		$h$	8,068.26	559.31	262.72
Two-mode	76,923	$x$	117.01	203.44	
		$\sigma^2$	15.77	14.00	
		$h$	8,378.88	512.53	
One-mode	80,792	$x$	120.00		
		$\sigma^2$	20.00		
		$h$	8,890.72		
Port Jefferson Harbor, 2008					
One-mode	6,711	$x$	111.00		
		$\sigma^2$	28.76		
		$h$	772.26		
Shinnecock Bay, 2007					
Three-mode	49,280	$x$	93.48	117.00	152.00
		$\sigma^2$	6.02	13.15	25.53
		$h$	2,948.52	2,089.32	719.38
Two-mode	49,819	$x$	94.82	126.01	
		$\sigma^2$	6.95	24.18	
		$h$	3,115.69	2,640.70	
One-mode	52,535	$x$	109.16		
		$\sigma^2$	23.12		
		$h$	5,752.23		
Shinnecock Bay, 2008					
One-mode	12,903	$x$	84.14		
		$s$	21.45		
		$h$	2,887.04		

Given the assumptions that the survival rate is constant and that settlement occurs at approximately 2–3 months posthatch, the time frame of settlement can be used as a proxy for spawning activity, thereby providing insight into the dynamics of age-0 year-classes (Sogard 1991; Pereira et al. 1999). Thus, Winter Flounder spawning in SB during 2007 likely began in late January and continued until mid-March, exhibiting two (and possibly three) peaks. Similarly, in PJ during 2007, three peak spawning periods were likely. The period from late February to early April comprises the normal spawning window for Winter Flounder in this region (Collette and Klein-MacPhee 2002). However, the potential spawning in late May to early June falls outside the commonly observed time frame for this species (Collette and Klein-MacPhee 2002; Klein-MacPhee 2002). Our results are similar to observations of July settlement (i.e., from an April spawning event) in New Jersey (Meise et al. 2003).

Does the combination of multiple spawning cohorts, the presence of migratory and resident fish, and weak genetic

differentiation among Winter Flounder populations support the observation of metapopulations with spatial or temporal overlap? Previous research on Winter Flounder has identified spawning periods lasting from January to April, with the presence of peaks in spawning activity (Stoner et al. 1999), which could explain the observed trends in settlement distributions. However, as additional evidence builds on observations that Winter Flounder exhibit natal spawning groups (Lobell 1939; Perlmutter 1947; Saila 1961) and local genetic structure (Buckley et al. 2008; O'Leary et al. 2013), the underlying mechanisms maintaining the population structure will have to be considered. Future research encompassing adult spawning, migratory behavior, stock structure, duration of the larval period, and settlement timing will be required to unravel the complex behavior of Winter Flounder (Frisk et al. 2014).

The regional stock structure of Winter Flounder has been studied (McBride 2014), but there remains a large amount of uncertainty regarding local life history diversity, including

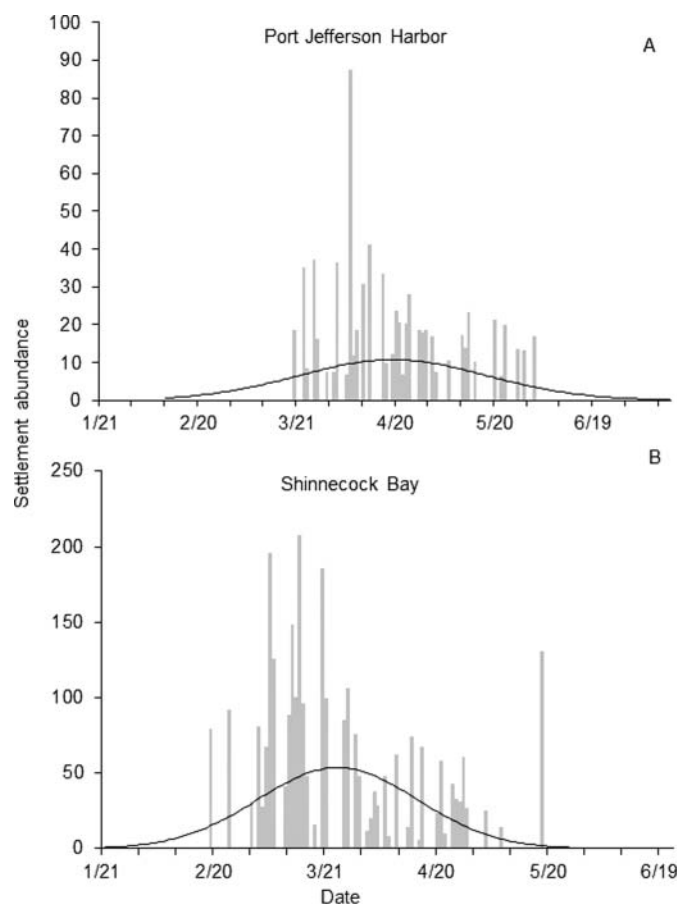


FIGURE 8. Frequency of abundance at settlement for Winter Flounder captured throughout spring and summer 2008 at (A) Port Jefferson Harbor and (B) Shinnecock Bay. Data are based on the daily instantaneous mortality rate and age-length relationship estimated for each region.

population, demographic, and genetic connectivity (Frisk et al. 2014). This paucity of information means that the extent to which Winter Flounder in Long Island bays are connected to ocean stocks is unknown. The difference in population status between the offshore stocks (at 9% of target levels; NEFSC 2008) and the Long Island populations that have experienced inbreeding suggests a degree of isolation between these two contingents (Secor 1999). Research is needed to link local productivity to competing drivers of density-dependent compensation and predation-based mortality in Winter Flounder. Finally, the conflicting genetic evidence for local population structure (Crivello et al. 2004; Buckley et al. 2008; O'Leary et al. 2013) and against such structure (Wirgin et al. 2014) in coastal Winter Flounder must be reconciled.

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