Predation on post-settlement winter flounder *Pseudopleuronectes americanus* by sand shrimp *Crangon septemspinosa* in NW Atlantic estuaries

David L. Taylor*

Marine Field Station, Institute of Marine and Coastal Sciences, Rutgers University, 800 c/o 132 Great Bay Boulevard, Tuckerton, New Jersey 08087-2004, USA

ABSTRACT: Assessing predation risk is necessary to evaluate the functional significance of estuaries as critical nursery habitats for juvenile fishes. The objective of this study was to quantify rates of sand shrimp *Crangon septemspinosa* predation on post-settlement winter flounder *Pseudopleuronectes americanus* in 3 NW Atlantic estuaries: Narragansett Bay (Rhode Island), Niantic River (Connecticut), and Navesink River/Sandy Hook Bay (New Jersey). Sand shrimp were collected from designated study sites in late spring and summer (2001 and 2002), and their stomach contents were analyzed with immunological assays to detect the presence of juvenile winter flounder in the diet. The results indicate that sand shrimp are possible sources of intense predator-induced mortality for newly settled winter flounder. There was a direct relationship between the incidence of winter flounder in shrimp stomachs and the body size and density of shrimp. The importance of sand shrimp as a mortality factor for winter flounder in the Navesink River/Sandy Hook Bay was minimal due to the low abundance of large shrimp (≥30 mm total length). Conversely, in Narragansett Bay and the Niantic River predation rates were high because of the presence of large shrimp during peak winter flounder settlement periods (May to early June), when the flatfish are small in size and vulnerable to predation. Thus, sand shrimp predation rates on winter flounder depend on the relative spatial and temporal overlap between the settlement of flounder to the benthos and the movement patterns of large shrimp that migrate into shallow estuaries to reproduce and feed.

KEY WORDS: *Crangon septemspinosa* · *Pseudopleuronectes americanus* · Sand shrimp · Winter flounder · Predation · Immunoassay · Estuaries

INTRODUCTION

The functional significance of estuaries as a critical nursery habitat is impacted greatly by the sources of mortality that affect year-class strength and recruitment of estuarine-dependent fish (Gibson 1994, Scharf 2000, Sogard et al. 2001). There is a general consensus that the size of a given year-class of fish is determined during the early life history stages, when mortality rates are substantial and highly variable (Bailey & Houde 1989). Of the multitude of factors thought to regulate year-class formation, predation is perhaps the most important (Bailey & Houde 1989). Predation risk is therefore a key determinant in establishing the role of estuaries as nursery habitat (Gibson 1994). For many species of flatfishes, survival during the post-settlement stage depends on the habitat suitability of resident estuaries. Nevertheless, relatively few studies have quantitatively examined the effect of predation on habitat suitability for juvenile flatfishes (exceptions include Pihl & Van der Veer 1992, Gibson 1994, Manderson et al. 1999). Moreover, very little is known regarding the spatial variability in predation risk within the geographic distribution of post-settlement flatfishes and their respective predators.

The winter flounder *Pseudopleuronectes americanus* Walbaum is a pleuronectid flatfish that has traditionally supported valuable commercial and recreational

fisheries. This species is distributed along the NW Atlantic coast, with maximal abundance occurring inshore between the Gulf of St. Lawrence and Chesapeake Bay (Collette & Klein-MacPhee 2002). Spawning occurs in estuaries during the winter and early spring, after which adult winter flounder migrate offshore as water temperatures exceed 15°C (Collette & Klein-MacPhee 2002). Several factors reduce the dispersion of early-stage winter flounder within natal estuaries, including production of demersal eggs, bottom-oriented larval behavior, and metamorphosis at a relatively small size (8 to 9 mm total length; Chambers & Leggett 1987). Moreover, young-of-the-year winter flounder demonstrate limited movement during their summer residence in shallow estuaries (Saucerman & Deegan 1991). These characteristics of limited mixing of adult populations and limited movements of early-stage winter flounder suggest that individual estuaries support discrete local populations.

The small size at which most post-metamorphic flatfishes settle to the benthos render the individuals vulnerable to a suite of crustacean and demersal fish predators (Manderson et al. 1999, 2000, Fairchild & Howell 2000, Taylor 2003a). Predation by crangonid shrimp (*Crangon* spp.), for example, is a source of high mortality for newly settled flatfish, and thus, possibly dictates year-class strength (Van der Veer & Bergman 1987, Seikai et al. 1993, Taylor & Collie 2003a). In particular, sand shrimp *Crangon septemspinosa* Say is a common estuarine decapod distributed along the NW Atlantic from Newfoundland to eastern Florida, hence spatially overlapping with the geographic distribution of winter flounder (Price 1962, Haefner 1979). Sand shrimp are omnivores and feed primarily upon detrital matter, mollusks, arthropods, annelids and fishes (Wilcox & Jeffries 1974, Taylor & Peck 2004). Based on laboratory feeding experiments, there is increasing evidence that sand shrimp are a significant source of mortality for post-settlement winter flounder (Witting & Able 1995, Taylor 2003a, Taylor & Collie 2003a). Despite these laboratory findings, however, there is limited information on the extent to which shrimp prey on winter flounder in the field (Witting 1995, Taylor 2004).

Visual estimates of a predator's stomach contents have traditionally been used to elucidate trophic linkages under field conditions. For example, previous attempts to identify winter flounder in the diet of sand shrimp have relied on the visual identification of flounder remains (otoliths, scales and fin rays) in the stomach contents of suspected shrimp predators (Wilcox & Jeffries 1974, Witting 1995). However, visually identifying fishes in the diet of shrimp is hampered due to the mastication of prey tissue by mandible and gastric mill grinding. Moreover, determining predation rates

through visual analyses may lead to erroneous conclusions because of suspected predators (1) ingesting particulate matter and other prey items that resemble the target prey, and (2) incomplete or partial predation events that do not result in the ingestion of identifiable remains (Feller 1991, Seikai et al. 1993).

As an alternative approach to visual estimations, biochemical techniques provide a means of positively identifying prey proteins in a predator's stomach. Immunological assays, for example, have been used to successfully identify the stomach contents of several marine crustaceans, including crangonid shrimp (Brodeur & Merati 1993, Van der Veer et al. 1998). In a recent study, Taylor (2004) developed winter flounder-specific antiserum that successfully identified juvenile flounder proteins in the stomach contents of sand shrimp. Moreover, preliminary analysis of the diet of field-collected sand shrimp revealed that this species is a predator of post-settlement winter flounder in natural populations (Taylor 2004). This paper is an extension of the previous research and attempts to quantify sand shrimp predation rates on winter flounder from 3 NW Atlantic estuaries. Moreover, differences in estuarine-specific attributes of both predator and prey (e.g. shrimp and flounder population density and size-structure, flounder growth) were analyzed relative to estimated predation rates to determine the impact on localized winter flounder mortality.

MATERIALS AND METHODS

Field sampling. Post-settlement winter flounder and sand shrimp were sampled from late spring to late summer over a 2 yr period (2001 and 2002) in 3 NW Atlantic estuaries (Table 1, Fig. 1). In 2001, 2 stations in Narragansett Bay (Rhode Island) were sampled from mid May to early June with weekly beam trawls (1.3 m width; 0.06 cm mesh size). At each station, 2 to 3 tows were made on each sampling date during the morning hours (06:00 to 08:00 h). Field sampling continued in Narragansett Bay from June to October, with monthly seine hauls, whereby 1 seine haul was conducted from a boat at each of the 2 stations on each sampling date with a 61 × 3.05 m beach-seine set (0.64 cm mesh size and 0.48 cm bunt). The 2002 field-sampling protocol in Narragansett Bay was the same as in the previous year, with the exception that the beam trawl survey began in late March and finished in late August.

Field sampling in the Niantic River (Connecticut) occurred at 2 stations from late May to the end of September in 2001 and 2002 (Table 1, Fig. 1). Fortnightly sampling was performed with two 1 m beam trawls equipped with tickler chains and nets of 0.08 and 0.16 cm mesh (1 mesh size per trawl frame); 4 tows

Table 1. Summary of field sampling protocol and habitat characteristics of Narragansett Bay (Rhode Island), Niantic River (Connecticut), and Navesink River/Sandy Hook Bay (New Jersey). nm: not measured

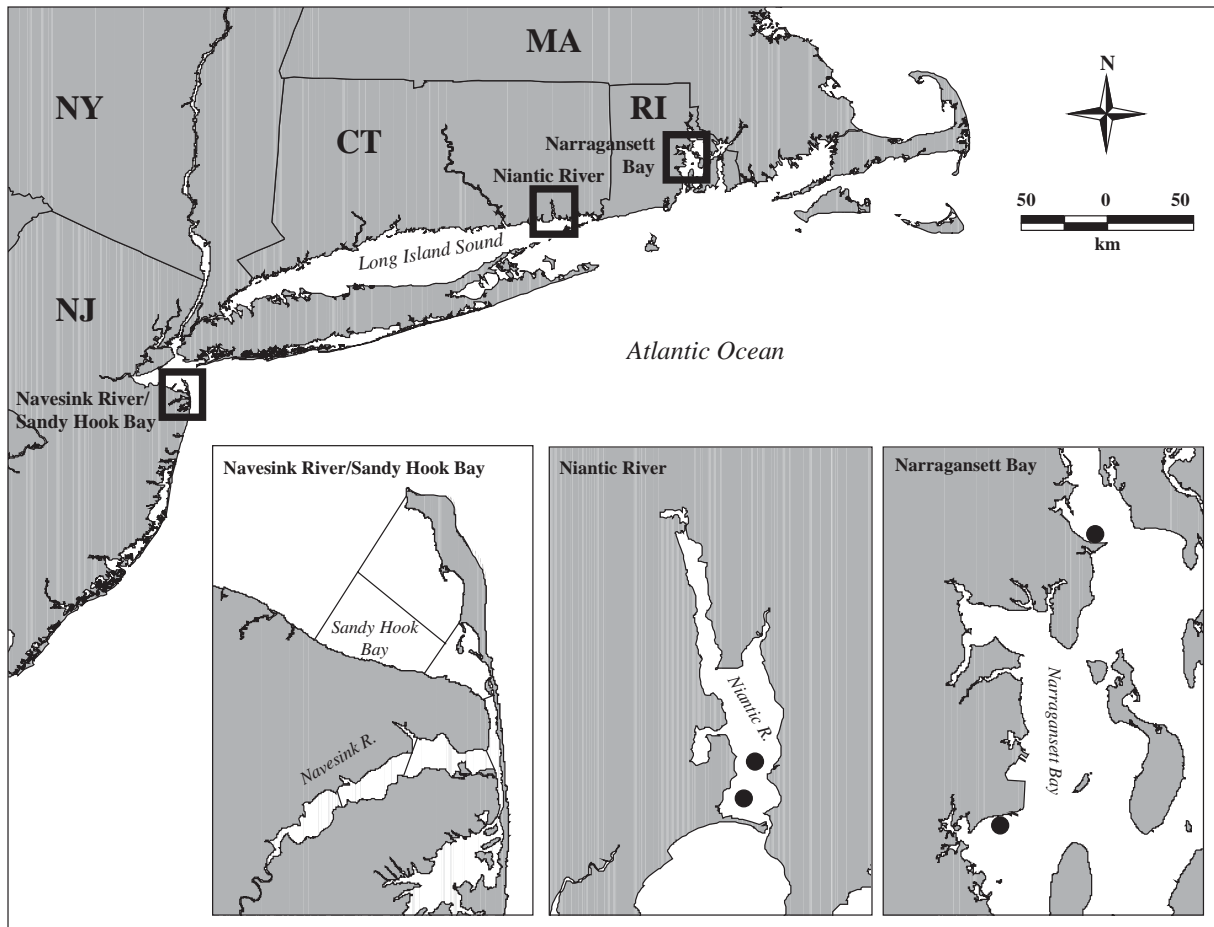|	Site			
	Narragansett Bay		Niantic River	Navesink River/ Sandy Hook Bay
Sampling protocol				
Sampling gear	Beam trawl	Beach seine	Beam trawl	Beam trawl
Date (2001/2002)	May–Jun/Mar–Aug	Jun–Oct/Jun–Oct	May–Sep/May–Sep	Apr–Sep/Apr–Jun
Time of day	Morning	Morning to midday	Morning to midday	Morning to midday
Tide (relative to high tide)	Variable	±2 h	±2 h	Variable
No. sites sampled	2	2	2	12
Area sampled effort^{-1} (m^2)	26	500	40–100	30–60
Sample frequency	Weekly	Monthly	Fortnightly	Weekly to fortnightly
Habitat characteristics				
Depth (m)	1–2	0–3	1–2	0.5–8
Salinity (ppt)	nm	26.2–32.7	28.0–30.7	10.3–29.1
Temperature (°C)	4.5–21.5	11.4–25.0	10.1–23.9	9.6–26.9
Substrate	Fine sands, medium sands	Fine sands, medium sands	Fine sands, shell hash	Silt, fine sands, coarse sands
Vegetation	None to intermittent macroalgae	None to intermittent macroalgae	None to intermittent macroalgae	None to intermittent macroalgae

Fig. 1. Location of sampling sites in NW Atlantic: Narragansett Bay (Rhode Island), Niantic River (Connecticut), and Navesink River/Sandy Hook Bay (New Jersey). Insets demarcate specific sampling areas in each respective estuary: (●) Narragansett Bay and Niantic River, and line-grid: Navesink River/Sandy Hook Bay

were made on each sampling date (2 from each beam trawl with nets of different mesh size).

Sampling in the Navesink River/Sandy Hook Bay (New Jersey) was conducted as a stratified random design with 12 stations chosen throughout the estuary in 2001 (Table 1, Fig. 1). Beam trawls (1 m width; 0.30 cm mesh size) were performed weekly from mid April to the end of June, after which fortnightly sampling occurred from June to the end of September. A similar, but less extensive, beam trawl survey was performed in 2002 in the Navesink River/Sandy Hook Bay.

Winter flounder and sand shrimp size-frequency and density. Winter flounder captured during field sampling were enumerated, measured to the nearest 1 mm for total length (TL), and returned to the place of capture. Collected sand shrimp were placed on ice after capture and then frozen at –20°C in the laboratory. Shrimp TL was determined to the nearest 1 mm by measuring with calipers from the tip of the antennal scale to the end of the telson. Moreover, shrimp collected in Narragansett Bay were grouped by sex and reproductive status. Shrimp measuring ≤20 mm TL were defined as juveniles, whereas individuals >20 mm TL were sexed by means of dimorphism observed on the endopodite of the first pleopod (Price 1962). The reproductive status of female shrimp (ovigerous or non-ovigerous) was determined by the presence or absence of an egg mass attached to the abdomen (Price 1962).

Winter flounder and sand shrimp size-frequency over time was estimated from the catch and length data averaged over monthly intervals. Catch data were standardized to number of individuals m^{-2} and calculated assuming 60 and 30% efficiency of the beam trawl and seine sampling gear, respectively (Kuipers 1975, Pierce et al. 1990, Kuipers et al. 1992). For winter flounder, length-frequency distributions were estimated for each sampling year from May to August in Narragansett Bay (excluding May 2001), Niantic River and Navesink River/Sandy Hook Bay (excluding 2002). For sand shrimp, length-frequency distributions were estimated from April to September in Narragansett Bay (excluding April 2001) and the Navesink River/Sandy Hook Bay (excluding 2002). Shrimp population density and size-structure was not quantitatively measured in the Niantic River.

The abundance of winter flounder in the 3 estuaries was determined at daily intervals by fitting a normal density function to catch data (no. flounder m^{-2}) over time by least-squares analysis:

$$\rho_{(f,t)} = \left[\frac{1}{\sigma\sqrt{2\pi}} e^{-0.5[(t-\mu)/\sigma]^2} \right] \cdot \varepsilon \qquad (1)$$

where $\rho_{(f,t)}$ is the density of flounder (no. flounder m^{-2}) at time t (day of year), μ is the arithmetic mean of the

distribution that indicates the day of year of maximum density, σ is the standard deviation of the distribution, and ε is a correction parameter that converts the probability mass function to units of density (no. flounder m^{-2}). Winter flounder catch data incorporated into Eq. (1) were pooled across years for Narragansett Bay and the Niantic River, and for the Navesink River/Sandy Hook Bay flounder density was only calculated in 2001. Pairwise Kolmogorov-Smirnov tests were performed on seasonal winter flounder abundance data to compare density distributions from 2 estuaries against the null hypothesis that both samples were from populations with the same parametric distribution (Sokal & Rohlf 1981).

The size-structure and density of adult sand shrimp (≥30 mm TL) was determined at daily intervals by fitting a least-squares second-order polynomial to catch (no. shrimp m^{-2}) and size (mm TL) data:

$$\rho_{(s,t)} = \alpha + \beta_1 t^2 + \beta_2 t + \beta_3 L_{(s,t)}^2 + \beta_4 L_{(s,t)} \qquad (2)$$

where $\rho_{(s,t)}$ is the density of shrimp (no. shrimp m^{-2}), α is the intercept parameter, β_{1-4} are the vectors of the slope parameters, and $L_{(s,t)}$ is the TL (mm) of individual shrimp collected at time t (day of year). Shrimp catch data incorporated in Eq. (2) were pooled across years for Narragansett Bay, and for the Navesink River/Sandy Hook Bay shrimp density was only calculated in 2001. Moreover, density calculations were based solely on the abundance of shrimp ≥30 mm TL because these individuals were the main predators of post-settlement winter flounder (see 'Results'). Kolmogorov-Smirnov tests were performed on the abundance of large shrimp over time to compare density distributions between 2 estuaries (Sokal & Rohlf 1981).

Winter flounder growth. Winter flounder annual growth rates analyzed separately for Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay were determined by first fitting the Ludwig von Bertalanffy (LVB) growth model to the mean body size of flounder measured during field sampling (2001 and 2002 combined):

$$L_{(f,t)} = L_{(f,\infty)}\left[1 - e^{-\kappa(t-t_0)}\right] \qquad (3)$$

where $L_{(f,t)}$ is the mean TL (mm) of flounder measured at time t (day of year), t_0 is a location parameter that indicates the x-intercept of the curve, and κ is the Brody growth coefficient, or curvature parameter, that dictates the speed with which the curve approaches asymptotic length, $L_{(f,\infty)}$. The asymptotic length of winter flounder was assumed to be 460 mm TL (Collette & Klein-MacPhee 2002). The remaining parameters of the LVB growth model (t_0 and κ) were estimated by non-linear least-squares analysis. The effect of day of year on winter flounder body size (i.e. growth rate) as a function

of site (Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay) was analyzed with the Fisher-Behrens statistic, whereby variances need not be constant across treatments and the statistic is compared to a critical value of a *t*-distribution (Cerrato 1990).

Results from the LVB model were used to estimate the daily growth rate of winter flounder (mm d^{-1}), averaged over the time period individuals were vulnerable to sand shrimp predation (i.e. mortality window). The timescale of the mortality window was defined from initial winter flounder settlement (body size = 8 mm TL; Chambers & Leggett 1987) and concluded once fish achieved a body size large enough to preclude them as prey for shrimp (25 mm TL; Witting & Able 1995, Taylor 2003a).

Sand shrimp stomach-content analysis. Qualitative immunoassays, utilizing the micro-Öuchterlony double-diffusion technique, were used to analyze the stomach contents of sand shrimp for the presence or absence of juvenile winter flounder proteins (Feller 1991, Taylor 2004). Specifically, 2 templates were placed on an agarose matrix, which in turn covered a microscope slide. Each template consisted of 5 wells, into which 20 µl of winter flounder-specific antiserum was pipetted into a single central well. The remaining 4 wells surrounding and equidistant from the template's central well were loaded with 20 µl of antigen solutions prepared from solubilized stomach material from an individual shrimp (1 stomach sample well^{-1}). Diffusion of the antiserum and antigen solutions occurred within the agarose matrix, and precipitin lines formed between the central well and peripheral wells if antibodies within the antiserum reacted with antigenic moieties in the stomach-content mixture. A positive reaction was defined as the formation of at least 1 distinct precipitin line, and the resulting reaction was confirmed with tests of identity (Taylor 2004).

Logistic regression analysis, employing the method of maximum likelihood, was used to test for a significant relationship between the response variable (shrimp stomach contents testing positive for flounder proteins) and explanatory variables (flounder and shrimp density and size). The natural logarithm of the ratio of response frequencies (logits) was used to estimate parameters of a linear model. The proportion of shrimp stomachs containing winter flounder proteins (P_t) was equal to:

$$\text{logit}(P_t) = \log\left(\frac{P_t}{1-P_t}\right) = \alpha + \beta_1\rho_{(f,t)} + \beta_2 L^2_{(f,t)} + \beta_3 L_{(f,t)} + \beta_4\rho_{(s,t)} + \beta_5 L_{(s,t)} \quad (4)$$

where α is the intercept parameter, β$_{1-5}$ are the vectors of the slope parameters, $\rho_{(f,t)}$ and $L_{(f,t)}$ is flounder density (no. flounder m^{-2}) and mean size (mm TL) at time t (Eqs. 1 and 3, respectively), and $\rho_{(s,t)}$ and $L_{(s,t)}$ are shrimp density (no. shrimp m^{-2}) and body size (mm TL) at time t (Eq. 2 and measured directly, respectively). The data were treated as frequency responses (presence or absence of flounder proteins in shrimp guts) rather than continuous responses, and thus, a chi-square value was calculated to test for the significance of the explanatory variables.

Modeling winter flounder mortality. Site-specific differences in winter flounder cumulative and average daily instantaneous mortality (*M* and *Z*) owing to sand shrimp predation were assessed with a deterministic model (Taylor 2003b). The model was developed to track the daily growth and survival of a single cohort of recently settled winter flounder in Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay as the fish progressed through a mortality window. The initial density of each cohort was 8 flounder m^{-2}. The timing of winter flounder settlement to the benthos, and thus, the start period of the model, was determined by first back-calculating growth to the day of the year that flounder were 8 mm TL (i.e. size at settlement). Winter flounder growth was back-calculated according to the site-specific LVB growth models presented earlier (Eq. 3). Winter flounder settlement was then estimated as a normal distribution, with the mean of the distribution equal to the day of the year the mean winter flounder body size was 8 mm TL and with a standard deviation of 10 d (Sogard et al. 2001). The size-structure and total abundance of juvenile winter flounder used in this investigation were calculated from published estimates from several estuaries of the NW Atlantic during spring and summer (Witting 1995, Sogard et al. 2001, Curran & Able 2002, DNC 2003).

Site-specific mean daily growth and the resulting body size of winter flounder were incorporated into a size- and density-dependent predation mortality model. The number of surviving winter flounder at a given daily time step was calculated as:

$$N_t = N_{t-1} - N_e \quad (5)$$

where N_t is the number of flounder m^{-2} surviving to time t, N_{t-1} is the number of flounder m^{-2} at the previous daily time step, and N_e is the number of flounder consumed daily (no. flounder eaten m^{-2}).

The number of winter flounder consumed at each daily time step (N_e) was estimated by summing the daily consumption rate of individual sand shrimp, each defined by a certain length $L_{(s,t)}$ (mm TL):

$$N_e = \sum_{L_{(s,t)}=30}^{70} P_{L_{(s,t)}} \cdot \rho_{(s,L_{(s,t)})} \quad (6)$$

where N_e is the number of flounder eaten m^{-2} d^{-1} at time t summed over the predator size range of 30 to 70 mm TL ($L_{(s,t)}$), P is the proportion of field-collected shrimp of length $L_{(s,t)}$ whose stomach contents tested positive for juvenile winter flounder proteins (Eq. 4), and $\rho_{(s)}$ is the density of shrimp (no. shrimp m^{-2}) of length $L_{(s,t)}$ (Eq. 2). Shrimp stomach samples testing positive for winter flounder proteins were assumed to represent the ingestion of 1 flounder (Taylor 2003a). The total abundance and size-structure of shrimp ($\geq$30 mm TL) incorporated into Eq. (4) were re-calculated daily based on Eq. (2). Moreover, the

equation explaining shrimp population structure in Narragansett Bay was also used for the Niantic River (DNC 2003, Taylor pers. obs.). The size of winter flounder incorporated into Eq. (4) was calculated as the mean size of individuals at time t (Eq. 3), whereas the density of winter flounder was re-calculated daily based on losses attributed to shrimp predation. Error analysis was performed by rerunning the deterministic model with ±1 SD of parameter estimates originally incorporated into the model, i.e. shrimp and flounder density and size-structure over time (Eqs. 1–3).
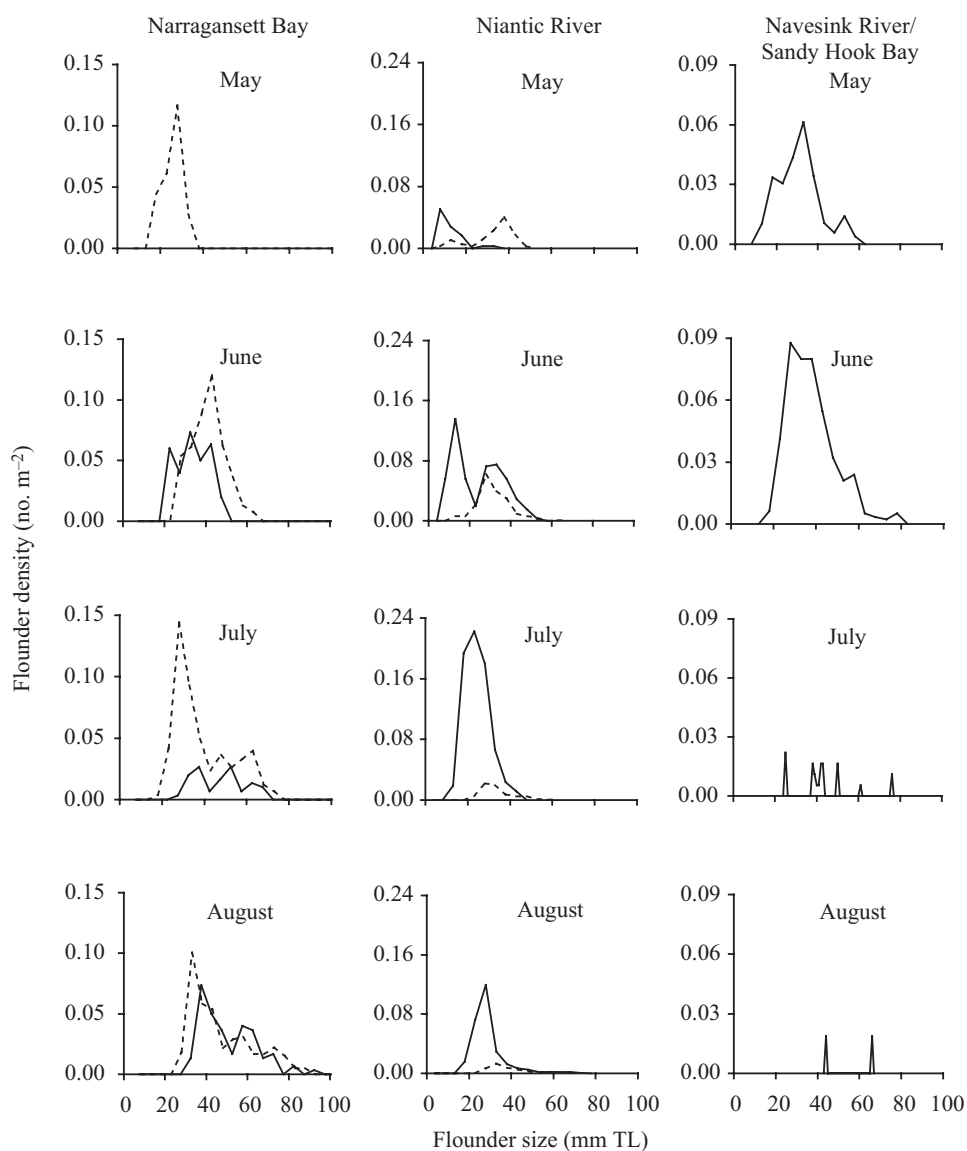

Fig. 2. *Pseudopleuronectes americanus*. Size-frequency (total length, TL) distribution of juveniles in Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay. Distributions were estimated from May to August in 2001 (continuous line; excluding May for Narragansett Bay) and 2002 (dashed line; Narragansett Bay and Niantic River only). Note that *y*-axes are scaled differently for the 3 estuaries

RESULTS

Winter flounder and sand shrimp size-frequency and density

Seasonal trends in juvenile winter flounder abundance and size-structure were relatively consistent among Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay, with size-frequency distributions approximating normality (Fig. 2). Only 2 departures from normality out of 19 comparisons were detected by 1-sample Kolmogorov-Smirnov (KS) tests (Navesink River/Sandy Hook Bay, July 2001: KS = 3.525, p < 0.0001; Navesink River/Sandy Hook Bay, August 2001: KS = 2.668, p < 0.0001). Despite general similarities, there were discernible differences in the temporal distribution and size-structure of winter flounder populations among the 3 estuaries (Fig. 2). The range of winter flounder size in Narragansett Bay during May was narrow (size range = 16 to 34 mm TL) in comparison to the Niantic River and Navesink River/Sandy Hook Bay (size range = 6 to 49 mm TL and 9 to 60 mm TL, respectively). Moreover, mean size of winter flounder in Narragansett Bay and the Niantic River during May (mean size = 25.7 and 25.1 mm TL, respectively) was smaller relative to the Navesink River/Sandy Hook Bay (mean size = 28.4 mm TL). The size-frequency distribution of winter flounder among the 3 study sites generally broadened in range and shifted to larger sizes as the summer progressed. However, the rate of increase in winter flounder size was not consistent across estuaries. Between May and August, for example, the mean size of winter flounder in Narragansett Bay and Navesink River/Sandy Hook Bay increased by 26.8 and 26.6 mm TL, respectively, whereas winter flounder in the Niantic River only increased by 6.1 mm TL during the same time period. Accordingly, small winter flounder (<25 mm TL) were routinely collected in May and June in all 3 estuaries; however, in the Niantic River small winter flounder were present into late July and early August.

Differences in winter flounder size-structure among estuaries may be caused by discrepancies in the water depths sampled at each site (Stoner et al. 2001, Manderson et al. 2004; Table 1). Therefore, the effect of winter flounder body size (mm TL) on depth distribution (m) was examined in the Navesink River/Sandy Hook Bay (depth range = 0.5 to 8 m) with a least-squares linear regression. For this analysis, winter flounder were grouped into 5 mm length classes ranging from 10 to 75 mm TL. Size-dependent depth distributions of winter flounder were not analyzed for the 2 northernmost estuaries because of the narrow range of water depths sampled at these sites (Narragansett Bay = 0 to 3 m and Niantic River = 1 to 2 m; Table 1).

Winter flounder in the Navesink River/Sandy Hook Bay did not distribute themselves across depths according to size (R^2 = 0.077, F = 0.671, df = 1, 9, p = 0.436). Conversely, all sizes of winter flounder (10 to 75 mm TL) were concentrated at depths of 2.0 to 2.5 m.

The magnitude and timing of peak winter flounder density differed among sites (Fig. 3). Winter flounder density was greatest in the Niantic River, reaching a maximum estimated value of 2.60 flounder m^{-2} on Day 183. Narragansett Bay experienced the lowest peak winter flounder density of the 3 estuaries (0.58 flounder m^{-2} on Day 172), but the width of the density distribution over time was greater than that estimated for the Niantic River and Navesink River/Sandy Hook Bay (σ = 46.2, 25.7, and 13.3 for Narra-
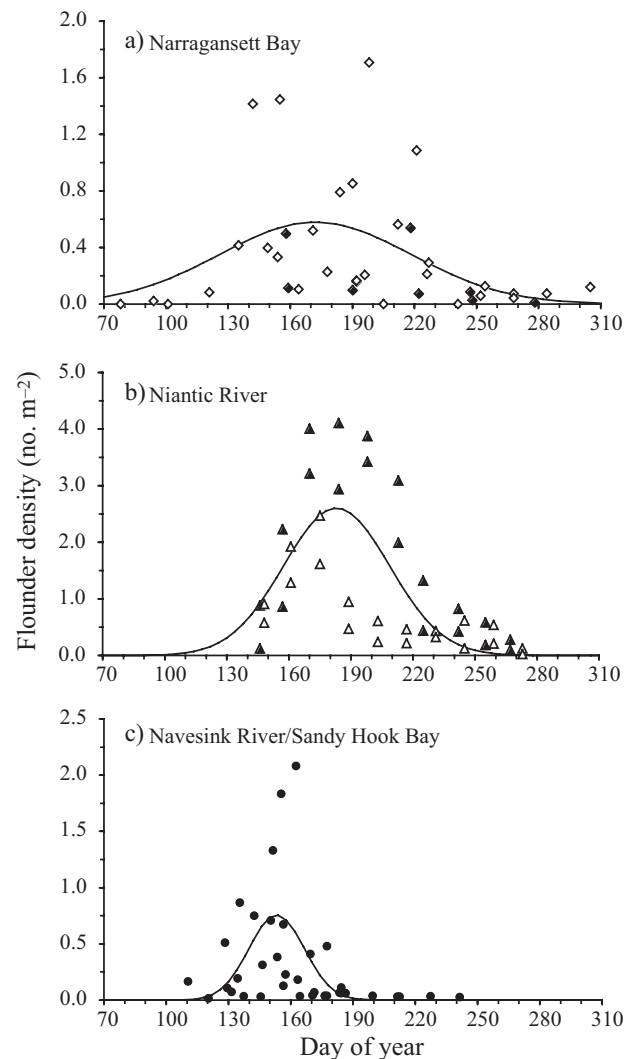

Fig. 3. *Pseudopleuronectes americanus*. Density of juveniles during late spring and summer in Narragansett Bay, Niantic River, and Navesink River/Sandy Hook Bay. Closed and open symbols: data from 2001 and 2002, respectively. Model fits of the normal density function (Eq. 1) are presented
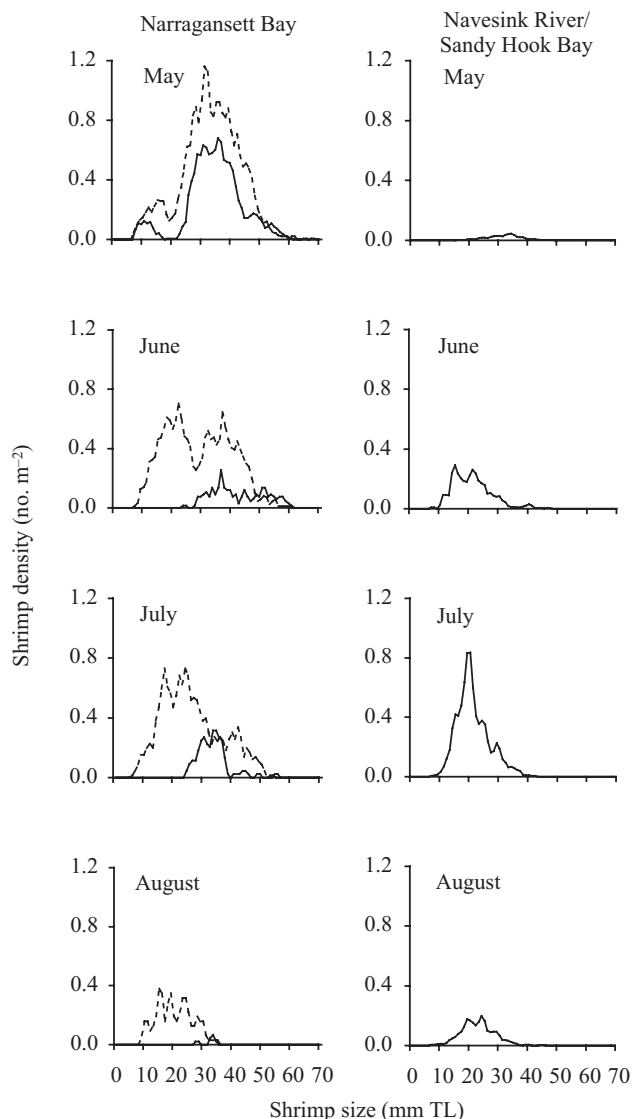
Fig. 4. *Crangon septemspinosa*. Size-frequency (TL) distribution in Narragansett Bay and Navesink River/Sandy Hook Bay. Distributions were estimated from May to August in 2001 (continuous line) and 2002 (dashed line; Narragansett Bay only)

gansett Bay, Niantic River and Navesink River/Sandy Hook Bay, respectively). Winter flounder in the Navesink River/Sandy Hook Bay reached maximum density (0.76 flounder m^{-2}) early in the year (Day 153) relative to Narragansett Bay and the Niantic River. Results from the 2-sample Kolmogorov-Smirnov tests indicated that the winter flounder density-distribution in the Niantic River was significantly different than the distributions observed in Narragansett Bay (KS = 1.412, p < 0.05) and the Navesink River/Sandy Hook Bay (KS = 1.779, p < 0.005), whereas distributional differences in winter flounder density between Narra-

gansett Bay and the Navesink River/Sandy Hook Bay were not significantly different (KS = 0.777, p = 0.5827).

The seasonal abundance and size structure of sand shrimp in the Navesink River/Sandy Hook Bay and Narragansett Bay differed in 2 distinct respects (Figs. 4 & 5). First, the total abundance of shrimp during the spring and early summer was substantially lower in the Navesink River/Sandy Hook Bay relative to Narragansett Bay. For example, the total density of sand shrimp in the Navesink River/Sandy Hook Bay in May and June equaled 0.5 and 3.6 shrimp m^{-2}, respectively, whereas shrimp densities in Narragansett Bay ranged between 16.9 and 22.5 shrimp m^{-2} during the same time period (Fig. 4). Second, large sand shrimp (≥30 mm TL) were rare in the Navesink River/Sandy Hook Bay (Figs. 4 & 5). Large shrimp reached maximum densities in the Navesink River/Sandy Hook Bay during July at a level of 0.94 shrimp m^{-2}. This represents a 16.8-fold decrease relative to the maximum density of large shrimp observed in Narragansett Bay during May (15.8 shrimp m^{-2}). These findings are consistent with the results of the 2-sample Kolmogorov-Smirnov test indicating that the pairwise difference in sand shrimp populations between Narragansett Bay and Navesink River/Sandy Hook Bay was significant (KS = 2.423, p < 0.0001).

Similar to winter flounder, previous research has demonstrated that sand shrimp exhibit size-dependent changes in depth distributions (Manderson et al. 2004). Consequently, the discrepancy in water depths sampled in the Navesink River/Sandy Hook Bay, relative to Narragansett Bay, could affect site-specific estimates of shrimp abundance and size-structure. To determine whether depth distributions of sand shrimp change with body size in the Navesink River/Sandy Hook Bay, a least-squares linear regression was used to test for a significant relationship between depth of occurrence and shrimp length (grouped into 5 mm length classes; 10 to 55 mm TL). Accordingly, sand shrimp depth distributions were independent of body size (R^2 = 0.010, F = 0.126, df = 1, 13, p = 0.729), and the majority of shrimp were concentrated at 2 m.

The abundance of large sand shrimp (≥30 mm TL) in Narragansett Bay increased considerably in April, irrespective of shrimp sexual status or reproductive condition (Figs. 5a & 6). By late April (Day 121), non-egg-bearing females constituted the largest percentage of the total (large) shrimp population (41.9%), followed by males and ovigerous females (34.2 and 23.8% of total population, respectively) (Fig. 6). From early May to early June, male and non-ovigerous female shrimp densities declined to <1.0 shrimp m^{-2}, while the abundance of ovigerous female shrimp initially increased to

7.3 shrimp m^{-2} and then declined to 3.4 shrimp m^{-2} by Day 154 (Fig. 6). During this time period (Days 137 to 154), ovigerous female shrimp were numerically dominant and constituted 69.0% of the adult shrimp population, whereas non-ovigerous females and males represented 18.6 and 12.4% of the population, respectively. Male shrimp densities remained low (<0.5 shrimp m^{-2}) from mid June to late August. After a modest increase in abundance in mid June (4.1 to 5.3 shrimp m^{-2}), densities of ovigerous and non-ovigerous female shrimp (presumably having recently shed eggs) also declined continuously for the remaining summer months.

Winter flounder growth

The site-specific LVB growth models adequately fit the mean winter flounder body-size data measured during field sampling in Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay (Fig. 7), as indicated by highly significant model fits (p < 0.0001) and relatively high R^2 values (R^2 = 0.510 to 0.778). Winter flounder in Narragansett Bay and the Navesink River/Sandy Hook Bay experienced similar growth rates (Narragansett Bay: mean = 0.34 mm d^{-1}, range = 0.33 to 0.34 mm d^{-1}; Navesink River/Sandy Hook Bay: mean = 0.37 mm d^{-1}, range = 0.36 to 0.38 mm d^{-1}). Conversely, winter flounder growth rates in the Niantic River were >2 times slower than rates measured in the other 2 estuaries (Niantic River: mean = 0.16 mm d^{-1}). The Brody growth coefficient (κ) estimated for the Niantic River was significantly lower than values obtained for Narragansett Bay (Fisher-Behrens test; z = 4.142, df = 2, 69, p < 0.0001) and the Navesink River/Sandy Hook Bay (Fisher-Behrens test; z = 2.880, df = 2, 66, p < 0.001), whereas there was no significant difference in κ between Narragansett Bay and the Navesink River/Sandy Hook Bay (Fisher-Behrens test; z = 0.449, df = 2, 61, p = 0.6549). Estimates of the LVB growth model location parameter (t_0) for each site were not significantly different (Fisher-Behrens test; Narragansett Bay–Niantic River: z = 1.401, df = 2, 69, p = 0.1658; Narragansett Bay–Navesink River/Sandy Hook Bay: z = 0.911, df = 2, 61, p = 0.3660; Niantic River–Navesink River/Sandy Hook Bay: z = 1.862, df = 2, 66, p = 0.0671). According to the site-specific LVB growth models, winter flounder settling to the benthos in the Niantic River remained vulnerable to shrimp predation for 106 d, i.e. the number of days required to grow from 8 to 25 mm TL (Witting & Able 1995, Taylor 2003a). Winter flounder in Narragansett Bay and the Navesink River/Sandy Hook Bay required 46 and 51 d after settlement, respectively, to achieve a size refuge from shrimp predation.

Sand shrimp stomach content analysis

A total of 2499 sand shrimp were collected from Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay from late March to late August, of which 177 (7.1%) of the stomachs examined tested positive for juvenile winter flounder proteins (Table 2, Fig. 8). The incidence of winter flounder in shrimp stomachs (averaged over all sites and years) was greatest from late May to early June (14.2%). This percentage then decreased abruptly until no winter flounder
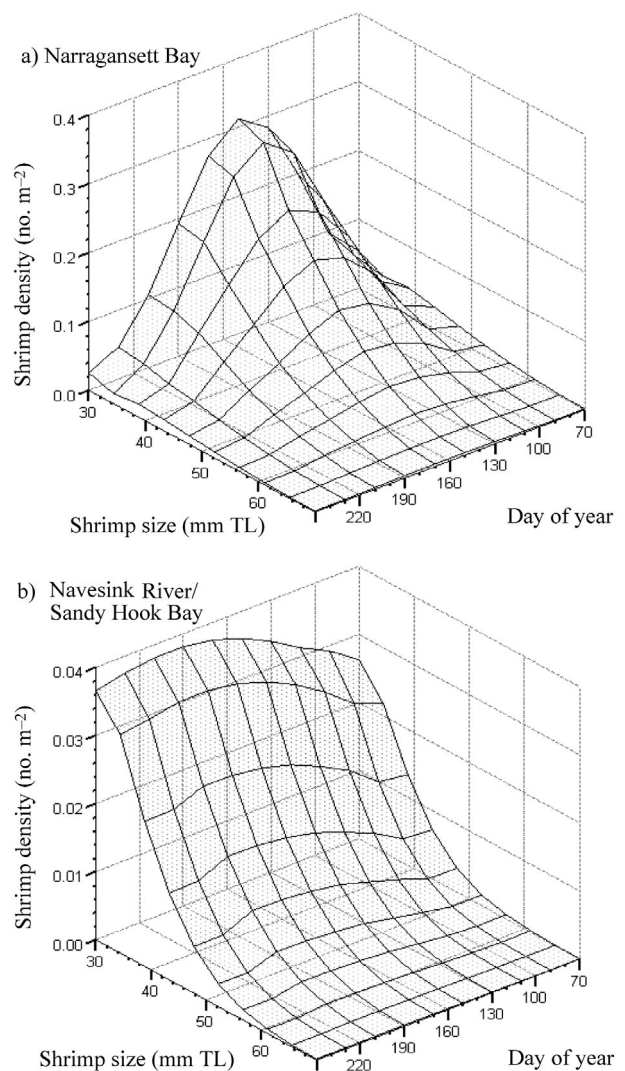

Fig. 5. *Crangon septemspinosa*. Predicted density of adults (≥30 mm TL) during late spring and summer in Narragansett Bay and Navesink River/Sandy Hook Bay. Response surfaces estimated from second-order polynomials (Eq. 2) fit to shrimp catch (no. shrimp m^{-2}) and size (mm TL) data over time (day of year). Note that *y*-axes are scaled differently for the 2 estuaries
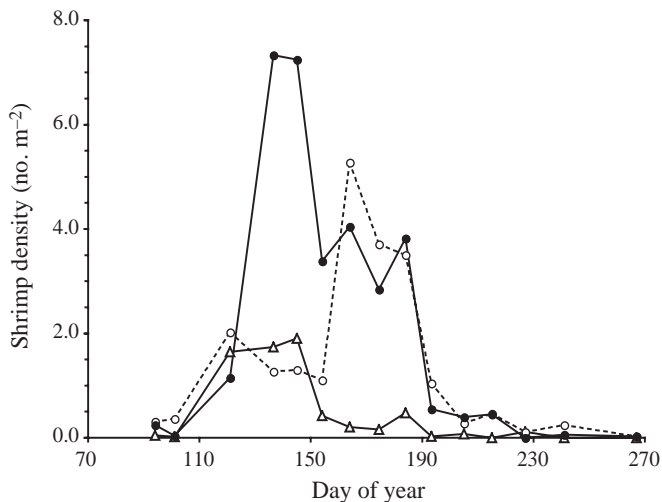
Fig. 6. *Crangon septemspinosa*. Density of adults (≥30 mm TL) over time in Narragansett Bay as a function of sexual and reproductive status; (△) male; (○) non-ovigerous female; (●) ovigerous female

were detected in shrimp stomach samples after early July (Fig. 8). There was little variation in detection responses in 2001 and 2002 in Narragansett Bay and the Niantic River (max. response = 14 and 15% for 2001 and 2002 in Narragansett Bay, and 13 and 20% in 2001 and 2002 in the Niantic River, respectively). Conversely, the proportion of shrimp stomach contents testing positive for juvenile winter flounder was substantially higher in 2002 relative to 2001 in the Navesink River/Sandy Hook Bay (max. response = 4 and 20% for 2001 and 2002, respectively). This dis-

crepancy was attributed to subsampling and analysis of larger shrimp in 2002 (average shrimp size = 41.2 mm TL; range = 32 to 50 mm TL), whereas sampling in 2001 consisted of smaller shrimp that were more indicative of the true population in the Navesink River/Sandy Hook Bay (average shrimp size = 37.3 mm TL; range = 24 to 55 mm TL) (Table 2, Fig. 4).

The proportion of sand shrimp stomachs containing winter flounder generally increased with increasing flounder density. Moreover, the proportion of predator stomach contents testing positive for winter flounder followed a dome-shaped response when analyzed graphically with respect to prey size. Maximum detection responses occurred when the mean flounder size was 29 mm TL. The characteristics of the winter flounder population (size and density), however, were non-significant factors in predicting the probability of shrimp preying on juvenile flounder

Table 2. *Crangon septemspinosa* and *Pseudopleuornectes americanus*. Number of sand shrimp stomach samples examined by immunological assay and number of stomach samples testing positive for juvenile winter flounder proteins. Shrimp were collected during late spring and summer (Days 78 to 241) in 2001 and 2002 from Narragansett Bay, Niantic River and Navesink River/Sandy Hook Bay. Average size (TL) and size range (in parentheses) of shrimp analyzed for stomach contents are presented

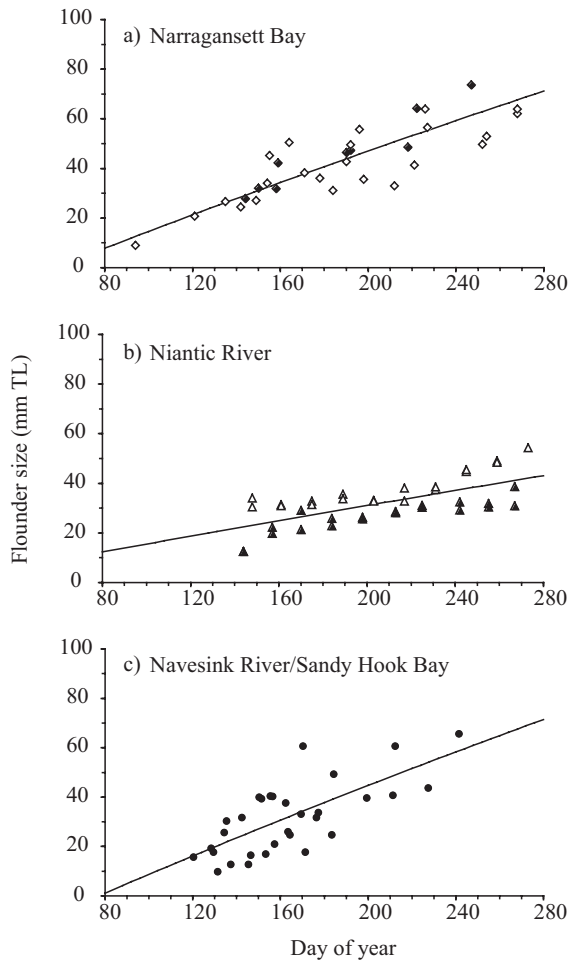|	Sampling dates (Days)	Sample size (n)	Positive samples (n)	Shrimp size (mm)
Narragansett Bay				
2001	140–228	311	28	46.6 (33–66)
2002	78–241	959	79	41.8 (20–68)
Niantic River				
2001	144–212	255	18	47.5 (36–64)
2002	148–189	354	45	42.9 (35–59)
Navesink River/Sandy Hook Bay				
2001	107–179	553	3	37.3 (24–55)
2002	120–176	67	4	41.2 (32–50)

Fig. 7. *Pseudopleuronectes americanus*. Mean body size during late spring and summer in Narragansett Bay, Niantic River, and Navesink River/Sandy Hook Bay. Filled and open symbols: data from 2001 and 2002, respectively. Model fits of Ludwig von Bertalanffy growth model (Eq. 3) are presented

(Table 3). Conversely, predation rates were dependent upon the attributes of the shrimp, such that an increase in predator density and body size resulted in a statistically significant increase in the proportion of stomach samples testing positive for winter flounder proteins (Table 3, Fig. 9). The range of shrimp size in which winter flounder were detected in stomach samples was 31 to 66 mm TL (Fig. 9b). Shrimp reproductive and sexual status (female, ovigerous female, or male) was not a statistically significant factor in the proportion of predator stomachs testing positive for winter flounder remains (1-way ANOVA: $F = 0.382$, df = 2, 1688, p = 0.6828).

Modeling winter flounder mortality

Estimated predator-induced mortality of winter flounder varied considerably across study sites. Modeled winter flounder mortality was greatest in the Niantic River, whereby the average daily consumption rate of sand shrimp (N_e) was 0.032 flounder eaten m^{-2} (range = 0 to 0.086), and the average daily instantaneous mortality rate (Z) of flounder equaled 0.0086 (±1 SD = 0.0471). Summing the number of winter flounder eaten daily over the entire predation period in the Niantic River resulted in a total consumption rate equal to 4.52 flounder eaten m^{-2} and a cumulative mortality (M) of 0.5651 (±1 SD = 0.2823). Winter flounder in Narragansett Bay also experienced substantial predator-induced mortality (average N_e = 0.025 flounder eaten m^{-2} d^{-1}), whereby sand shrimp predation accounted for an average daily instantaneous mortality rate of 0.0059 (±1 SD = 0.0030), and cumulative mortality of 0.4347 (±1 SD = 0.2481). In contrast to the Niantic River and Narragansett Bay, the juvenile winter flounder cohort modeled for the Navesink River/Sandy Hook Bay experienced relatively low rates of mortality owing to shrimp predation: average N_e = 0.002 flounder eaten m^{-2} d^{-1} (range = 0 to 0.003), average Z = 0.0003 (±1 SD = 0.0004), and M = 0.0464 (±1 SD = 0.0243).

DISCUSSION

Site-specific variability in modeled winter flounder mortality

Immunological assays successfully identified sand shrimp as predators of post-settlement winter flounder in natural populations. Predator-induced mortality of winter flounder, however, varied substantially among 3 NW Atlantic estuaries. Predation was more intense in the 2 northerly located estuaries, where shrimp con-
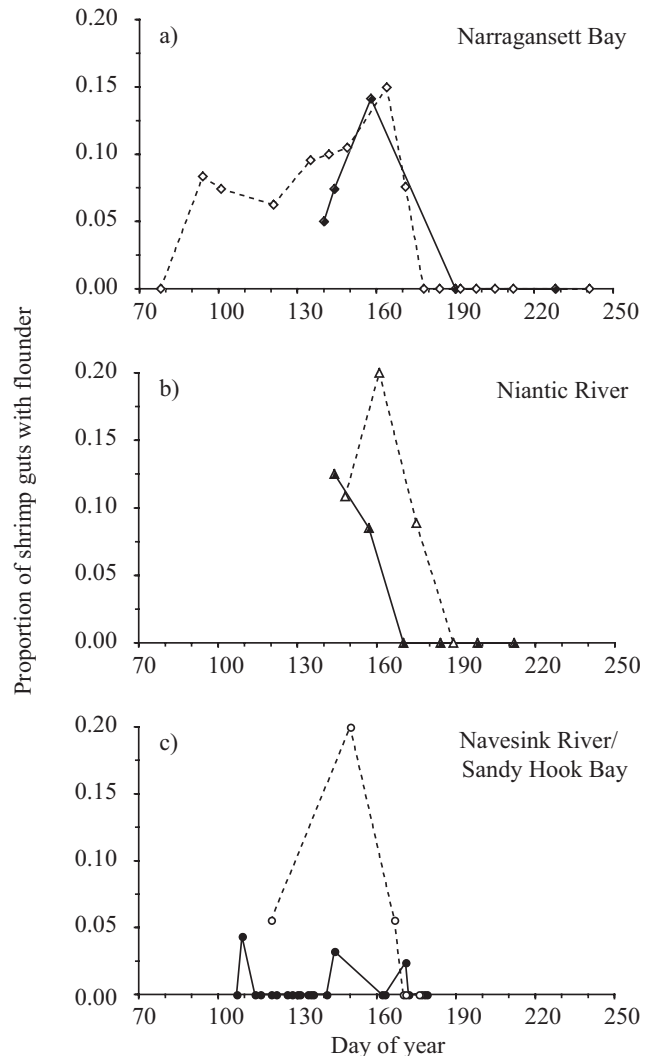

Fig. 8. *Crangon septemspinosa* and *Pseudopleuronectes americanus*. Proportion of sand shrimp stomach contents testing positive for juvenile winter flounder proteins. Shrimp were collected during late spring and summer in 2001 (filled symbols) and 2002 (open symbols) from Narragansett Bay, Niantic River, and Navesink River/Sandy Hook Bay

sumed 43.5 and 56.5% of the total winter flounder year-class in Narragansett Bay and the Niantic River, respectively. Conversely, shrimp in the Navesink River/Sandy Hook Bay only accounted for a 4.6% loss to the flounder year-class. The most critical factor underlying the difference in modeled winter flounder mortality across sites was the difference in the abundance and size-structure of local sand shrimp populations. The importance of sand shrimp as a mortality factor for winter flounder in the Navesink River/Sandy Hook Bay was minimal due to the low abundance of large shrimp (≥30 mm TL). Conversely, in Narragansett Bay and the Niantic River predation rates were

Table 3. *Crangon septemspinosa* and *Pseudopleuornectes americanus*. Summary statistics and mean (SE) parameter estimates for logistic regression of proportion of sand shrimp stomachs containing winter flounder proteins (*P*) as a function of prey density (ρ_f; no. flounder m^{-2}), prey size (L_f; mm; TL), predator density (ρ_s; no. shrimp m^{-2}), and predator size (L_s; mm TL). Proportions are natural logarithm of the ratio of response frequencies (logits). logit (*P*) = log [*P*/(1–*P*)]

Variable	Symbol	Parameter estimate (SE)	df	Chi-square	p-value
Intercept	α	−7.128 (1.214)	1	34.49	<0.0001
Flounder density	ρ_f	−0.006 (0.157)	1	0.002	0.9695
Flounder size	L_f	0.017 (0.097)	1	0.032	0.8588
Flounder size^2	$L_f{}^2$	−0.0003 (0.0017)	1	0.042	0.8380
Shrimp density	ρ_s	0.328 (0.077)	1	41.89	<0.0001
Shrimp size	L_s	0.082 (0.013)	1	18.26	<0.0001

high because of the presence of large sand shrimp during peak winter flounder settlement periods (May to early June), when flounder are small in size and vulnerable to predation.
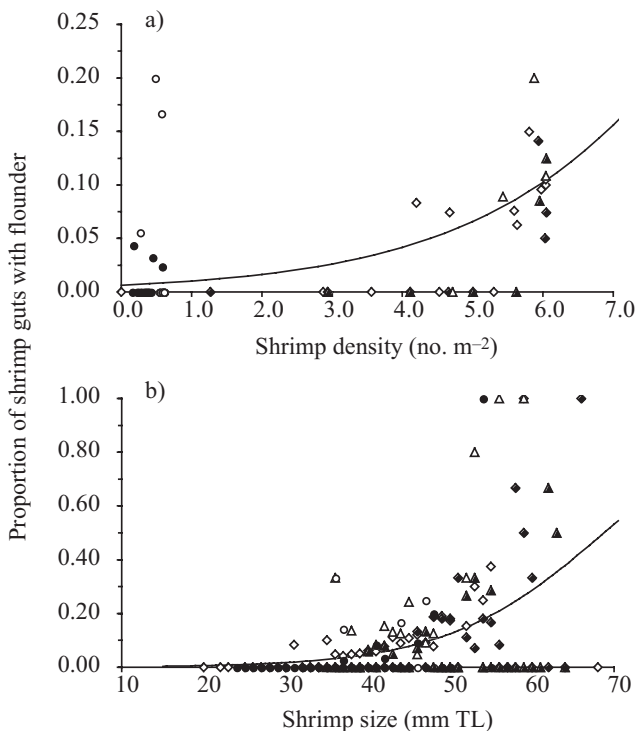

Fig. 9. *Crangon septemspinosa* and *Pseudopleuronectes americanus*. Proportion of sand shrimp stomach contents testing positive for juvenile winter flounder proteins as a function of (a) shrimp density (no. shrimp m^{-2}) and (b) size (mm TL). Shrimp were collected during late spring and summer in 2001 (filled symbols) and 2002 (open symbols) from Narragansett Bay (♦, ◊), Niantic River (▲, △), and Navesink River/Sandy Hook Bay (●, ○). Logistic regressions estimated from maximum-likelihood analysis were fit to data (continuous lines)

The incidence of winter flounder in the stomachs of sand shrimp increased significantly with increasing shrimp size, and the smallest shrimp identified as a predator of winter flounder was 31 mm TL. This trend may be partially explained by morphological constraints of the shrimp, in that a reduction in shrimp length coincides with a decrease in stomach volume (Gibson et al. 1995). Consequently, smaller shrimp are unable to retain enough prey tissue within their stomachs to be effectively detected with immunological assays (Taylor 2004). It is also likely that larger crangonid shrimp have an increased capture efficiency and ability to consume flatfishes (Taylor 2003a). *Crangon affinis* predation on juvenile Japanese flounder *Paralichthys olivaceus*, for example, is governed by predator–prey size relationships (Seikai et al. 1993). *C. affinis* between 20 and 30 mm TL are unable to successfully capture large flounder (25 to 29 mm TL), whereas increases in shrimp size (44 to 48 mm TL) markedly improve the shrimp's ability to feed on equally-sized fish (Seikai et al. 1993). Similarly, *C. crangon* predation on juvenile plaice *Pleuronectes platessa* is restricted to shrimp >30 mm TL, beyond which increasing predator size results in shrimp consuming more juvenile plaice (Van der Veer & Bergman 1987, Wennhage & Pihl 2001).

The relative magnitude of sand shrimp predation on juvenile winter flounder is also influenced by flounder growth and their resulting body size at age (Van der Veer & Bergman 1987, Gibson et al. 1995, Witting & Able 1995, Taylor 2003a). Winter flounder are susceptible to sand shrimp predation shortly after initial settlement (8 mm TL), until a size-refuge is attained after flounder grow to 25 mm TL (Witting & Able 1995, Taylor 2003a). In this study, positive identification of juvenile winter flounder proteins in the stomach contents of sand shrimp occurred when the mean body size of flounder ranged between 12 and 37 mm TL. It is more likely, however, that shrimp selectively preyed on the smaller flounder in the population (size range = 8 to 25 mm TL) (Wennhage & Pihl 2001, Taylor 2003a). Similar conclusions were made in the western Wadden Sea, where *Crangon crangon* preyed on post-settlement plaice until late May and early June, ceasing once the fish achieved a size of 30 mm (Zijlstra et al. 1982, Van der Veer & Bergman 1987).

Growth rates of post-settlement winter flounder determined in this study (0.16 to 0.37 mm d^{-1}) are consistent with previous estimates from several mid-Atlantic and southern New England estuaries. A series of short-

term field caging experiments in Narragansett Bay revealed that juvenile winter flounder grew at rates between 0.22 and 0.60 mm d^{-1} from early June to early July (Meng et al. 2001). Field enclosure studies estimated winter flounder growth rates of –0.03 to 0.21 mm d^{-1} and 0.0 to 0.88 mm d^{-1} in the Hammonasset River (Connecticut) and the Navesink River/Sandy Hook Bay, respectively (Phelan et al. 2000, Manderson et al. 2002). Moreover, the analysis of otolith increment counts of winter flounder determined that growth rates during and shortly after settlement ranged between 0.25 and 1.91 mm d^{-1} in the Navesink River/Sandy Hook Bay (Sogard et al. 2001, Manderson et al. 2003, Meise et al. 2003). This study indicates that winter flounder in the Niantic River experienced growth rates 2.1 to 2.3 times slower than conspecifics in Narragansett Bay and the Navesink River/Sandy Hook Bay. The slow growth of winter flounder observed in the Niantic River, and the resulting exposure to size-dependent predation, contributes to the higher rates of mortality recorded in this estuary (Taylor & Collie 2003b).

Differences in winter flounder growth rates across sites may be attributable to several unique characteristics of the estuaries, including temperature (Meng et al. 2000, Manderson et al. 2002), adequate food resources and substrate characteristics (Phelan et al. 2001, Manderson et al. 2002) and density-dependent processes (DeLong et al. 2001, DNC 2003). The presence of small winter flounder (<25 mm TL) in the Niantic River from late spring to late summer may also be an artifact of a protracted settlement period. An extended settlement period would explain the rapid increase in the abundance of recently settled winter flounder in mid-summer (e.g. July 2002) that were unaccounted for in preceding months. Although advanced stages of winter flounder larvae (Stage IV = left eye at midline) in the Niantic River achieved maximum abundance in late spring, pre-metamorphic larvae were collected from the estuary as late as mid June (DNC 2003). Otolith analysis of juvenile winter flounder has revealed similar occurrences of a protracted settlement period in the Navesink River/Sandy Hook Bay (Manderson et al. 2003, Meise et al. 2003). Conversely, the date of metamorphosis of winter flounder in several other New Jersey estuaries occurred within a restricted time period (2 to 3 wk) from mid March to mid May (Sogard et al. 2001). In another study, significant differences in the size-frequency distribution of post-settlement winter flounder were observed in a single year (1990) among 4 separate estuaries in New Jersey (Sogard & Able 1992). Based on otolith analysis that estimated settlement patterns and growth rates, 2 mechanisms accounted for the decreased size of winter flounder in 2 regions: protracted or late settlement period of flounder (Sandy Hook Bay) and slow growth rates (Great Bay). A similar analysis of otolith microstructure for winter flounder collected from the Niantic River would help distinguish between the effects of settlement period and growth rates on observed flounder body size.

Differences in modeled winter flounder mortality among the 3 estuaries may be explained by temporal patterns of field sampling and detection limits of immunological assays. For example, the ability to detect winter flounder in the stomachs of sand shrimp is contingent on collecting shrimp shortly after foraging events. The detection limit of juvenile winter flounder proteins in sand shrimp stomachs is 9.4 h after initial feeding (Taylor 2004). In Narragansett Bay, shrimp were collected shortly after first light, whereas shrimp in the Niantic River and Navesink River/Sandy Hook Bay were collected over a range of daylight hours (typically midday). If predation events occurred much earlier then field sampling (nocturnal feeding; Pihl & Rosenberg 1984, Ansell & Gibson 1993), then the proportion of shrimp stomachs testing positive for winter flounder proteins may have been underestimated. Dietary analysis of a congener species, however, revealed that *Crangon crangon* preyed on fishes during morning crepuscular periods, and to a lesser extent during other periods of the diel cycle (Ansell et al. 1999). Assuming that sand shrimp exhibit similar foraging behavior as other crangonid shrimp (Price 1962, Haefner 1979, Van der Veer & Bergman 1987), immunoassays performed in this study adequately examined the time period when predation events most likely occurred, regardless of the estuary from which the shrimp were collected.

Because the deterministic model presented in this study relies on site-specific field data (e.g. shrimp and flounder density and size-structure), estimates of winter flounder mortality may be influenced by differences in sampling design, time of day (Mattila et al. 1999), tidal cycle (Tyler 1971, Kuipers 1975, Van der Veer & Bergman 1987), habitat- and species-specific gear efficiency (Kuipers 1975, Pierce et al. 1990, Kuipers et al. 1992), and local environmental conditions (e.g. water depth, substrate, vegetation; Phelan et al. 2000, 2001, Stoner et al. 2001, Manderson et al. 2003, 2004). In this study, for example, field sampling of the 2 northern most estuaries occurred at shallow water depths (0 to 3 m), whereas sampling in the Navesink River/Sandy Hook Bay occurred over a range of depths (0.5 to 8 m). Previous research in the Navesink River/Sandy Hook Bay determined that winter flounder and sand shrimp demonstrate size-dependent depth distributions, with larger individuals (shrimp >30 mm TL and flounder >25 mm TL) more strongly associated with shallow habitats (<3 m)

(Stoner et al. 2001, Manderson et al. 2004). Consequently, in this study the density of winter flounder susceptible to sand shrimp predation (flounder <25 mm TL; Witting & Able 1995, Taylor 2003a) may have been overestimated in the Navesink River/Sandy Hook Bay relative to Narragansett Bay and the Niantic River. Similarly, the density of sand shrimp capable of feeding on post-settlement winter flounder (shrimp >30 mm TL; this study) may have been underestimated in the Navesink River/Sandy Hook Bay because sampling included water depths >3 m. In this study, however, neither species demonstrated a depth preference according to body size. Conversely, the depth of occurrence for all sizes of winter flounder and sand shrimp occurred at approximately 2 m in the Navesink River/Sandy Hook Bay — a depth that was also adequately sampled in Narragansett Bay and the Niantic River. It is therefore concluded that differences in the population structure of winter flounder and sand shrimp among the 3 NW Atlantic estuaries is real, and not an artifact of field sampling design.

Geographic variability in sand shrimp population size-structure

Although sand shrimp have a broad geographic distribution encompassing most of the eastern coastline of North America (Gulf of Saint Lawrence to eastern Florida; Haefner 1979 and references therein), the species is categorized as a subarctic–boreal form with peak abundances between the Chesapeake Bay and the Bay of Fundy (Haefner 1979) (Fig. 10). The maximum body size of sand shrimp is variable within its geographic range, with larger individuals (>30 to 40 mm TL) more prevalent in southern New England and areas extending to the Bay of Fundy (Taylor 2003b). Suboptimal growth conditions may account for the reduced size of shrimp in its southern geographic range. Sand shrimp are a cold-water species, and thus, the warmer temperatures (>20°C) prominent at southern latitudes depress growth because a disproportionate amount of energy is devoted to increased metabolism, thereby reducing energy for somatic development (Price 1962, Haefner 1972, Taylor & Peck 2004).

Another possible mechanism causing a reduction in sand shrimp body size at southern latitudes is shrimp allocating energy to gonadal or egg development, as opposed to somatic growth (Price 1962). Corey (1987) concluded that within their geographic range, sand shrimp demonstrate different reproductive strategies according to the environment's thermal regime. Specifically, 2 separate spawning periods (late spring

and fall) are predominant in northern latitudes (total duration ≈2 mo), whereas the spawning period of shrimp in southern ranges is generally longer and occurs as a single, continuous process (total duration ≈11 mo) (Fig. 10). Shrimp demonstrating the latter reproductive strategy produce several broods per year, and consequently devote more energy to reproduction and less to somatic development, which in turn decreases their overall body size.

Effects of sand shrimp predation on winter flounder year-class strength

The predator-induced mortality of juvenile winter flounder calculated in this study agrees with other published estimates of crangonid shrimp predation on newly settled flatfishes. Fin rays and otoliths of juvenile plaice were identified in 6% of the stomach samples of *Crangon crangon* collected from the Gullmars fjord on the Swedish west coast (Wennhage & Pihl 2001). Similarly, there was a 5% incidence of juvenile plaice in the stomach contents of *C. crangon* collected from tidal flats of the western Wadden Sea (Van der Veer & Bergman 1987). These shrimp were estimated to cause a daily instantaneous mortality rate between 0.02 and 0.15 d^{-1}, and subsequently account for 40% of the observed mortality in juvenile plaice per month (Van der Veer & Bergman 1987). In the present study, the daily instantaneous mortality rate for post-settlement winter flounder owing to sand shrimp predation ranged between 0.0059 and 0.0086 for Narragansett Bay and the Niantic River, respectively. Total daily instantaneous mortality rates of juvenile winter flounder have been estimated as between 0.0123 and 0.0400 (average = 0.0235) (Pearcy 1962, Howell 1993, Meise et al. 1999, DeLong et al. 2001). Thus, sand shrimp predation on post-settlement winter flounder may account for 14.8 to 69.9% (average = 30.9%) of the fish's total daily mortality.

Year-class strength of juvenile winter flounder in northern-temperate estuaries is impacted by the spatial and temporal overlap with predatory sand shrimp (Taylor & Collie 2003b). The spatial and temporal overlap between predator and prey is determined by the relative timing of seasonal onshore migrations of the shrimp (Price 1962, Haefner 1969, 1979) and the settlement of post-metamorphic winter flounder to the benthos (Laurence 1975, Chambers & Leggett 1987). Crangonid shrimp undergo seasonal onshore migrations, triggered by the increase in spring water temperature. The natural warming of water temperature during spring initiates a return migration of shrimp back to shallow estuaries from deeper water, presumably because these areas provide greater food resources
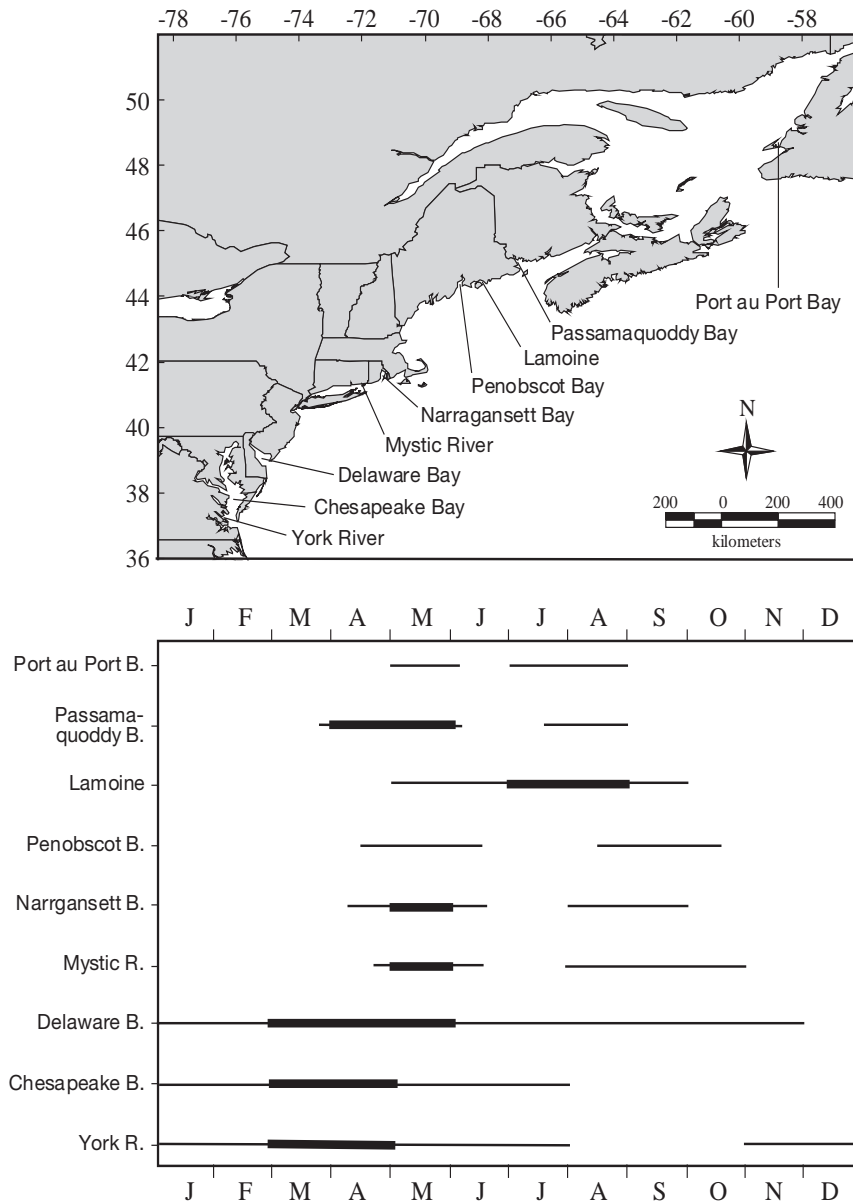
in the season, whereas smaller egg-bearing shrimp (<40 mm TL) progressively replace the larger females and become numerically dominant during the summer and early fall (Modlin 1980, Corey 1987, Whitehouse 1994, this study). Consequently, the timing of winter flounder settlement to the benthos may occur simultaneously with the migration of large (ovigerous) sand shrimp into flatfish nursery areas. In years when the spring migration, and thus, spawning period of sand shrimp coincides with winter flounder settlement, the fish suffer extensive predator-induced mortality, resulting in a weak flounder year-class. Conversely, when winter flounder settlement does not coincide temporally with the migration of large shrimp, fish benefit from reduced predator densities, supporting a strong flounder year-class. At southern latitudes, the relative spatial and temporal overlap between sand shrimp and winter flounder is of minor consequence to flounder survival because of the low abundance of predatory shrimp in these regions.

In summary, the results from this study suggest that predator–prey relationships can vary dramatically across geographic distributions according to differences in the population structure of both predator and prey. Specifically, mortality of newly settled winter flounder owing to sand shrimp predation was site-specific because of differences in shrimp population structure across latitudes. Moreover, winter flounder growth rates, and thus the ability to obtain a size-refuge from predation, was important to fish survival in estuaries where large shrimp were in high abundance during spring and early summer. It is concluded that annual rates of winter flounder survival in northern-temperate estuaries is maximal when flounder settle early to the benthos and grow rapidly to decrease exposure to high densities of late arriving shrimp (Gibson 1994, Taylor & Collie 2003b). Juvenile winter flounder, however, grow through a series of critical periods in which they are vulnerable to different predators, including crabs (Witting 1995, Fairchild & Howell 2000), demersal fishes (Manderson et al. 1999, 2000), and avian piscivores

Fig. 10. *Crangon septemspinosa*. Spawning period across the species primary geographic distribution (~37 to 49°N). Thin lines represent seasonal occurrence of gravid shrimp in shallow-water habitats; thick lines demarcate periods of peak abundance of gravid shrimp. Field surveys were conducted in Port au Port Bay, Newfoundland, Canada (Squires 1965), Passamaquoddy Bay, New Brunswick, Canada (Corey 1981, 1987), Lamoine, Maine (Haefner 1972), Penobscot Bay, Maine (Haefner 1979), Narragansett Bay, Rhode Island (Whitehouse 1994, this study), Mystic River, Connecticut (Modlin 1980), Delaware Bay, Delaware (Price 1962), Chesapeake Bay and York River, Maryland/Virginia (Haefner 1976, 1979)

and optimal conditions for reproduction (Haefner 1969, 1979). As previously discussed, sand shrimp exhibit 2 spawning periods at northern latitudes: spring–early summer (March to early June) and summer–early fall (late July to September) (Price 1962, Modlin 1980, Corey 1987, this study) (Fig. 10). Large females (40 to 70 mm TL) dominate the reproductive population early

(DNC 2003). The relative spatial and temporal distribution of several predator types varies geographically, and thus, can have important consequences on the overall year-class strength of early-stage winter flounder. It follows that the predation processes affecting winter flounder survival cannot be ascertained from the analysis of a single species-specific predator–prey interaction. Conversely, to properly assess the functional significance of estuaries as critical nursery habitats for winter flounder, future research must focus on the communal effects of all predator fields.

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