

# Identification of Winter Flounder (*Pseudopleuronectes americanus*) Estuarine Spawning Habitat and Factors Influencing Egg and Larval Distributions

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**Abstract** A long-term (2002–2011), spatially robust, ichthyoplankton sampling program conducted in the New York/New Jersey Harbor produced 3,033 epibenthic samples from which the relationships between winter flounder egg and larval distributions and environmental parameters were examined. Variations in water temperature, sediment characteristics, and tidal phase were all significantly associated with egg distributions. Inferences about spawning habitats were based on the presence of early-stage eggs (ES1 and ES2). In the Lower Bay (LB), these habitats were primarily non-channel and characterized by more sandy substrates, averaging 96.5 % sand, 2.3 % silt/clay, 0.2 % total organic carbon (TOC), and shallower water (average depths of 5.3 m) compared to LB non-channel stations without ES1 and ES2 eggs (50.2 % sand, 42.0 % silt/clay, 2.1 % TOC, and 7.9 m depths). Occurrences of all stages of eggs in channels were associated with strong tides and severe cold winter water temperatures. These conditions increase the probability of egg transport from shallow spawning sites through increased vertical mixing (strong tides) and delayed development that prolongs the risk of displacement (cold temperatures). Yolk-sac (YS) and Stage-2 larvae were smaller in 2010 when spring water temperatures were highest.

Overall, YS larval size decreased with warmer winters (cumulative degree-days for the month preceding peak YS larval collections,  $r^2=0.82$ ,  $p<0.05$ ). In all years, YS larvae collected in LB were smaller and Stage-3 larvae collected in channels were larger and possibly older than those from non-channel habitat. Because estuarine winter flounder populations are highly localized, adverse effects experienced during egg and larval stages are likely to propagate resulting in detrimental consequences for the year class in the natal estuary.

**Keywords** New York/New Jersey Harbor · Temperature · Strong tide · Sediment · Yolk-sac larvae

## Introduction

Management practices designed to protect and restore declining fisheries have transitioned from targeting single species primarily through catch limits, gear restrictions, fishery closures, and fish size limits, to include protecting ecologically important habitats. Potential disturbances to these habitats by human activities, such as navigation dredging and construction, commonly are restricted seasonally and spatially by policy in order to minimize adverse biological impacts. The effectiveness of these management practices, however, is complicated by limited data and an incomplete understanding of the complexities between fishes and estuarine habitat use (Phelan 1992; Able 1999; Schultz and Ludwig 2005). Site-specific information is sometimes needed to manage human activities more efficiently in estuaries while protecting important fishery resources. One example is the challenge of identifying and protecting winter flounder, *Pseudopleuronectes americanus*, spawning habitat while managing dredging activities in the New York/New Jersey Harbor (harbor). Current management practices

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include seasonally restricted dredging during February 1 to May 31, which is believed to be the period of high vulnerability of eggs and benthic associated larvae. Although winter flounder is a well-studied species that supports commercial and recreational fisheries, there is little specific knowledge about its spawning sites and habitats in the estuary or the features of estuarine habitats that affect egg survival (Able and Grothues 2007; Schultz et al. 2007). The general understanding that winter flounder spawn in shallow estuarine habitats in the northeastern United States and Canada (Able and Fahay 1998; Pereira et al. 1999) has been inferred either from relative catch rates of pre-spawning, ripe, or spent adults in trawls (McCracken 1963; Kennedy and Steele 1971), telemetry of adults during the spawning season (Pereira et al. 1994; Able and Grothues 2007), or the inshore presence of larvae (Crawford and Carey 1985; Witting et al. 1999; Chant et al. 2000; Curran and Able 2002). Investigations of estuarine spawning habitat via epibenthic sled sampling have been limited to a few estuaries in Rhode Island (Crawford and Carey 1985; Hughes 1999), New Jersey (Scarlett and Allen 1992), and Connecticut (Schultz et al. 2007). In recognition that site-specific information was needed for the harbor, the New York District Army Corps of Engineers and the Port Authority of New York and New Jersey, in coordination with the National Marine Fisheries Service and New York and New Jersey environmental resource agencies, developed the Aquatic Biological Survey (ABS) to improve our understanding of habitat use within the harbor by winter flounder and other demersal species. In this study, we examined 10 years (2002 through 2011) of the ABS epibenthic ichthyoplankton data to determine spatial and temporal patterns of winter flounder spawning within the harbor. Specifically, we examine associations between environmental variables and (1) the distribution of eggs and larvae throughout the harbor, (2) the seasonal timing of egg and larval occurrences, and (3) variation in larval size.

Winter flounder occur along the east coast of North America from North Carolina to Newfoundland (Bigelow and Schroeder 1953) and have declined in abundance to historic lows; inshore New York populations are less than 10 % of the peak levels observed in the 1980s (ASMFC 2006; Sagarese and Frisk 2011). A description of spawning of captive fish in large-volume tanks by Stoner et al. (1999) included a convergence of males around females and elevation and circling of the group in the water column, with multiple males involved in the fertilization of eggs during a single spawning event. Historically, spawning has been described as occurring offshore for winter flounder on Georges Bank and inshore, following fall and early winter migrations, for more southerly populations (Bigelow and Schroeder 1953; Pereira et al. 1999; Stoner et al. 1999). Recently, however, evidence of spawning in nearshore

coastal habitats has emerged for winter flounder in the Gulf of Maine (DeCelles and Cadrin 2010; Fairchild et al. 2012) and the New York Bight (Wuenschel et al. 2009; Able et al. 2010) as well.

Spawning in New York Bight estuaries occurs from January to March/April (Scarlett and Allen 1992; Stoner et al. 1999) with spawning peaks observed in February (Scarlett and Allen 1992). Egg and larval development are temperature dependent. For example, time until hatching occurs at 63 days at  $-1.8$  °C and 11 days at  $8.0$  °C (Williams 1975), and the duration of the larval period lasts from 80 days at  $5$  °C to 49 days at  $8$  °C in captivity (Laurence 1975). Larvae are bottom-oriented and negatively buoyant (Pearcy 1962; Pereira et al. 1999). The demersal nature of winter flounder eggs and larvae is believed to be adaptive by facilitating their retention within estuaries (Pearcy 1962; Crawford and Carey 1985). This characteristic also makes these life stages vulnerable to benthic disturbances such as dredging (Crawford 1990; Able and Grothues 2007). Consequently, a better understanding of winter flounder egg and larval spatial and temporal distributions within the harbor is needed in order to identify the most effective dredging practices and protection measures.

## Materials and Methods

### Study Site

New York/New Jersey Harbor is a heavily industrialized and urbanized estuary, with much of the shoreline occupied by oil refineries, docking facilities for container ships, chemical plants, and other manufacturing sites. An extensive network of navigation channels provide access to berthing areas in one of the busiest ports in the world, generating over \$25 billion annually in support of the regional economy (USACE 2008). Dredging activity is necessary to maintain and deepen shipping channels to accommodate deep draft vessels. The greatest influence on water movement within the estuary is tidal, with vertical stratification occurring during weak tides and well-mixed conditions occurring during strong spring tides (Geyer and Chant 2006).

### Sampling Methods

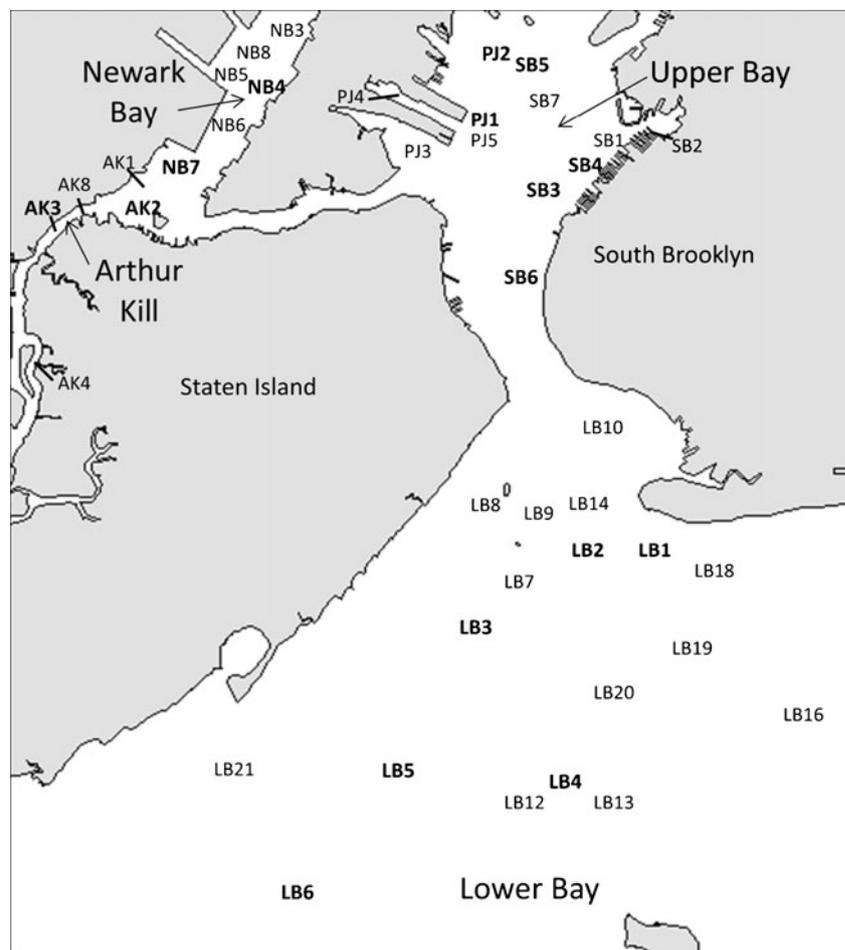
Since its inception in 1998, the ABS program has been modified and enhanced to reflect data needs and concerns of the supporting agencies. The sampling protocol was standardized in 2002 and focused on winter flounder spawning and the habitats associated with early life stages. A gear comparison study conducted in 2002 examined relative catch rates of winter flounder eggs and larvae using modified sleds with the plankton net mounted at alternative

heights (51 and 89 mm) above the substrate and a standard sled modified with a tickler chain (USACE 2002). Results of the gear comparison study indicated that modifications to the standard epibenthic sled design (0.5-mm mesh plankton net with an opening of 0.25 m<sup>2</sup> and the lowest point of the net ringer mounted 178 mm above the substrate) did not significantly affect the capture of winter flounder eggs or larvae, therefore the standard sled design was used for the remainder of the study. Data analyzed in this study were obtained from epibenthic sampling conducted bi-weekly from approximately mid-January to mid-June during 2002 through 2011 throughout the harbor (Fig. 1). For this study we identified three major subareas of the harbor: Arthur Kill/Newark Bay (AKNB), Lower Bay (LB), and Upper Bay (UB). Between 26 and 29 stations at fixed locations across all three subareas in navigation channel (hereafter, channel) and non-channel habitats were sampled each year. In the early years of the survey (2002 to 2007), sampling effort was similar among harbor areas. In later years (2008 to 2011), new sampling stations were added in the LB in order to more fully explore the use of shallow non-channel habitats by winter flounder for spawning. Sixteen stations

were sampled all 10 years (hereafter referred to as the core stations; Table 1, Fig. 1) by 10-min sled tows into the current. Samples were fixed in 10 % buffered formalin containing Rose Bengal and returned to the laboratory for sorting. Viable eggs were counted in all years and egg developmental stages were determined from 2008 to 2011. Eggs were staged 1 to 5 corresponding to cleavage, blastula, gastrula, early embryo, and late embryo stages, respectively (as described by Martin and Drewry 1978, pp. 196–200). Egg developmental stages are used here to distinguish recently spawned eggs from older eggs, the latter at higher risk of being transported from their spawning site (Schultz et al. 2007). Because winter flounder eggs develop more slowly at colder temperatures (Williams 1975; Keller and Klein-MacPhee 2000), the age of eggs determined for each stage at 20.6 °C by Martin and Drewry (1978) did not apply to this study as eggs were collected in the harbor at colder (1.1 °C to 10.2 °C) water temperatures.

Starting in 2008, non-viable eggs, which included non-fertilized eggs and eggs that were opaque or had other obvious signs of deterioration, also were counted. Winter flounder larvae were identified as either yolk-sac (YS) or

**Fig. 1** Location of stations sampled during the Aquatic Biological Survey conducted from 2002 through 2011 in the New York/New Jersey Harbor. Station labels for the harbor subarea Arthur Kill/Newark Bay (AKNB) begin with AK or NB, Lower Bay (LB) begin with LB, and Upper Bay (UB) begin with PJ (Port Jersey) or SB (South Brooklyn). **Boldface** labels depict the 16 core stations



**Table 1** Percent of annual viable egg densities collected at each station (annual columns sum to 100 %)

Station	Subarea	Station physical characteristics				% of eggs collected annually at each station									
		Type	Sed	% TOC	Depth (m)	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
PJ-2	UB	NC	SS	2.0	3.0	24	0	0	47	41	12	6	22	36	3
LB-5	LB	NC	S	0.2	6.4	31	26	6	0	0	24	0	1	2	0
LB-1	LB	NC	S	0.1	5.2	23	2	21	1	0	6	0	10	2	2
LB-4	LB	CH	SS	2.7	11.3	9	28	10	10	0	0	0	3	1	5
SB-6	UB	CH	S	0.2	14.6	1	27	0	9	0	2	2	0	0	0
PJ-1	UB	NC	GS	2.3	5.8	0	1	0	8	0	19	3	0	0	0
LB-2	LB	CH	S	0.1	16.5	1	1	24	0	3	0	0	0	1	2
NB-7	AKNB	NC	SS	2.9	3.4	4	0	0	9		1	7	2	1	1
LB-6	LB	CH	S	0.5	14.0	3	1	18	0	0	0	0	2	0	0
SB-3	UB	NC	S	0.4	5.5	0	5	0	2	1	10	0	4	0	0
SB-4	UB	CH	SCS	2.9	12.2	1	5	7	4	1	0	0	3	0	0
SB-5	UB	CH	SS	2.1	14.3	0	0	0	2	0	0	0	5	0	0
LB-3	LB	NC	SiS	0.7	6.1	2	0	5	0	0	0	0	0	0	0
AK-2	AKNB	CH	SCS	2.8	15.8	0	0	3	0	2	0	0	0	0	0
NB-4	AKNB	NC	SCS	3.0	3.7	0	0	0	0	0	0	0	0	0	0
AK-3	AKNB	CH	SS	4.3	15.2	0	0	0	0	0	0	0	0	0	0
AK-1	AKNB	NC	NS	–	5.8	0	0	2	0						
AK-4	AKNB	NC	SS	5.5	6.1	0	0	0	0						
SB-1	UB	NC	NS	–	8.2	0	0	0	0	2	0				
SB-2	UB	NC	NS	–	9.1	0	0	0	4	0	0				
PJ-3	UB	NC	NS	–	3.0	1	3	0	0	31	25	80			
PJ-4	UB	CH	SCS	3.1	15.5	0	0	0	3	2	0	0			
PJ-5	UB	CH	SCS	3.4	12.8	0	0	0	2	16	0				
NB-6	AKNB	CH	SCS	2.7	14.0	0	0	3	0	0	0			0	0
NB-3	AKNB	NC	SiS	2.2	3.0	1	0	0	0	0	0				
NB-5	AKNB	CH	SCS	3.8	12.8	0	0	0	0	0	0				
NB-8	AKNB	CH	SCS	4.5	13.1								0	0	0
LB-9	LB	NC	SiS	2.1	9.1							0	2	0	0
LB-8	LB	NC	S	0.2	6.1							1	1	1	1
LB-7	LB	NC	SCS	2.8	9.4							0	0	0	
LB-14	LB	CH	SiS	2.4	15.8							0	1	2	0
LB-13	LB	NC	S	0.2	5.8							1	45	6	13
LB-12	LB	NC	S	0.3	7.6							0	0	8	30
LB-10	LB	NC	SS	1.4	9.1							0	0	0	
LB-16	LB	NC	S	0.1	5.5									35	7
SB-7	UB	CH	NS	–	16.5									1	
AK-8	AKNB	CH	SCS	3.2	14.6										0
LB-18	LB	NC	S	0.1	3.7										7
LB-19	LB	NC	S	0.1	4.3										3
LB-20	LB	NC	G	3.5	5.8										0
LB-21	LB	NC	S	0.3	3.7										25

Harbor subareas are identified as Upper Bay (UB), Lower Bay (LB), and Arthur Kill/Newark Bay (AKNB). Habitat type is identified as channel (CH) or non-channel (NC). Sediment characterizations (Sed) are based on Folk (1974) and are abbreviated as follows: *G* gravelly, *GS* gravelly silt, *S* sand, *SS* sandy silt, *SiS* silty sand, *SCS* silt/clayey silt, *NS* no sample. % total organic carbon (TOC) is given for each station. The first 16 stations were sampled in all 10 years (core stations), with the exception of station NB7

post-yolk-sac (PYS) for all years of sampling. Starting in 2007, all larvae were further classified into four stages of larval development (Laroche 1981) as follows:

- Stage 1 Larvae are recently hatched; with yolk-sac present and eyes lacking pigment (YS larvae).
- Stage 2 Larvae have fully pigmented eyes and lacked a yolk-sac, but had yet to exhibit a loop or coil in their gut or to show signs of flexion of the notochord.
- Stage 3 Larvae have some fin rays, flexion has begun, and the gut possesses a loop or coil, but the left (migrating) eye has past the midline.
- Stage 4 Larvae have a left eye past the midline, but lack full juvenile characteristics (loss of pigmentation on left side and full pigmentation near fin base).

For 5 years of sampling (2003, and 2008 to 2011), total length (TL) was measured for subsamples of larvae. For each sample, calibrated images were taken of up to 25 randomly selected larvae for each larval stage and TLs were measured to the nearest 0.1 mm. For the 2003 data, only YS larvae were included in analyses because PYS larvae were not further delineated into stages 2 through 4.

Dissolved oxygen (DO), temperature, and salinity were measured at 0.3 m above the substrate at each station using a water quality meter (YSI Model 85). Water temperature data also were obtained from records for an NOAA gauge (station ID 8518750) located at the southern tip of Manhattan Island (the Battery, at 40°42.0'N, 74°0.8'W), where the temperature sensor is located at 2.385 m below mean sea level (MSL). These temperature data were collected 2–25 km from our stations and provide a continuous record of water temperature, allowing an examination of the duration and magnitude of conditions experienced throughout egg and larval development, which is not possible using the bi-weekly water quality data collected during the ABS sampling. Tidal phase for 2011 was evident in the periodicity of water height data recorded at the NOAA gauge (station ID 8518750). Samples occurring on days when water heights exceeded  $\pm 1$  m from MSL were grouped as strong tide samples and the remaining samples were grouped as weak tide samples.

In 2011, single sediment samples were collected using a 0.1-m<sup>2</sup> Smith McIntyre dredge at 38 of the stations throughout the harbor that had been sampled during the 10 years of the ABS program (Table 1). The upper 10 cm of each grab sample was processed using standard methods for percent grain size and total organic carbon (TOC) analyses. The percent grain size data were used to classify sediments at stations into one of the following five categories based on the Wentworth classification (see Folk 1974): gravelly, gravelly silt, sand, sandy silt, silty sand, and silt/clayey-silt.

## Data Analysis

Egg and larval densities were computed for each sled tow and are expressed as number per 1,000 m<sup>3</sup>. Comparisons of egg and larval densities across years use data from the 16 core stations sampled each year (Table 1). Interannual variation in the seasonal timing of spawning was examined by plotting the cumulative percent of total annual egg densities against time for each year. Spatial variation in egg distributions was examined among harbor subareas (AKNB, LB, UB) and habitat type (channel, non-channel) with relation to severity of winter temperature (severe vs. moderate water temperatures) using a three-factor analysis of variance (ANOVA). Because total annual egg densities at each station were not normally distributed and the interactions among independent factors were of interest, egg densities among stations within harbor subarea and habitat type combinations were aggregated for each year and log-transformed to meet the normality and variance assumptions of the test. Year was used as the replicate after tests for interannual dependencies in annual egg densities using 1-, 2- and 3-year time lags demonstrated no significant autocorrelations for these lag periods. The severity of winter factor was determined by grouping years into either a severe ( $n=4$ ) or moderate ( $n=6$ ) winter temperature category based on whether the cumulative average daily temperatures for the first 8 weeks of the calendar year were below or above 200 degree-days (defined as the sum of daily average temperatures), respectively (Table 2, Fig. 2). Cumulative degree-days also were used in Spearman rank correlations to examine associations between temperature and the timing of egg and larval occurrences. The sampling periods at which 10 % of the annual collection of eggs and 95 % of annual collection of PYS larvae were collected were used to estimate the beginning and end of egg and larval occurrences in the harbor, respectively. Cumulative degree-days were summed over the first 8 weeks of the year for eggs and for February and March for larvae to encompass time periods over which gamete, embryonic, and larval development were occurring in the harbor.

The spatial distributions of larvae were examined using mixed model nested ANOVAs. The annual sums of YS and PYS larval densities at each station were analyzed in separate ANOVAs using harbor subarea and habitat type as fixed effects and station as a random factor nested within harbor subarea  $\times$  habitat type. Larval densities were log-transformed to meet the normality and variance assumptions of the test. Tests for autocorrelations in annual total larval densities at 1-, 2- and 3-year time lags were conducted using regression analysis and were not significant for any of these lag periods. Variation in larval TL was examined by three-factor ANOVAs that tested for differences in size by year, harbor subarea, and habitat type for each larval stage using

**Table 2** Statistical summary of select data on tows, annual biological variables, and annual environmental data

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Sampling start date	1/22	1/21	1/21	1/10	1/24	1/29	2/5	1/5	1/4	1/19
Sampling end date	7/11	7/10	7/7	7/7	7/7	7/11	7/9	6/19	6/16	6/8
Total number of ichthyoplankton tows	312	339	309	327	283	289	314	288	284	288
# of viable eggs at 16 core stations	123	580	30	36	19	589	62	106	150	212
# of viable eggs at all stations	123	608	32	40	49	814	378	213	327	1,553
# of non-viable eggs at 16 core stations							200	151	48	0
# of non-viable eggs at all stations							1,146	206	140	3
# of days water temperature <2 °C	0	48	31	14	0	8	0	0	0	23
Cumulative degree-days through 8 weeks <sup>1</sup>	305	124	116	166	270	279	285	281	291	126

Temperature parameters were calculated from the NOAA gauge (station ID 8518750) located just offshore of Manhattan Island, New York (the Battery, 40°42.0'N, 74°0.8'W). Cumulative degree-days is the sum of daily average water temperature

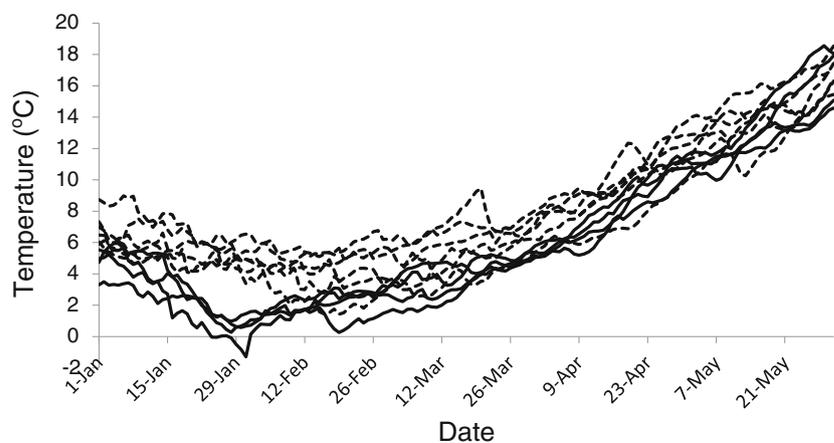
<sup>1</sup> Start January 1

data collected in 2003 and 2008 to 2011 from core stations. Average larval TL by station was the dependent variable in these analyses. Small sample sizes prevented an examination of variation in larval TL among stations through nested ANOVAs. The potential relationship between temperatures experienced during embryonic and early larval development and YS larval size (TL) was examined using a least-squares regression that compared cumulative degree-days for the month preceding peak YS larval collections to annual mean YS larval TL.

Kruskal–Wallis tests were used to test for differences in the densities of early (ES1 and ES2) and late (ES3 to ES5) stage eggs between channel and non-channel habitat for eggs collected in 2011. Separate analyses were conducted for strong and weak tidal phases. To identify habitat characteristics of stations where early-stage eggs were collected, a non-metric multidimensional scaling (nMDS) ordination was used to depict the relative similarity of 14 stations in non-channel habitat in LB based on the stations' physical characteristics, which included water depth, substrate composition (i.e., % sand, % silt/clay, % TOC), temperature

(average difference between station temperature and average LB non-channel station temperature), and distance to mouth of harbor. Environmental data were normalized and Euclidean distances used to create similarity matrices. The relative position of stations in the nMDS plot indicates the similarity of environmental conditions among stations, with similar stations positioned more closely than stations with dissimilar environmental conditions. The analysis was restricted to LB stations to allow an examination of spawning activity within an area with relatively homogeneous salinity conditions. Stations were assigned to a presence/absence category for early-stage (ES1, ES2) eggs based on data from the time period when egg stage determinations were made (2008 to 2011) and an ANOSIM (analysis of similarity, PRIMER version 6.1; Clarke and Warwick 2001) test was used to determine whether physical conditions differed between stations with and without early-stage eggs. SIMPER (similarity percentages, Clarke and Warwick 2001) was used to determine the relative contribution of each physical parameter in distinguishing between stations with and without early-stage eggs.

**Fig. 2** Winter and spring water temperatures recorded at the southern tip of Manhattan Island (NOAA gauge station ID 8518750) for the 10 years (2002 to 2011) that the ABS sampling was conducted. Years described here as severe or moderate winter water temperatures are depicted by *solid* and *dotted* lines, respectively



## Results

### Environmental Factors

Physical conditions measured during bi-weekly sampling were within the general reported tolerances of winter flounder eggs and larvae (Pereira et al. 1999). DO concentrations ranged from 5 to 11 mg/l. The harbor subareas had distinct seasonal salinity ranges, with the lowest monthly averages ranging from 17 to 21 psu in the AKNB area, intermediate salinities (21 to 24 psu) in the UB, and highest salinities (25 to 28 psu) in the LB. Temperatures varied considerably among years during the study period, particularly in the extent of prolonged and cold winter temperatures (winter severity). In 4 years (2003, 2004, 2005 and 2011), extreme low water temperatures (<1 °C), were recorded at the Manhattan NOAA gauge (Fig. 2) and cumulative degree-days for the first 8 weeks of these years averaged 133 degree-days compared to 288 degree-days for other years (Table 2). Differences in water temperature between channel and non-channel stations within a harbor subarea during a sampling event, which usually lasted 3 to 4 days, were typically less than 0.5 °C, and differences among harbor subareas generally ranged from 1 °C to 2 °C, with more extreme temperatures in the AKNB area that were typically colder in the winter and warmer later in the spring than other harbor subareas.

Sediments at the ABS stations were similar to characterizations made of harbor sediments in earlier studies (Coch 1986; Iocco et al. 2000). The AKNB subarea was dominated by silty material in varying quantities at most stations, with the exception of Elizabeth Flats (NB-7) where the sand content was higher (Table 1). LB sediments were comprised primarily of sand and UB sediments were transitional, ranging from silt to gravelly sand. TOC values ranged from 0.1 % to 5.5 %, with the lowest values at LB stations and the highest values in the AKNB subarea (Table 1).

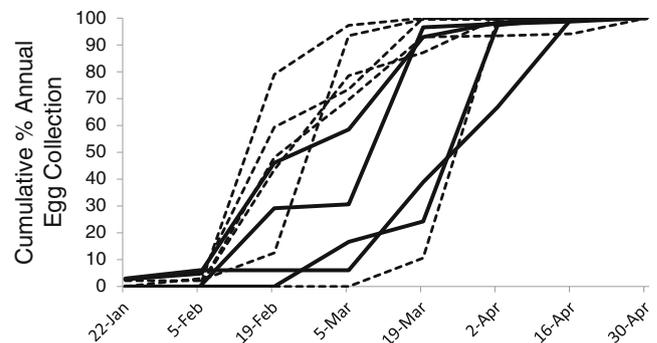
### Egg Distribution Patterns

A total of 3,033 ichthyoplankton tows was conducted in the harbor during the ABS program from 2002 to 2011, ranging from 283 to 339 tows annually (Table 2). The total annual number of viable eggs collected varied more than 10-fold over the 10 years of sampling, with collections ranging from 19 to 589 eggs per year at the 16 core stations (Table 2). Substantially more viable eggs were collected in 2011 at all stations sampled ( $n=1,553$ ), which was in large part due to high egg densities at two LB stations (LB12 and LB21) that were not among the core stations sampled (Table 1). The relative number of viable to non-viable egg collections was highly variable and episodic. Overall, only 6 % of samples collected during the spawning seasons of 2008 to 2011

contained non-viable eggs, whereas 21 % of samples contained viable eggs. Non-viable eggs accounted for <1 % (2011) to 75 % (2008) of total annual egg collections (Table 2). In 2008, the high percentage of non-viable eggs was due to the collection of 1,130 unfertilized eggs at two UB non-channel stations (PJ-2 and PJ-3) on February 20. Unfertilized eggs had a wrinkled surface membrane compared to dead eggs, which were opaque or murky in nature, with obvious signs of deterioration. All results reported hereafter pertain to viable eggs only.

The beginning of the spawning season, as characterized by the first collection of eggs, varied annually and ranged from initiating before sampling began in mid-January in some years (2004, 2010, and 2011), to initiating in February (2002, 2003, 2007, 2008, 2009) and March (2005, 2006) in other years. Temperature parameters (e.g., cumulative degree-days for the first 8 weeks of the calendar year and number of days <2 °C) were not correlated with either the timing of first egg collections or the sampling period by which 10 % of the annual egg total was collected. Eggs collected at core stations before February 1 never accounted for more than 3 % of the total egg abundance for any single year and on average accounted for 0.8 % of annual egg collections (Fig. 3). The majority of egg collections occurred later in the spring during severe cold years than in other years, with collection of 50 % of eggs by week-of-year 12.5 (late March) during cold years compared to week 9.2 (early March) for all other years (Fig. 3).

Egg densities were consistently lower in AKNB than in other harbor subareas ( $F=8.99$ ,  $p<0.001$ ; Table 3; Fig. 4) and varied between channel and non-channel habitats based on the severity of winter water temperatures. During years with moderate winters, egg densities throughout the harbor were significantly higher in non-channel than channel habitats, whereas severe winter egg densities did not differ between channel and non-channel habitats ( $F=5.27$ ,  $p<0.05$ ; Table 3; Fig. 4). The inverse relationship between



**Fig. 3** Cumulative percentage of total annual viable egg abundances depicted for all 10 years (2002 to 2011) of sampling. *Solid and dotted lines* correspond to years with severe and moderate winter water temperatures, respectively

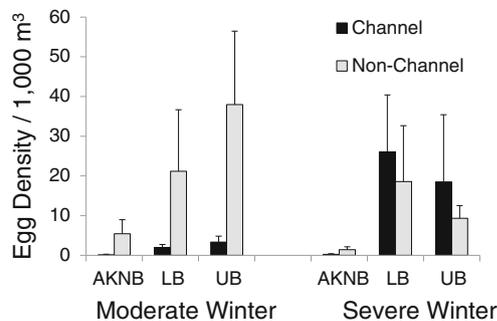
**Table 3** Results of the analysis of variance (ANOVA) comparing egg densities by harbor subarea (AKNB, LB, UB), habitat type (channel vs. non-channel), and severity of winter (SOW)

	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Subarea	2	11.70	8.99	<0.001
Habitat	1	7.90	6.07	0.017
Severity of winter (SOW)	1	0.19	0.15	0.704
Subarea × Habitat	2	1.22	0.94	0.398
Subarea × SOW	2	2.40	1.85	0.169
Habitat × SOW	1	6.86	5.27	0.026
Subarea × Habitat × SOW	2	0.47	0.36	0.700
Error	48	1.30		

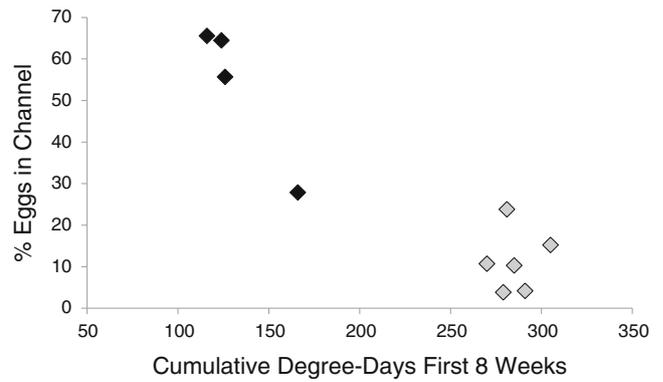
Years were assigned to SOW categories of severe and moderate based on whether the sum of daily average water temperatures for the first 8 weeks was less or more than 200 degree-days, respectively

egg density in channels and temperature is further demonstrated by the significant inverse relationship between the annual % of eggs collected at channel stations and the cumulative degree-days for the first 8 weeks of the year (Spearman  $r = -0.76$ ,  $p < 0.01$ ; Fig. 5), indicating the highest incidences of eggs in the channels occurred in years with prolonged low temperatures.

The occurrence of eggs in channels was also associated with tidal phase. When sampling occurred during weak tidal phases in 2011, egg densities were significantly greater at non-channel stations for both early (ES1 and ES2; Mann–Whitney  $U = 6.5$ ,  $p < 0.005$ ) and late (ES3, ES4, and ES5; Mann–Whitney  $U = 8.0$ ,  $p < 0.05$ ) stage eggs (Fig. 6a). When sampling occurred during strong tidal phases, there were no significant differences in egg densities between channel and non-channel stations for either early or late stage eggs (Fig. 6b). The association between tidal phase and early-stage egg collections in channels was most pronounced during the second sampling period in March 2011 which coincided with a perigee (super moon) phenomenon in

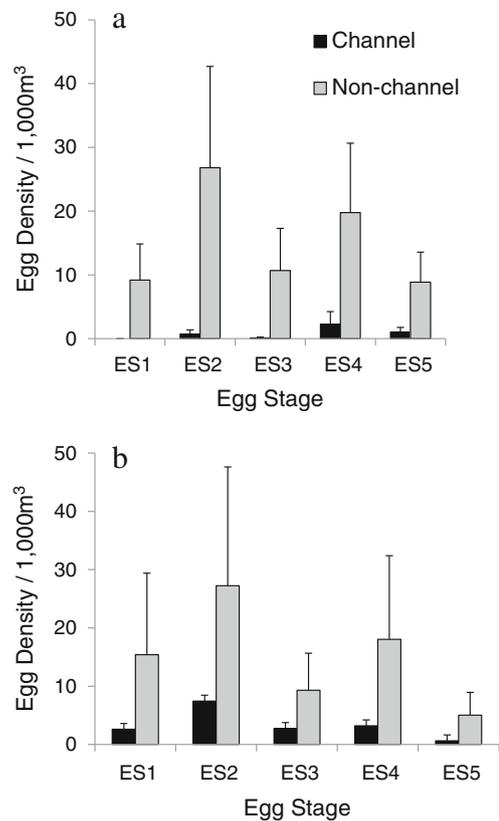


**Fig. 4** Annual mean ( $\pm$ SE) viable egg densities collected in Arthur Kill/Newark Bay (AKNB), Lower Bay (LB), and Upper Bay (UB) at channel (black bars) and non-channel (gray bars) habitat from 2002 to 2011 (see Fig. 1). Temperature profiles of years categorized as having severe and moderate winters are depicted in Fig. 2. Data from 16 core stations are presented (see Table 2, Fig. 1)



**Fig. 5** Relationship between the % of viable eggs collected at channel stations annually and the cumulative degree-days for the first 8 weeks of each year (Spearman  $r = -0.78$ ,  $p = 0.009$ ). Water temperature data are from the southern tip of Manhattan Island (NOAA gauge station ID 8518750). Data from 16 core stations are presented (see Table 2, Fig. 1) with black and gray symbols depicting severe and moderate winter water temperatures, respectively

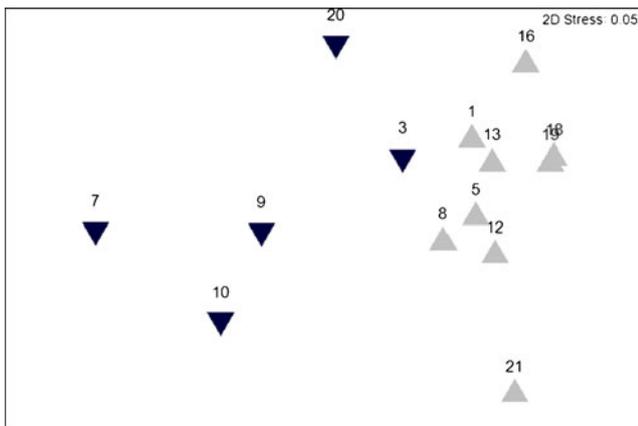
which the timing of the moon being at the closest point of its elliptical orbit around earth coincided with a full moon causing unusually large spring tides. The resultant strong tidal currents in conjunction with spring pulses of snowmelt



**Fig. 6** Mean ( $\pm$ SE) viable egg densities by egg stage (ES1–ES5) collected in 2011 at channel (black bars) and non-channel (gray bars) stations for sampling days that coincided with a weak and b strong tides

and rainfall flood waters created some of the strongest non-storm currents (2.2 m/s) recorded in the Hudson (Stevens Institute of Technology, Hoboken, NJ) during this March 21–24 sampling period. Forty-four of the 69 early-stage eggs collected in channels in 2011 were collected during the perigee event. Minimum bottom velocities of one knot (0.51 m/s) are estimated to be required to suspend winter flounder eggs into the water column (Signell et al. 2000; Schultz et al. 2007), which is roughly one-fourth that observed during this sampling period. Of the 1,418 early-stage (ES1 and ES2) eggs collected at all stations sampled during the 4 years eggs were staged (2008 to 2011), 79 eggs were collected from channel stations, 77 of which were collected during a strong tidal phase.

Physical characteristics of LB non-channel stations where early-stage (ES1 and ES2) eggs were collected differed significantly from that of other LB non-channel stations (ANOSIM  $R=0.65$ ; Fig. 7). Substrate parameters contributed most substantially to discriminating between stations with and without early-stage eggs (SIMPER), with percent TOC contributing the most (21.1 %), followed by percent sand (20.6 %), percent silt/clay (19.5 %), water depth (16.9 %), temperature difference (11.6 %), and distance from the harbor mouth (10.1 %). At LB stations where early-stage eggs were collected (LB stations 1, 5, 8, 12, 13, 16, 18, 19 and 21), depth averaged 5.3 m and substrate parameters averaged 96.5 % sand, 2.3 % silt/clay, and 0.2 % TOC, whereas LB non-channel stations without early-stage eggs averaged 7.9 m depth and had substrates averaging 50.2 % sand, 42.0 % silt/clay, and 2.1 % TOC.



**Fig. 7** Non-metric multidimensional scaling (*nMDS*) ordination plot depicting 14 Lower Bay non-channel stations by the presence (*gray*) or absence (*black*) of early-stage (ES1 or ES2) eggs in samples from 2008 to 2011. Symbol labels indicate LB station number. Juxtaposition between stations indicates similarity based on physical characteristics that include station depth, substrate composition (% sand, % silt/clay, and % total organic carbon), temperature, and distance from harbor mouth

## Larval Distribution Patterns

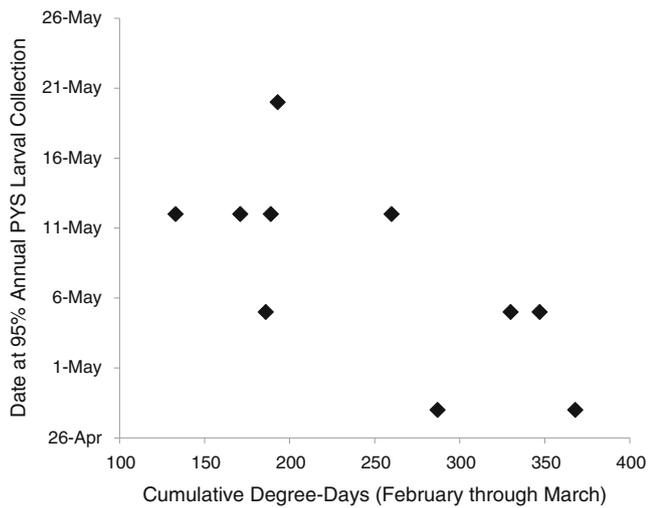
Densities of YS larvae differed among harbor subareas ( $F=3.39$ ,  $p<0.05$ ), but did not differ between channel and non-channel habitats (Table 4), with significantly higher densities in the LB than the AKNB area (Bonferroni pairwise comparisons,  $p<0.01$ ). YS larval densities also varied among stations within subarea  $\times$  habitat type groupings ( $F=2.74$ ,  $p<0.01$ ). PYS larval densities also differed by harbor subarea ( $F=44.8$ ,  $p<0.001$ ), with no difference due to habitat type (Table 4). PYS larval densities in AKNB were significantly lower than in UB and LB, which had the highest densities (Bonferroni pairwise comparisons,  $p<0.01$ ). When PYS densities were further analyzed by developmental stage (2008 to 2011), both ST2 and ST3 densities reflected the previously described PYS larval distribution patterns, however, ST4 densities were significantly greater at channel than non-channel stations (Mann–Whitney  $U=185.0$ ,  $p<0.01$ ) and did not differ among harbor subareas.

PYS larvae were present in the harbor later in the spring in years with severe winter water temperatures. The sampling period by which 95 % of PYS were collected each year was inversely correlated with the cumulative degree-days from February through March (Spearman  $r=-0.63$ ,  $p<0.05$ , Fig. 8). In most years of sampling, 95 % of PYS were collected in the harbor by the second week of May.

YS larval size ( $n=812$  measured larvae from 2003 and 2008 to 2011) differed among years ( $F=16.1$ ,  $p<0.001$ ) and harbor subareas ( $F=19.8$ ,  $p<0.001$ ; Fig. 9a.), but not between channel and non-channel habitats (Table 5). YS larvae were smaller in 2010 (mean TL=3.16 mm) than in other years (mean TL=3.71 mm) and were consistently smaller in LB (mean TL=3.37 mm) than in the other subareas (mean TL=3.79 mm, Fig. 9a). Stage-2 larvae ( $n=923$ ), which recently transitioned from subsisting on endogenous to exogenous energy resources, also were smaller in 2010 than in other years ( $F=9.3$ ,  $p<0.05$ ) and were smaller in LB ( $F=$

**Table 4** Results of nested ANOVAs comparing annual total yolk-sac and post-yolk-sac larval densities by harbor subarea (AKNB, LB, UB), habitat type (channel vs. non-channel) and station nested within subarea  $\times$  habitat

	Yolk-sac larval density				Post-yolk-sac larval density		
	<i>df</i>	MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
Subarea	2	6.96	3.39	0.037	34.02	44.80	<0.001
Habitat	1	1.05	0.51	0.477	0.01	0.01	0.916
Subarea $\times$ Habitat	2	3.28	1.60	0.206	3.62	4.76	0.100
Station (Subarea $\times$ Habitat)	10	5.64	2.74	0.004	1.04	1.36	0.202
Error	143	2.06			0.76		



**Fig. 8** Sampling period at which  $\geq 95\%$  of PYS larvae had been collected each year at core stations versus the winter temperature regime (cumulative degree-days from February 1 through March 31)

4.2,  $p < 0.05$ ) and did not differ by habitat type (Fig. 9b, Table 5). Stage-3 larvae ( $n = 3,270$ ) were significantly larger at channel than at non-channel stations ( $F = 26.3$ ,  $p < 0.001$ ) and did not differ in size among years or subareas (Fig. 9c, Table 5). Sample sizes of stage-4 larvae were small ( $n = 92$ ) and the majority (92 %) of these larvae were collected at channel habitats and no significant differences in size were observed among subareas or years.

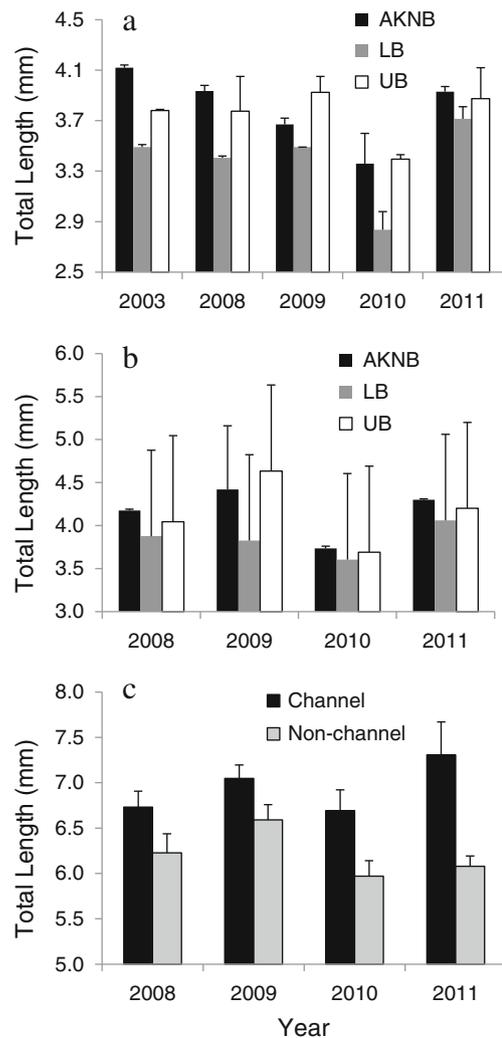
Variation in size of YS larvae among years was related to water temperatures during the month preceding peak YS larval collections each year ( $r^2 = 0.82$ ,  $p < 0.05$ ). YS larvae were larger when eggs were developing in colder water conditions (Fig. 10).

**Correlations Among Egg and Larval Densities**

Total YS larval densities for the entire harbor were positively correlated with total annual egg densities of the same year ( $r^2 = 0.54$ ,  $p < 0.05$ ). The relationship between annual egg and PYS larval densities was weaker ( $r^2 = 0.33$ ,  $p = 0.08$ ). Winter water temperature (average March temperature and cumulative degree-days) was not related to total annual densities of either eggs or larvae.

**Discussion**

Characteristics of winter flounder estuarine spawning habitat are not well described, largely because it is difficult to synoptically sample eggs in sufficient numbers to relate distribution patterns to physical features of the benthic environment (Able and Grothues 2007). In addition, in shallow, well-mixed estuaries, eggs may be transported from



**Fig. 9** Mean ( $\pm$ SE) total length of **a** YS ( $n = 812$ ) and **b** Stage-2 larvae ( $n = 923$ ) in Arthur Kill/Newark Bay (AKNB, black bars), Lower Bay (LB, gray bars) and Upper Bay (UB, open bars) and **c** mean ( $\pm$ SE) total length of Stage-3 larvae ( $n = 3,270$ ) at channel (black bars) and non-channels (gray bars) stations from 16 core stations.

spawning sites as they develop, thus staging information is needed to identify spawning habitat more reliably. Winter flounder eggs are adhesive, and in culture, diatomaceous earth is used to prevent eggs from clumping or adhering to container walls (Smigielski and Arnold 1972; Chambers and Leggett 1987; Buckley et al. 1991a). In estuaries, suspended sediments may adhere to eggs as they descend through the water column, thus reducing their adhesive potential once on the substrate (J. Smith et al., unpublished data). In our study, collected eggs were not adhered to each other or to pieces of debris or substrate, which is similar to the solitary condition of eggs collected by epibenthic sled in two Connecticut estuaries (Schultz et al. 2007). The long-term, spatially robust nature of the ABS sampling program provides an unusual opportunity to explore associations between winter flounder egg distributions and environmental

**Table 5** Results of ANOVAs comparing larval total length (TL) by year, harbor subarea (AKNB, LB, UB), and habitat type (channel vs. non-channel) for yolk-sac, stage-2 (ST2) and stage-3 (ST3) larvae

	Yolk-sac larval TL				ST2 larval TL				ST3 larval TL			
	<i>df</i>	MS	<i>F</i>	<i>p</i>	<i>df</i>	MS	<i>F</i>	<i>p</i>	<i>df</i>	MS	<i>F</i>	<i>p</i>
Year	4	0.84	16.11	<0.001	3	0.82	9.26	<0.001	3	0.63	1.77	0.168
Subarea	2	1.03	19.77	<0.001	2	0.38	4.25	0.022	2	0.14	0.39	0.677
Habitat	1	0.10	1.89	0.178	1	0.13	1.50	0.228	1	9.31	26.28	<0.001
Year × Subarea	8	0.08	1.63	0.149	6	0.18	2.02	0.087	6	0.42	1.18	0.337
Year × Habitat	4	0.05	0.89	0.481	3	0.21	2.31	0.092	3	0.34	0.95	0.425
Subarea × Habitat	2	0.03	0.50	0.610	2	0.16	1.80	0.179	2	0.56	1.57	0.221
Year × Subarea × Habitat	8	0.06	1.21	0.321	6	0.18	1.98	0.093	6	0.28	0.79	0.583
Error	38	0.05			38	0.09			40	0.35		

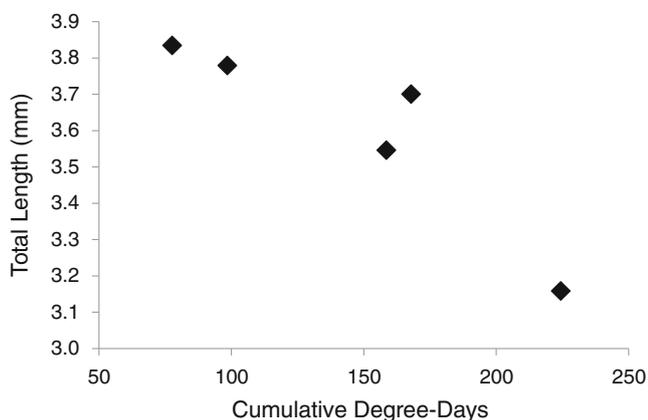
factors. Overall, winter flounder egg densities were highest in relatively shallow non-channel habitats. In LB, early-stage eggs (ES1 and ES2), which presumably were collected close to spawning sites, were present on sediments with higher sand and lower % TOC content and at depths that were on average 2.6 m shallower than other non-channel LB areas where early-stage eggs were not collected (Fig. 7). These results are consistent with previous findings that winter flounder spawn in shallow estuarine habitat and indicate that within shallow estuaries, spawning site selection is non-random. In other estuaries, eggs (not identified by developmental stage) have been collected in association with algal mats (Bigelow and Schroeder 1953) and gravel (Crawford and Carey 1985), and early-stage eggs were collected on sandy and silt/clay substrata in low current areas (Schultz et al. 2007). Site selection may vary based on the types of habitat available at the time of spawning, but in the LB of New York/New Jersey Harbor, the selection of shallow, sandy habitat is evident. In LB, late-stage eggs and YS larvae were collected at non-channel stations with a broader range of physical features than at stations where

early-stage eggs were collected, suggesting egg viability was unaffected by transport from spawning sites.

Egg collections in channels were associated with severe winter water temperatures (Figs. 4 and 5) and strong tides (Fig. 6), both of which increase the probability of transport from shallow spawning sites. In particular, egg development is delayed under cold conditions, thus prolonging residence times within the estuary and increasing the opportunity for eggs to be advected from spawning sites. Strong tides induce vertical mixing, which also increases the probability of egg advection from spawning sites.

Egg densities were consistently low in the AKNB subarea of the harbor where sediments were composed of higher percentages of silt/clay and TOC (Table 1). Both YS and PYS larval densities remained relatively low in AKNB (i.e., less than 10 % of the total harbor CPUE; thus, this area does not appear to provide high value habitat for winter flounder eggs or larvae. Feeding-stage larvae (Stage-3) are more common in channels than non-channel habitat (Fig. 9c) and Stage-4 larvae, which are nearing metamorphosis to the benthic juvenile phase, were collected primarily in channels, certain reaches of which may be organically rich depositional areas, a prime characteristic of winter flounder settlement habitat (Howell et al. 1999; Manderson et al. 2003).

The influence of water temperature on winter flounder egg and larval development has been demonstrated through both controlled laboratory experiments (Laurence 1975; Williams 1975; Rogers 1976; Keller and Klein-MacPhee 2000) and correlative field studies (Jefferies and Johnson 1974; Sogard et al. 2001). Specifically, under warm conditions, egg and larval development is faster (Laurence 1975; Williams 1975), survival is lower (Rogers 1976) and size is smaller (Keller and Klein-MacPhee 2000). These effects on eggs and larvae correspond to annual variation observed in juvenile and adult populations. For instance, in Narragansett Bay, Rhode Island, annual winter flounder adult abundance is negatively correlated with winter temperature from the appropriately lagged spawning season, indicating that

**Fig. 10** Annual mean total length (mm) of all YS larvae versus the cumulative degree-days for the month prior to peak YS larval collections in 2003 and 2008 to 2011. Data from 16 core stations

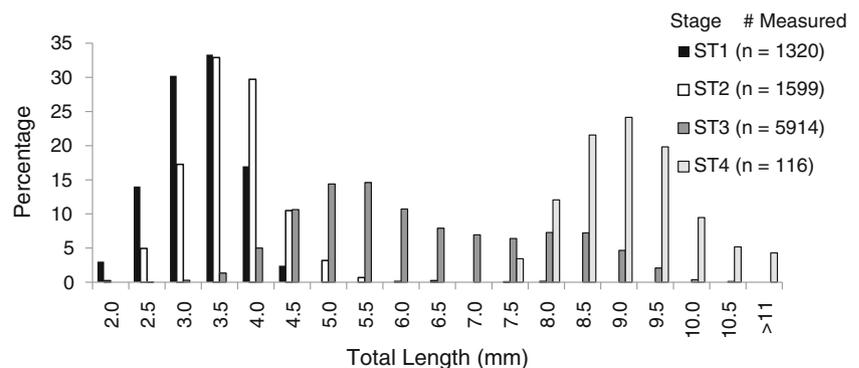
warmer temperatures experienced by eggs and larvae result in fewer adult fish (Jefferies and Johnson 1974; Keller and Klein-MacPhee 2000), perhaps due to greater predation from sand shrimp on eggs (Taylor and Danila 2005) and newly settled juveniles (Taylor and Collie 2003) under warmer conditions. The effect of temperature on winter flounder early life stages was also evident in the harbor, affecting the timing of egg and larval occurrences as well as larval size. Peak egg collections occurred later in March and PYS larvae were collected later in May (Fig. 8) in colder years, which is consistent with the delayed development observed in laboratory experiments (Rogers 1976; Laurence 1975). Similar correlations have been observed in other estuaries (Sogard et al. 2001; DNC 2011).

YS larval size decreased with increasing temperatures experienced by embryos (Fig. 10), which is consistent with laboratory studies in which larval size is larger at the lowest combination of acclimation and rearing temperatures (Buckley et al. 1990; Keller and Klein-MacPhee 2000). In particular, YS and Stage-2 larval sizes were smallest in 2010 when mean March water temperature was the warmest of the years for which larval size was examined by stage (7.0 °C versus 3.2 °C, 5.2 °C, 6.2 °C and 4.2 °C for other years). In addition, YS larval size was consistently smaller in the LB (Fig. 9a) where salinities were highest and generally exceeded the 25 psu maximum salinity for optimal egg viability at temperatures above 3 °C (Rogers 1976). Salinity effects on larval size are variable among marine fishes and less dramatic than the influence of temperature (Chambers 1997), but high temperature and salinity combinations are stressful for winter flounder early life stages and result in low egg survival under laboratory conditions (Rogers 1976). The absence of size differences among areas and years for Stage-3 larvae may reflect larval dispersal or the broader size range included in this developmental stage (Fig. 11) may increase variability and weaken statistical power. Larval size does not continually diverge throughout winter flounder development (Bertram et al. 1997). The larger size of Stage-3 larvae in channels may indicate that Stage-3 larvae in channels are older than those in non-channel

habitat, and thus, larger. Winter flounder larvae at this stage feed primarily on polychaete larvae, nauplii, and invertebrate eggs (Shaheen et al. 2004), but the relative prey availability between habitat types is not known. Over a third of the measured Stage-4 larvae, collected almost exclusively in channels, exceeded 9.5 mm TL (Fig. 11). Larger size is advantageous at each stage of larval development. Survival for the first month of life is lower for smaller larvae at the yolk-sac stage (Buckley et al. 1991a). Larger size for feeding larval stages improves survival because of the greater potential to avoid size-dependent predation, capture food, and survive periods of low prey availability (Buckley et al. 1990). The escape response of larval winter flounder tends to be slower than that of other comparably sized plankton leaving it more susceptible to predation by contact predators, such as copepods and amphipods (Williams and Brown 1992). In addition, escape response speed is positively correlated with winter flounder larval size; therefore, smaller larvae are slower and less able to escape predation (Williams and Brown 1992). Other factors that affect larval size include paternal (Fraboulet et al. 2009) and maternal (Buckley et al. 1991b; Chambers and Leggett 1996) influences, time of spawning (egg size decreases as the spring progresses, Buckley et al. 1991b; Chambers and Leggett 1996), and egg contaminants (size at hatch is smaller for larvae hatched from eggs contaminated with PCBs; Black et al. 1988). Of these alternative influences, we are only able to examine the potential influence of the time of spawning. Although egg size was not determined in this study, winter flounder egg and larval size at hatching are positively correlated (Chambers et al. 1988; Buckley et al. 1991b); therefore, the smaller larval size in LB could result from later spawning in the spring in this subarea.

In addition to overfishing and the general decline in estuarine habitat quality, the adverse effects of elevated water temperatures on eggs and larvae have been included among factors potentially responsible for the persistent decline in winter flounder populations since the 1980s (Keller and Klein-MacPhee 2000; Manderson 2008; Sagarese and Frisk 2011). Previous linkages among winter flounder life

**Fig. 11** Length–frequency histogram of winter flounder larvae by stage of development for all larvae measured from 2008 to 2011



history stages have relied on abundances of spawning stock females (e.g., Danila 2000; Brodziak et al. 2001; DNC 2011) as a proxy variable to estimate potential egg production for an area. To our knowledge, our study provides the first field evidence that the density of viable winter flounder eggs developing on the substrate is positively correlated with YS larval densities within an estuarine system. Factors, therefore, that could disrupt this relationship, such as temperature-mediated predation on eggs by crustaceans (Taylor and Danila 2005) or temperature-related egg mortality (Rogers 1976) if present, were not substantial enough to eliminate the simple correlation between annual egg and early larval abundances. The significant relationship between warm temperatures and small YS larval size provides an alternative mechanism by which local population strength is adversely affected by warm temperatures. Winter flounder juvenile and larval populations can be closely associated within estuaries (Buckley et al. 2008), and local residency within the natal estuary may extend through the adult phase, at least for a contingent of the population (Sagarese and Frisk 2011). Therefore, negative impacts that occur during the egg and larval stages, such as those associated with small larval size, may be propagated through juvenile and adult stages, thus affecting local population structure.

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