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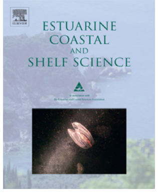

Winter flounder (*Pseudopleuronectes americanus*) estuarine habitat use and the association between spring temperature and subsequent year class strength

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ABSTRACT

Winter flounder habitat use in New York/New Jersey Harbor was examined through a long-term (2002–2010) bottom trawl sampling program (Aquatic Biological Survey) in which 5234 winter flounder were captured in 2069 samples collected at approximately 26 stations throughout the harbor. Interannual variability in catch-per-unit-effort (CPUE) primarily was attributable to fluctuations in Year-1 juvenile CPUE, which was positively correlated with total annual egg abundances from the previous year. Adult male CPUE during the spawning season was positively correlated with total egg abundances of the same year, whereas adult female CPUE was unrelated to annual egg abundances in the harbor. Annual variation in adult male densities in the harbor during the spawning season reflects the intensity of estuarine spawning activity, whereas adult female densities may include non-reproductive, foraging individuals. Seasonal fluctuations in condition indices reflected energy use during the spawning season, with relatively high condition in January, reduced levels in March and April, and elevated condition again in May. Adult CPUE peaked in April, coincident with the critical feeding period that follows spawning. Mean April water temperatures were positively correlated with egg abundances the following year and Year-1 juvenile CPUE two years later. A similar correlation between April temperatures and Year-1 juvenile abundances two years later was demonstrated using published data for winter flounder collected in Niantic Bay, CT. Higher April water temperatures may enhance benthic secondary production during the critical feeding period, and thus increase prey availability for foraging adults that need to restore energy reserves in order to reproduce the following year. A direct examination of benthic secondary production and variation in winter flounder estuarine foraging and subsequent spawning activity is needed to more fully understand this relationship.

1. Introduction

Declines in both estuarine habitat quality and associated fish populations over the last several decades have focused management efforts on reducing negative biological impacts in estuaries where many human activities and critical life history functions of fish overlap. Factors associated with estuarine habitat degradation (e.g., pollution, coastal development, and climate change) and recurring human activities (e.g., vessel traffic, dredging, and power plant operations) are varied in nature and scale of impact (both spatial and temporal). The degree to which protective regulatory measures implemented locally may affect a declining fishery, therefore, is linked to the influence of the regulated activity on the fish population relative to other factors. New York/New Jersey Harbor (harbor) is a heavily industrialized and urbanized estuary with an extensive network of navigation channels leading to ports that are among the busiest in the world. Winter flounder (*Pseudopleuronectes americanus*), a commercially and recreationally important flatfish, use portions of this estuary as spawning, nursery, and foraging habitat. Dredging to maintain and deepen shipping channels within the harbor is one factor that may affect winter flounder, which is demersal throughout its life cycle (Pereira et al., 1999; Schultz et al., 2007). Because mortality rates associated with early life history stages may strongly influence fish recruitment processes (van der Veer, 1986; Houde, 1987; Nash and Dickey-Collas, 2005), protecting winter flounder eggs and larvae from

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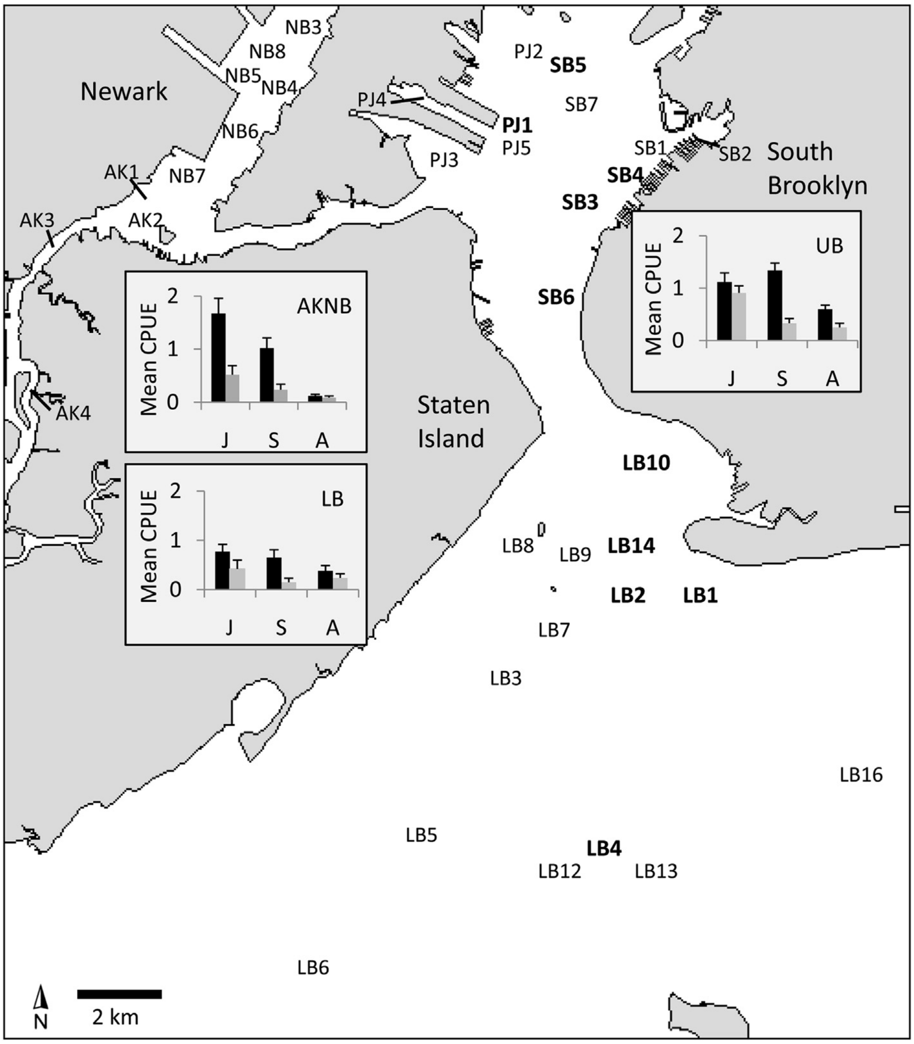

Fig. 1. Location of stations sampled by bottom trawl during the Aquatic Biological Survey conducted from 2002 through 2010 in the New York/New Jersey Harbor. Station labels for the harbor subarea Arthur Kill/Newark Bay (AKNB) begin with AK or NB, Lower Bay (LB) begin with LB, and Upper Bay (UB) begin with PJ (Port Jersey) or SB (South Brooklyn). Boldface labels indicate stations where five or more adult winter flounder were collected in single samples during the April/May critical feeding period. Histograms depict mean (+1 standard error) CPUE of juveniles (J), subadult (S), and adult (A) winter flounder at channel (black bars) and non-channel (gray bars) stations in each harbor subarea.

detrimental impacts is important to local population recovery. Knowledge of local habitat use is needed for management practices, such as seasonal dredging restrictions, to be effective. Therefore, a multi-year biological monitoring program (Aquatic Biological Survey – ABS) was designed by 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 the state environmental agencies of New York and New Jersey to better understand harbor habitat use by winter flounder and other demersal fish. ABS sampling was conducted in the winter and spring and included epibenthic sled collections (2002–2011) of winter flounder eggs and larvae (Wilber et al., 2013) and bottom trawl sampling (2002–2010) of juveniles and adults.

As with other inshore populations (e.g., Danila, 2000; Manderson, 2008; Fairchild et al., 2013), winter flounder abundances in New York estuaries have declined dramatically since the 1980s (ASMFC, 2006; Sagarese and Frisk, 2011) in association with more frequent high winter and spring temperatures, overfishing, and overall habitat degradation (Keller and Klein-MacPhee, 2000; Sagarese and Frisk, 2011). The conventional understanding of inshore winter flounder reproductive movements entails adult migrations into estuaries and shallow embayments in the early spring to spawn (Bigelow and Schroeder, 1953; Crawford and Carey, 1985; Pereira et al., 1999) in areas conducive to larval retention (Crawford and Carey, 1985; Chant et al., 2000). Recently, spawning activity of inshore populations has been observed in nearshore coastal habitat as well (Weunschel et al., 2009; DeCelles and Cadrin, 2010; Fairchild et al., 2013). Factors that underlie variable inshore spawning habitat use are not well described, although it is established that annual reproductive activity is greatly influenced by feeding success after spawning the previous spring (Burton and Idler, 1987; Wuenschel et al., 2009). Winter flounder prey primarily on benthic invertebrates (Pereira et al., 1999; Stehlik and Meise, 2000) that include clam siphons, polychetes and ampeliscidae amphipods in the New York/New Jersey area (Franz and Tanacredi, 1992; Carlson et al., 1997; Steimle et al., 1994, 2000). In this study, we use the ABS bottom trawl data to examine juvenile and adult winter flounder distribution patterns within the harbor, document correlations in annual abundances among eggs, juveniles and adults, and examine the relationship between the spring temperatures experienced by foraging adults and recruitment at the egg and Year-1 juvenile stages in subsequent years.

2. Methods

2.1. Field sampling and processing

The ABS program began in 1998 and was modified in response to the data needs of supporting agencies. The sampling protocol was standardized in 2002, and from 2002 to 2010, bottom trawl surveys were conducted in the winter (beginning in late December or early January) and spring (ending in May or June), which bracketed the winter flounder spawning season. A corresponding ABS epibenthic ichthyoplankton sled survey was conducted over the same time period (Wilber et al., 2013). Bottom trawl sampling (10 min tow duration) was conducted using a 9.1-m otter trawl with 2.5 cm square mesh wings and body and a 1.9 cm square mesh cod end with a 0.6 cm square mesh liner. A single tow was conducted at each station during each sampling period at approximately two week intervals from January through March and monthly thereafter. The total number of bottom trawls conducted each year ranged from 194 to 286 at fixed stations in channel and non-channel areas in the Arthur Kill/Newark Bay (AKNB), Lower Bay (LB) and Upper Bay (UB) subareas of the harbor (Fig. 1). Station locations were selected to provide information on habitat use for all harbor subareas and were influenced by practical considerations, such as avoiding vessel traffic and obstructions. The number of stations sampled annually ranged from 24 to 29 with the concentration of effort shifting increasingly toward LB non-channel stations in later years (Table 1) as it became increasingly apparent from the ABS ichthyoplankton surveys that winter flounder spawning in the AKNB areas was uncommon and shallow, non-channel areas (more common in LB) were favored as spawning sites (Wilber et al., 2013). Sixteen stations (eight channel and eight non-channel) were sampled by the bottom trawl all nine years and are hereafter referred to as the core stations (Table 1). Spatial coverage of all harbor subareas was maintained by the core stations, which were located in LB ($n = 6$), UB ($n = 6$), and AKNB ($n = 4$).

Bottom trawl sampling was conducted at night (between 1 h after sunset and 1 h before sunrise) from 2002 to 2004 and, due to

Table 2

Number (n) of adults (≥250 mm TL) identified by sex through March 31st each year. The total number of eggs collected at 16 core stations sampled by epibenthic sled is given for each year as reported in Wilber et al. (2013). The total adult abundance in April at 16 core bottom trawl stations indicates adult abundances during the post-spawning feeding period.

Year	Female n thru March	Male n thru March	% sex ID	F:M	Female CPUE	Male CPUE	Egg#	Adult n April
2002	25	9	89	2.78	0.23	0.08	123	12
2003	12	14	96	0.86	0.11	0.13	580	51
2004	3	2	100	1.50	0.04	0.03	30	9
2005	8	0	50	8+	0.09	0.00	36	26
2006	10	3	100	3.33	0.11	0.03	19	17
2007	15	16	100	0.94	0.16	0.17	589	20
2008	7	2	100	3.50	0.11	0.03	62	23
2009	3	4	100	0.75	0.03	0.04	106	6
2010	17	8	100	2.13	0.15	0.07	150	29

Table 1

Percentages of the combined total abundance of juvenile and adult winter flounder at each station each year (annual columns sum to 100%). Empty cells indicate that station was not sampled that year, whereas zero values indicate the station was sampled, but winter flounder were not collected. Harbor subareas are identified as Upper Bay (UB), Lower Bay (LB), and Arthur Kill/Newark Bay (AKNB). Station type is indicated as channel (CH) or non-channel (NC). The first 16 stations were sampled in all nine years (core stations). Most stations at the bottom were added to the survey in later years to examine shallow, non-channel habitat (more common in LB) more fully because it was favored spawning habitat (Wilber et al., 2013).

Station	Area	Station type	2002	2003	2004	2005	2006	2007	2008	2009	2010
AK-3	AKNB	CH	2.5	2.5	4.4	1.1	0.9	7.7	45.8	33.5	34.6
SB-5	UB	CH	11.8	6.7	1.1	16.4	21.6	14.4	15.4	28.0	5.1
LB-6	LB	CH	4.6	4.0	1.7	35.4	3.5	7.0	2.7	0.7	4.8
SB-4	UB	CH	1.9	3.1	6.3	1.1	10.6	17.7	3.2	6.0	4.9
AK-2	AKNB	CH	1.9	10.3	8.4	0.9	3.0	3.4	6.2	7.4	12.7
LB-2	LB	CH	14.1	1.3	1.2	17.0	5.7	1.4	4.0	3.9	1.7
PJ-1	UB	NC	8.9	11.7	7.2	1.1	2.2	3.0	2.4	3.7	6.2
SB-3	UB	NC	3.6	7.7	2.3	2.2	4.2	8.6	0.7	0.0	2.2
NB-7	AKNB	NC	9.7	9.6	3.8	1.9	0.0	0.3	0.3	2.0	1.0
SB-6	UB	CH	3.3	1.4	6.4	10.4	1.4	0.2	0.7	1.1	0.8
PJ-2	UB	NC	0.7	6.8	3.9	0.8	2.1	1.8	0.5	2.8	0.8
LB-4	LB	CH	3.6	3.6	3.7	1.1	2.1	1.6	1.5	0.5	0.4
LB-1	LB	NC	0.9	2.7	1.9	0.6	0.4	0.2	0.0	0.0	0.4
NB-4	AKNB	NC	2.0	1.8	0.7	0.5	0.0	0.0	0.0	0.2	0.1
LB-3	LB	NC	0.6	0.5	1.1	1.1	0.0	0.2	0.2	0.2	1.3
LB-5	LB	NC	0.5	0.2	3.0	0.0	0.0	0.2	0.1	0.0	1.1
PJ-5	UB	CH	6.8	7.5	14.6	0.4	12.0	21.8			0.0
NB-6	AKNB	CH	9.2	3.8	6.9	0.7	8.6	3.4			0.5
AK-1	AKNB	NC	1.1	1.0	11.0						0.0
PJ-4	UB	CH	2.2	2.8	1.5	0.0	10.5	3.4	5.1		0.0
NB-5	AKNB	CH	1.9	1.6	4.3	4.6	2.5	1.1			0.0
SB-1	UB	NC	0.9	2.1	0.0	0.0	4.6	1.8			0.0
NB-3	AKNB	NC	3.3	2.9	1.0	1.2	0.7	0.2			0.0
AK-4	AKNB	NC	2.6	0.2	2.0	0.8					0.0
PJ-3	UB	NC	1.0	3.7	0.7	0.7	0.4	0.5	0.3		0.0
SB-2	UB	NC	0.5	0.6	0.9		2.8	0.0			0.0
LB-14	LB	CH							7.3	3.9	5.3
SB-7	UB	CH									7.1
NB-8	AKNB	CH								3.2	2.8
LB-10	LB	NC							2.2	0.9	3.6
LB-12	LB	NC							0.1	1.4	1.1
LB-7	LB	NC							0.1	0.2	0.5
LB-9	LB	NC							0.6	0.0	0.1
LB-13	LB	NC							0.4	0.2	0.0
LB-16	LB	NC									0.2
LB-8	LB	NC							0.1	0.0	0.3

safety restrictions, during the day (between 1 h after sunrise and 1 h before sunset) from 2005 to 2010. All fish were counted and total length (TL) was measured to the nearest millimeter (mm). For those winter flounder ≥250 mm TL, if sex could not be determined in the field via extrusion of eggs or milt, fish were returned to the laboratory and gonads were dissected and examined. The number of adults examined in the laboratory was limited by a collector's permit. Beginning in 2008, all fish ≥250 mm TL returned to the laboratory were weighed. In most years, sex determinations were made for nearly all fish ≥250 mm TL collected through the end of March (Table 2), which corresponded with peak spawning activity (Wilber et al., 2013).

2.2. Statistical methods

Winter flounder catch-per-unit-effort (CPUE) was calculated as the number of fish captured per 10-min trawl and was standardized by trawl duration if tows were shorter due to obstructions. Analyses that compare CPUE across years use data from only the 16 core stations sampled each year to prevent confounding potential differences related to station location with other factors of interest. Because both juvenile (Casterlin and Reynolds, 1982) and adult (Stoner et al., 1999) winter flounder are nocturnal, the change from night to daytime sampling after 2004 may influence interannual comparisons of winter flounder abundances. A three-factor Analysis of Variance (ANOVA) was used to test for differences in overall winter flounder CPUE among harbor subareas (AKNB, LB, UB), station type (channel and non-channel) and time of sampling (night vs. day). Year was used as a source of replication after Pearson correlations among annual total CPUEs using one, two and three year time lags demonstrated no significant autocorrelations for these lag periods. Data were aggregated among stations by subarea × station type combinations for each year and log-transformed prior to analysis to satisfy assumptions of normality and homoscedasticity (Sokal and Rohlf, 1995). Bonferroni post-hoc comparisons were used to distinguish statistically different means. Similar three-factor ANOVAs were conducted separately for each of three size classes and results of two-factor ANOVAs (harbor subarea, station type) are reported because time of sampling was not included in any significant results in these tests. Size classes were designated to roughly correspond to approximate age categories based on both fish size and the date of collection (Witherell and Burnett, 1993; Able and Fahay, 2010; McBride et al., 2013). Size classes were designated as Year-1 juveniles (80–149 mm TL and <80 mm TL collected before May), subadult (150–249 mm TL), and adult (≥250 mm TL) and are hereafter referred to by these categories. Young-of-year (YOY, <80 mm TL collected in May and June) were collected primarily in June; however, sampling was not conducted in June for all years. In addition, other sampling methods, such as beam trawls (Goldberg et al., 2002) and beach seines (Manderson, 2008) are more appropriate gear types for reliably capturing these smaller individuals, therefore results for this age class are reported anecdotally and are not statistically analyzed. The minimum size for the adult size class (250 mm TL) is based on adult gonad development at 250 mm TL and attainment of sexual maturity between 280 mm and 300 mm TL (Witherell and Burnett, 1993), however, use of this size threshold may have missed some smaller mature males (B. Phelan, NOAA pers. comm.) and included some immature females (McBride et al., 2013). Potential differences in adult female size during the peak spawning season (January through March) between years with relatively low (2004, 2005, and 2006) vs. high (2003 and 2007) egg production in the harbor (Table 2; Wilber et al., 2013) were tested by harbor subarea (LB and UB) with a two-factor ANOVA. The AKNB harbor subarea was not included in this analysis because egg collections in this area were uncommon. A condition index (Burton and Idler, 1984; Wuenschel et al., 2009; Pereira et al., 2012) was estimated for each individual as its residual from the log–log regressions of mass to length (Le Cren, 1951; Jakob et al., 1996) and was calculated separately for females (Fig. 2a) and males (Fig. 2b). Fluctuations in condition indices reflected energy depletion and accumulation in adults during and after the spawning season, respectively.

Associations among egg, juvenile, and adult annual abundances were explored using Pearson correlations that incorporated appropriate time lags into the analyses. Total annual egg abundances at 16 core stations sampled in the ABS ichthyoplankton survey (Wilber et al., 2013) were square-root transformed to meet normality and variance assumptions of the analyses. Juvenile and adult abundances were adequately represented by untransformed CPUE. Water temperature data recorded at the NOAA gage (station ID 8518750) located at the Battery in New York City were used in tests of potential associations between temperature parameters and annual winter flounder egg and Year-1 juvenile abundances. Similar analyses were conducted using data from another estuarine system for which both long-term winter flounder monitoring and temperature data were available (Niantic Bay, Connecticut near the Millstone Power Station; DNC, 2011) to explore whether results observed in the harbor matched those of another estuarine system.

3. Results

Bottom trawls ($n = 2069$) conducted in the winter and spring of 2002–2010 captured a total of 5234 winter flounder (3030 juveniles, 1655 subadults, and 549 adults). The total number of winter

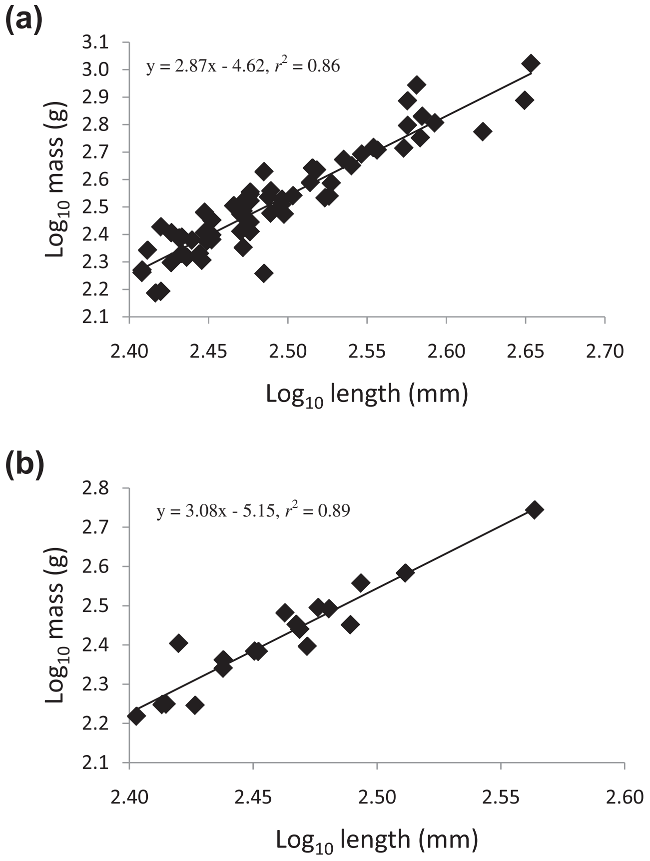

Fig. 2. Log–log regression of mass and total length from adult (a) female and (b) male winter flounder collected from December/January through March from 2008 to 2010. Individual condition is estimated as the residual from these regressions.

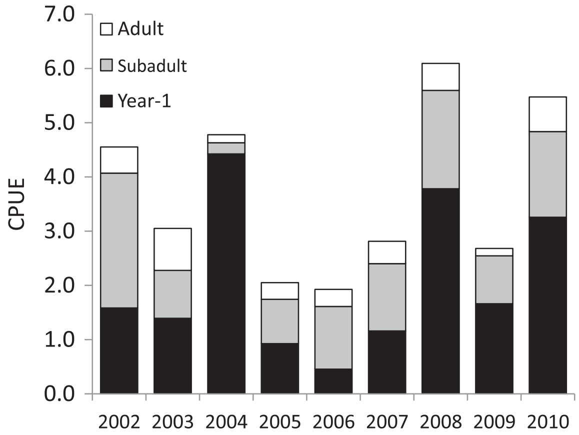

Fig. 3. Annual mean CPUE for Year-1 juveniles (black; 80–149 mm TL and <80 mm TL collected before May), subadult (gray; 150–249 mm TL), and adult (white; ≥250 mm TL), at the sixteen core stations. Young-of-year CPUE is not displayed because of interannual sampling biases that may have affected this size class. Sampling was conducted at night from 2002 to 2004 and during the day thereafter.

founder collected per trawl ranged from 0 to 161 fish. Variation in total fish CPUE among years largely was caused by variation in Year-1 juvenile abundances, which were relatively high in 2004, 2008, and 2010 (Fig. 3). Sex determinations were made for 406 winter flounder ≥250 mm TL (290 females, 116 males) including nearly all adults collected through March (Table 2), coincident with peak spawning activity (Wilber et al., 2013). Sex determinations were made on a lower percentage of fish collected later in the spring because quotas specified in collection permits had been reached by that time.

3.1. Spatial distribution patterns

Total winter flounder CPUE differed significantly by the time of sampling (day vs. night) and station type (channel vs. non-channel) interaction (Table 3). CPUEs were higher at channel than non-channel stations in years with daytime sampling, whereas there was no significant difference in CPUE between station types when sampling was conducted at night (Bonferroni $p < 0.001$). This result is consistent with a pattern of nocturnal activity in which winter flounder occupy channels during the day and move to shallow non-channel habitat at night. When fish distributions were analyzed separately for each size class, the time of sampling was not part of any significant results in the three-factor ANOVAs. Year-1 juvenile CPUE was significantly higher at channel stations in AKNB than in other harbor areas by station type combinations (Bonferroni, $p < 0.05$; Table 4). Subadult and adult CPUE differed by both harbor subarea and station type, with no interactions (Table 4). Subadult and adult densities were higher in the channels and subadult CPUE was higher in UB than LB (Bonferroni, $p < 0.05$), whereas adult CPUE was lower in AKNB than in UB and LB (Bonferroni, $p < 0.05$). YOY individuals were collected in years when sampling was conducted in June (2002–2007) and were relatively abundant in some years, (e.g., $n = 118$ in 2002) and uncommon in others ($n = 2$ in 2005 and $n = 1$ in 2006). Nearly all of the YOY individuals collected were captured in the AKNB (54%) or UB (44%) subareas and at non-channel stations (69%).

Table 3
Analysis of variance (ANOVA) results comparing total winter flounder CPUE by harbor subarea (AKNB, LB, UB), station type (channel vs. non-channel), and time of sampling (day vs. night).

	df	MS	*F*	*p*
Subarea	2	1.35	4.45	0.018
Station type	1	6.08	20.00	<0.001
Time of sampling	1	1.21	3.98	0.052
Subarea × station type	2	0.31	1.02	0.370
Subarea × time of sampling	2	0.01	0.01	0.991
Station type × time of sampling	1	2.21	7.27	0.010
Subarea × station × time of sampling	2	0.27	0.87	0.425
Error	42	0.30		

Stations with relatively high abundances in single catches were identified to potentially locate important spawning, nursery, and foraging habitat based on fish size and time of year. Twenty or more winter flounder were collected in a single trawl ten or more times at channel stations (AK-3 and SB-5). The high abundance collections at AK-3 all occurred from 2008 to 2010 and involved primarily Year-1 juveniles. Sediments at station AK-3 are sandy silt with a relatively high total organic content (4.3% TOC, Wilber et al., 2013). Adults dominated the high abundance catches at SB-5, where sediments are sandy silt with 2.1% TOC (Wilber et al., 2013). Five or more adults captured in single trawls occurred exclusively in the LB and UB areas primarily in April and May (Table 5), which is the critical post-spawning feeding period.

3.2. Temporal patterns

Adult abundances peaked in April, declining sharply in May, with few adults captured in June. Although interannual variation in abundances was not as pronounced for adults as for Year-1 juveniles (Fig. 3), there was considerable variation among years in the number of adults collected during the spawning season, especially for males (Table 2). Annual adult male and female CPUEs during the spawning season were not correlated ($r = 0.48$, $p > 0.1$). Condition indices for females were mostly positive prior to spawning in January, reflecting relatively high energy reserves, followed by more negative indices in March and April, which corresponds to the end of the spawning season and the depletion of stored energy (Fig. 4a). Condition indices returned to mostly positive values in May when energy reserves are being restored. A similar seasonal fluctuation in condition indices occurred for males (Fig. 4b). Adult sex ratios were female-biased during the spring spawning season in six of the nine years of sampling (Table 2). The spatial distribution of winter flounder among harbor areas and by station type did not differ by sex. The size of females collected during the spawning season did not differ between years with high vs. low egg production, however overall, female size in LB (mean ± standard error = 336 ± 14 mm TL) was significantly larger ($F = 4.0$, $p < 0.05$) than in UB (298 ± 7 mm TL). Adult male size did not differ between time periods or harbor subareas.

3.3. Associations among life history stages

Annual egg abundances were positively correlated with adult male ($r = 0.95$, $p < 0.001$; Fig. 5a), but not adult female ($r = 0.33$, $p > 0.1$; Fig. 5b) CPUE during the spawning season. The strength of the positive correlation for males increased ($r = 0.97$, $p < 0.001$) when the size threshold was increased to ≥280 mm TL, whereas increasing the size threshold (using 280, 300, 320 and 350 mm TL) for females did not produce any significant correlations with egg abundances. Larger sizes may be better estimates of the size of reproductive maturity for females in this area (McBride et al., 2013). Annual egg abundances were positively correlated with Year-1 juvenile CPUE the following year ($r = 0.89$, $p = 0.003$; Fig. 6).

Table 4
Results of separate ANOVAs that compare winter flounder CPUE between harbor subareas and station types for each age class.

	Year-1 juvenile				Sub-adults			Adults		
	df	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
Subarea	2	1.28	4.10	0.023	0.84	5.37	0.008	0.47	9.62	<0.001
Station	1	4.36	13.99	0.001	7.86	50.21	<0.001	0.44	8.94	0.004
Subarea*station	2	1.17	3.72	0.031	0.28	1.80	0.176	0.12	2.38	0.103
Error	48	0.31			0.16			0.05		

3.4. Associations with temperature

Mean April water temperatures were positively correlated with both annual egg abundances the following year ($r = 0.69$, $p < 0.05$; Fig. 7) and Year-1 juvenile CPUE two years later ($r = 0.75$, $p < 0.01$). Similarly,Year-1 juvenile winter flounder CPUE in Niantic Bay, CT was positively correlated with mean April temperatures (with a two-year time lag) over the same time period (2002–2010; $r = 0.89$, $p = 0.001$; Fig. 8). Other spring temperature parameters (e.g., March and April mean temperatures, spring maxima) were used in analyses with a one-year time lag to discern a potential influence of temperature on larval development. However, these were not significant variables in correlations with Year-1 abundances for either the harbor or Niantic winter flounder populations. In addition, tests for correlations between April temperatures and adult winter flounder abundances were not significant.

4. Discussion

4.1. Associations with temperature

High water temperatures are negatively associated with winter flounder larval size (Keller and Klein-MacPhee, 2000; Wilber et al., 2013) and the survival of early life stages (Rogers, 1976; Taylor and Collie, 2003; Taylor and Danila, 2005; Manderson, 2008). Yet, warmer water temperatures also enhance benthic secondary production (Edgar, 1990; Tumbiolo and Downing, 1994), which is needed to replenish depleted energy reserves following spawning. The feeding season that follows spawning is a nutritionally sensitive period for early gametogenesis in female winter flounder,

Table 5
Month and stations where five or more adult winter flounder were captured in a single sample listed by harbor subarea (LB and UB) and station type (channel vs. non-channel).

Year	Month	Station	Harbor subarea	Station type	# of adults in sample
2002	May	LB-2	LB	CH	8
2003	April	LB-1	LB	NC	15
2003	April	PJ-1	UB	NC	11
2003	April	SB-3	UB	NC	9
2003	April	SB-4	UB	CH	5
2003	May	LB-4	LB	CH	12
2003	May	LB-6	LB	CH	7
2003	May	PJ-1	UB	NC	8
2005	March	SB-5	UB	CH	10
2005	April	SB-6	UB	CH	17
2006	April	SB-5	UB	CH	14
2007	April	SB-4	UB	CH	19
2008	April	SB-5	UB	CH	16
2008	April	LB-14	LB	CH	13
2008	April	LB-6	LB	CH	5
2009	April	SB-5	UB	CH	5
2010	April	LB-10	LB	NC	5
2010	April	SB-5	UB	CH	12
2010	April	LB-6	LB	CH	5
2010	April	LB-6	LB	CH	5

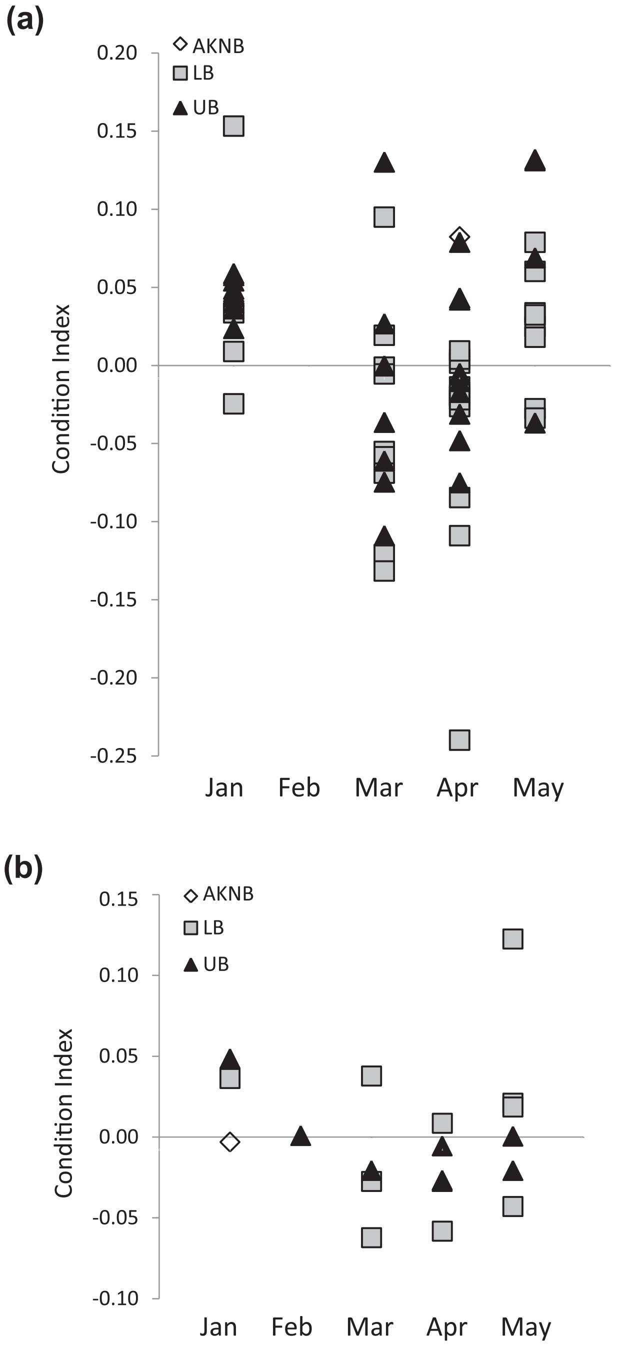

Fig. 4. Condition index (residual from the log–log regression of mass to length) for (a) female and (b) male winter flounder (≥250 mm TL) collected from 2008 to 2010 for each harbor subarea, Arthur Kill/Newark Bay (AKNB), Lower Bay (LB), and Upper Bay (UB) during each month of sampling.

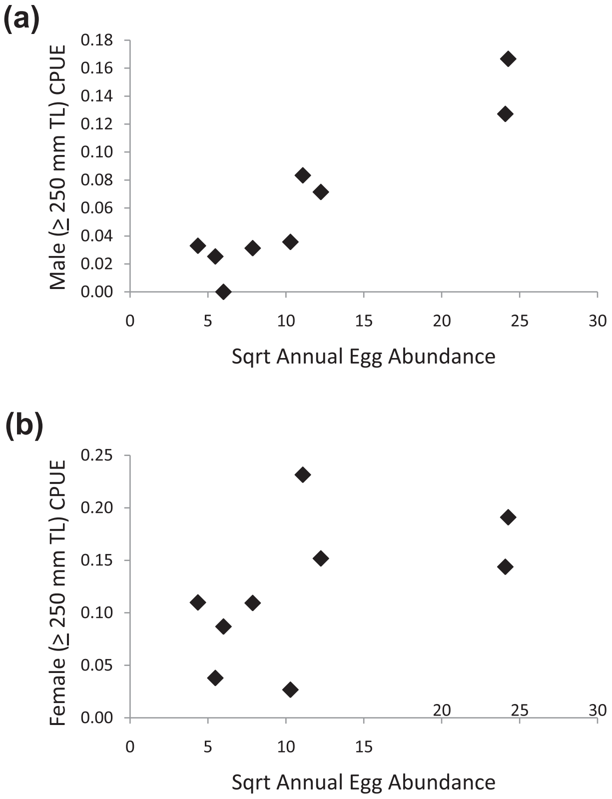

Fig. 5. Correlations between annual egg abundances (square-root transformed) and adult (a) male ($r = 0.95$, $p < 0.001$), and (b) female ($r = 0.33$, $p > 0.1$) CPUE during the spring spawning season. Both egg and adult abundances were calculated from core stations sampled each year from 2002 to 2010.

which may become non-reproductive the following spawning season if food is limited (Burton and Idler, 1987; Burton, 1994; Wuenschel et al., 2009). The timing of warmer spring temperatures, therefore, may be important to determining winter flounder reproductive success. Results of this study suggest that when warm temperatures coincide with the limited time period between spawning and adult emigration to deeper coastal habitat that is triggered by rising temperatures (Danila and Kennish, 1981; DeCelles and Cadrin, 2010), winter flounder reproductive activity in the estuary is high the following year.

Recent genetic evidence indicates that winter founder in six New York estuaries are inbred, with few mature adults spawning in the estuaries (O'Leary et al., 2013). The small number of spawning adults may reflect nutritional deprivation that results in “skipped” spawning, which has been observed in 5–30% of winter flounder throughout its range (McElroy et al., 2013). The strategy of sacrificing reproduction to maintain body size in times of food shortages (Tyler and Dunn, 1976; Burton, 1991) also occurs in plaice *Pleuronectes platessa* (Kennedy et al., 2008) and males of some species (Rideout and Tomkiewicz, 2011). Benthic prey resources in the harbor were not quantified during this study, however, the corresponding relationship between April temperatures and juvenile winter flounder abundances two years later in Niantic Bay, CT indicates the temporal overlap between benthic secondary production and adult winter flounder foraging activity in estuaries deserves further study. Temperature's effect on winter flounder populations is complex and evident on a regional scale (e.g., Manderson, 2008; current study). The potential effect of management measures designed to minimize local impacts on pressed winter flounder populations, therefore, should be considered relative to the demonstrated associations between annual fluctuations in temperature and year-class strength. Effective management also requires spatially and temporally explicit information on estuarine habitat use.

4.2. Harbor habitat use

Juvenile and adult winter flounder occupied New York/New Jersey harbor differently. Juveniles were most abundant in Arthur Kill channels where silt/clay and %TOC were relatively high, similar to other observations of juveniles in muddy habitats (Howell et al., 1999; Meng et al., 2005). In contrast, adults did not use the AKNB subarea extensively either for foraging or spawning. During the April feeding period, adults were concentrated near clam and mussel beds in UB (Iocco et al., 2000, Fig. 1) and occurred in LB where their benthic amphipod prey, *Ampelisca abdita*, (Steimle et al., 2000) has historically comprised >50% of the benthos (Cerrato, 2006).

Studies that sample concurrently in both estuarine and nearshore coastal habitat for winter flounder are needed to improve our understanding of their relative spawning habitat use. In this study, males were uncommon during the spawning season in years with low egg abundances and may have been with spawning females in shallow coastal habitat, resulting in female-biased sex ratios in the harbor. Winter flounder larvae occur in the nearshore and surf zone

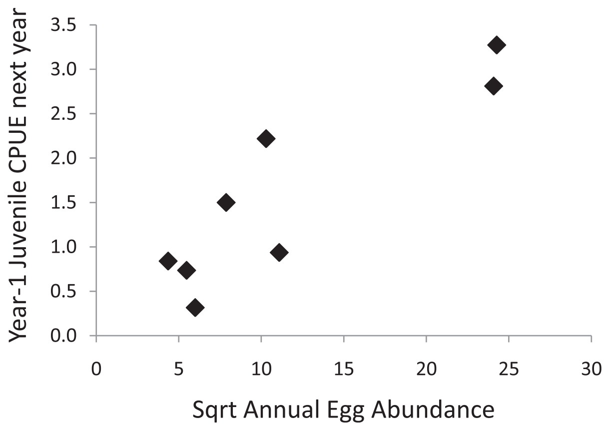

Fig. 6. Correlation between annual egg abundances (square-root transformed) and Year-1 juvenile CPUE one year later ($r = 0.89$, $p = 0.003$).

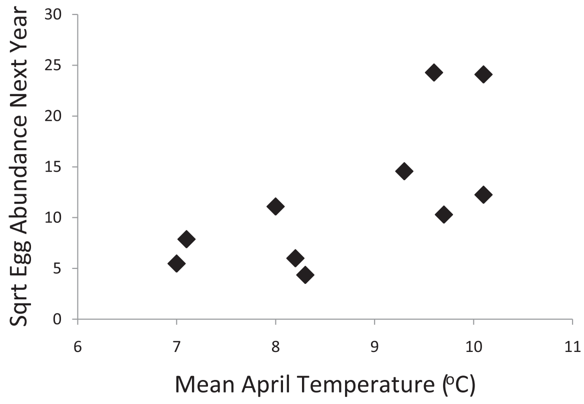

Fig. 7. Mean April water temperature from 2001 to 2010 (NOAA gage 8518750) plotted against annual winter flounder egg abundances (square-root transformed) in the harbor the next year (2002–2011). Egg abundances were calculated from 16 core stations sampled each year (Table 2, Wilber et al., 2013).

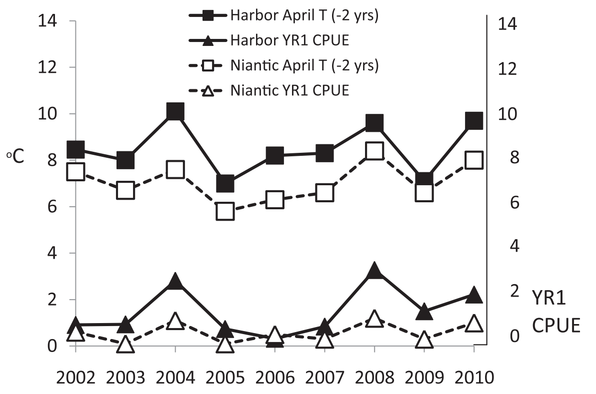

Fig. 8. Mean April water temperatures (2000–2008) in the harbor and Niantic Bay (black and white squares, respectively) plotted with a two-year lag and a plot of Year-1 juvenile CPUEs for the harbor and Niantic Bay (black and white triangles, respectively).

environments of northern New Jersey (Able et al., 2010). The strong correlation between annual egg production and adult male CPUE during the spawning season and the absence of a similar correlation for females suggests that adult males in the estuary during the spawning season are reproductively active, whereas some adult females are non-reproductive and may be foraging. Female-biased sex ratios have become increasingly common in another inshore population (Niantic River and Bay, CT) over the last several decades (DNC, 2011). Nearshore spawning on the inner continental shelf of New Jersey (Wuenschel et al., 2009) and in the Gulf of Maine (Fairchild et al., 2013) may result from a division of spawning site selection for contingents within populations (DeCelles and Cadrin, 2010) or alternate states (estuarine vs. nearshore spawning) that vary annually for the majority of a population. Spawning within estuaries promotes a localized population structure from the egg through the juvenile stages (DeCelles and Cadrin, 2010) and limited movement by juveniles further restricts connectivity among estuarine populations (Buckley et al., 2008; Manderson, 2008; Sagarese and Frisk, 2011). The positive correlation between annual egg production and Year-1 juvenile CPUE the following year for the harbor population is further evidence that estuarine populations are highly localized through the early life stages.

The positive association between April water temperatures experienced by foraging adults and subsequent winter flounder year-class strength suggests a previously unrecognized mechanism by which temperature may affect declining inshore winter flounder populations as well as other benthic-feeding species. The relative use of estuarine vs. nearshore habitat for spawning by winter flounder may further influence inshore population recovery because estuarine spawning populations, in at least some cases, are small and inbred, which may lower survival and reproductive rates (O'Leary et al., 2013). Our finding that adult male abundances during the spawning season are closely correlated with the magnitude of estuarine spawning activity may be useful to other studies for estimating the relative contribution of estuarine spawning to overall reproductive effort for inshore winter flounder populations.

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