

Winter flounder settlement dynamics and the modification of settlement patterns by post-settlement processes in a NW Atlantic estuary

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ABSTRACT: For fishes with bipartite life cycles, locations of high quality nursery grounds are determined by processes controlling larval supply as well as those affecting early juvenile mortality and emigration. From April through June 2000, distributions of settling and early juvenile winter flounder *Pseudopleuronectes americanus* were measured to examine how pre- and post-settlement processes determine the location of the primary nursery ground in the Navesink River/Sandy Hook Bay estuarine system (NSBES), New Jersey. The settlement pattern, measured with fine mesh (3 mm) traps that captured flounder ≤ 8 d into the post-metamorphic age but excluded predators and prevented emigration, was spatially dynamic. Fish settled on organically rich substrata (organic content = 5 to 12% by weight) 2 wk earlier in the Navesink River (mid-April through mid-May) than on similar substrata just 15 km downstream in Sandy Hook Bay (May through mid-June). Local retention mechanisms combined with spatial variation in spring warming, which probably affected larval-stage durations, appeared to be responsible for the dynamic settlement pattern. To determine whether spatial patterns of flounder settlement were dramatically altered by post-settlement processes, we compared settler supply (measured using traps) with juvenile distributions (measured using beam trawls, which do not prevent post-settlement mortality and emigration). The index of settler supply explained 95% of the variation in juvenile abundance patterns in the Navesink River ($p < 0.001$) where larger juveniles > 20 mm standard length were commonly trawled. However, larger juveniles were nearly absent in Sandy Hook Bay, where juvenile distributions were not related to settlement ($r^2 = 0.15$, $p = 0.31$). Thus, the upstream distribution of juvenile winter flounder in the NSBES, which is similar to that observed in other estuarine nurseries, appeared to be produced by the rapid modification of settlement patterns by post-settlement processes. However, pre-settlement processes that produce spatial variation in the timing of settlement could affect the ways in which settlement patterns are modified by age, time and/or size dependent post-settlement processes.

KEY WORDS: Dynamic habitat · Nursery · Supply side processes · Post-settlement processes

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INTRODUCTION

Most marine demersal fishes and invertebrates have complex life histories in which eggs hatch dispersive larvae that metamorphose and settle as relatively sedentary juveniles. For these species, locations of primary nursery grounds are established by processes controlling larval supply and settlement.

Settlement patterns may remain stable through the early juvenile period or may be dramatically altered by spatially structured mortality and/or emigration during the first few days to weeks of demersal life (Levin 1994, Wennhage & Pihl 2001, Booth 2002, Moksnes 2002, Steele & Forrester 2002, Webster 2002). As a result, better understanding of processes controlling nursery-ground formation often demands

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simultaneous assessment of the ways in which early juvenile distributions are shaped by supply-side and post-settlement processes. Relationships between pre- and post-settlement processes and year-class strength in fishes and invertebrates, including mobile flatfishes, have been extensively studied (Zijlstra et al. 1982, van der Veer 1986, Houde 1987, Beverton & Iles 1992, Hines & Ruiz 1995, Jager et al. 1995, Nash & Geffen 2000, van der Veer et al. 2000). However, studies of the combined effects of pre- and early post-settlement processes on the spatial distributions of juveniles have largely been confined to site-attached invertebrates and reef fishes (Caselle & Warner 1996, Eggleston et al. 1998, Shima 2001, Steele et al. 2002, but see Wennhage 2002).

Winter flounder *Pleuronectes americanus* is a NW Atlantic flatfish that ranges from Labrador to Georgia. With the exception of populations on Georges Bank and Nantucket shoals, the species uses estuaries as primary spawning and nursery grounds (Howe et al. 1976, Pierce & Howe 1977, Pereira et al. 1999). Adults spawn demersal eggs in the upper reaches of estuaries during winter and spring (Saila 1961, Crawford & Kerry 1985, Scarlett 1991, Phelan 1992, Stoner et al. 1999). Pelagic larvae remain in the water column from 5 to 8 wk and larval duration is strongly temperature-dependent (Laurence 1975, Keller et al. 1999, Chambers et al. 2001). Studies of estuarine circulation and larval distributions suggest that larvae are retained near spawning grounds (Pearcy 1962, Crawford & Kerry 1985, Chant et al. 2000), where they settle as benthic juveniles during the spring and early summer (Lobell 1939, Perlmutter 1947, Saila 1961, Pearcy 1962). Juveniles are generally more abundant in upstream reaches of estuaries, which are considered to be primary nursery grounds (Pearcy 1962, Armstrong 1995, Meng & Powell 1999, Stoner et al. 2001). Although these studies suggest that early juvenile winter flounder habitat associations are primarily determined by supply side processes, the extent to which post-settlement processes also contribute to the formation of upstream nursery grounds has not been explored.

We studied contributions of supply-side and early post-settlement processes to the formation of a winter flounder nursery ground in a mid-Atlantic estuarine system. We used settlement traps that captured newly settled fish but limited predation and emigration to test the null hypothesis that settler supply did not vary in space and time throughout the estuary. We then determined whether early juvenile flounder distributions were primarily controlled by supply-side processes by comparing settlement patterns, measured using traps, with juvenile distributions, measured using fine-mesh trawls that do not limit post-settlement mortality or emigration.

MATERIALS AND METHODS

Study area and study design. We used a nested experimental design to examine abundance patterns of settlement and juvenile stage winter flounder in the Navesink River/Sandy Hook Bay estuarine system (NSBES), a known spawning and nursery ground for the species (Fig. 1; Phelan 1992, Stoner et al. 1999, 2001, Sogard et al. 2001, Manderson et al. 2002). The study area was divided into 6 sectors along gradients of salinity, depth, and sediment characteristics associated with changes in fish and invertebrate community structure (Fig. 1; see Manderson et al. 1997 for details). Sectors A and B were located in Sandy Hook Bay in deep, high salinity areas with fine sand and silty substrata. Sediments are generally more coarse in Sector A, which contains the navigational channel to the Atlantic Ocean. Sediments are also fine sands and silts in Sectors E and F, located in shallow, lower salinity areas of the Navesink River. The primary freshwater source for the river drains into Sector F, where salinities are relatively low. Networks of sandbars and channels with high-velocity tidal currents are characteristic of Sectors C in the inner bay and D in the lower river, where sediments are coarse and medium sands. Three sectors were nested within 2 regions; the bay (Sectors A, B, C) and river (Sectors D, E, F; Fig. 1).

In each sector we randomly selected 3 stations from transects previously used in synoptic surveys (Fig. 1; Manderson et al. 1997, Stehlik & Meise 2000, Stoner et al. 2001). Thus, 3 stations were nested within each of 3 sectors, nested within each of 2 regions. This hierarchical design allowed for analysis of flounder abundance at 3 spatial scales (among regions, \bar{x} distance [D] = 10.9 km \pm 3.5; among sectors, \bar{x} D = 4.1 km \pm 1.3; among stations, \bar{x} D = 1.7 km \pm 0.8).

Collection techniques. Newly settled fish: We measured patterns in the supply of settlement-stage winter flounder with traps that captured newly settled fish <14 mm standard length (SL) but excluded predators. The traps were constructed of rectangular 3 mm nylon mesh bags (0.75 \times 0.75 \times 0.40 m) secured within steel reinforcing bar frames (0.85 \times 0.85 \times 0.45 m). The mesh bags had zippers that were tightly closed when the traps were deployed. Two to 3 cm of sediment penetrated through the bottoms of traps deployed on the substratum (see Able et al. 1999). The mesh size allowed fish <3 mm in body depth (BD; \leq 13 mm standard length [SL]; SL in mm = 1.68 \times BD in mm + 6.09, $R^2 = 0.67$) to enter the traps. Fish growing to 3 mm BD (SL \sim 14 mm) were retained in the gear. Winter flounder larvae undergo eye migration and metamorphosis from 7 to 13 mm SL (1 to 3 mm BD; Chambers & Leggett 1987, Able & Fahay 1998) and slightly larger fish (17 to 28 mm SL) grow \sim 0.8 mm SL d⁻¹ in encl-

tures identical to the traps (Manderson et al. 2002). Thus the traps captured fish during and just after settlement.

We fished replicate settlement traps ($N = 3$) at the 18 stations during eight, 13 d experiments conducted from March 7 through June 27, 2000 (Table 1). During each experiment the traps were retrieved after 13 d, emptied of flounder and other organisms, washed with freshwater and redeployed the following day. We measured (SL and BD in mm) trapped flounder and preserved them in 95% ethanol for age determination using otolith increment analysis.

We estimated post-metamorphic ages of trapped flounder by counting increments external to accessory primordia in sagittae otoliths. Accessory primordia form in the otoliths of fish undergoing eye-migration and settlement from pelagic to benthic habitats (Chambers & Leggett 1987, Sogard 1991). Otolith increments are then deposited daily in newly settled flounder with growth rates exceeding $0.25 \text{ mm SL d}^{-1}$ (Sogard 1991). We extracted left sagittae otoliths from 2 fish selected at random from each trap collection. Otoliths were embedded in Crystal Bond thermoplastic glue and then polished with sandpaper (800 and 1200 grit) and alumina powder (0.3μ) along

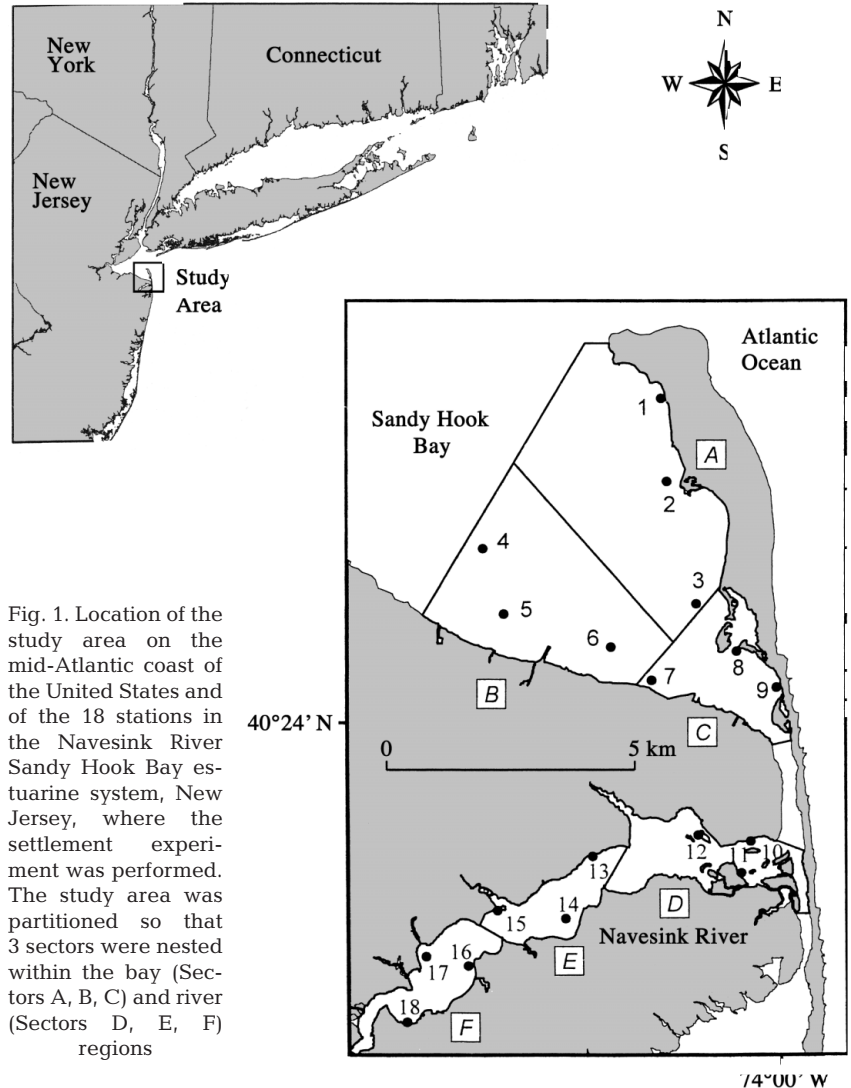


Fig. 1. Location of the study area on the mid-Atlantic coast of the United States and of the 18 stations in the Navesink River Sandy Hook Bay estuarine system, New Jersey, where the settlement experiment was performed. The study area was partitioned so that 3 sectors were nested within the bay (Sectors A, B, C) and river (Sectors D, E, F) regions

Table 1. *Pseudopleuronectes americanus*. Dates of winter flounder sampling and processes measured with settlement traps and beam trawls in the Navesink Sandy Hook Bay estuarine system. Beam trawls were also used to measure abundances of potentially important crustacean predators

Expt	Gear:	Process:	Duration	1 m beam trawl	Sampling dates
	Settlement traps	Settlement		Settlement + mortality and emigration	
1			March 7–21		March 15
2 ^a			March 22–April 3		March 29
3			April 4–18		April 12
4 ^a			April 19–May 1		April 25
5			May 2–16		May 9
6 ^a			May 17–30		May 24
7			May 31–June 13		June 5
8 ^a			June 14–28		June 19
9					July 5

^aReplicate ($N = 3$) sediment cores were collected at each station during the experiment

the sagittal plane until the cores were exposed. Otolith increments were counted 3 times under $400\times$ and $1000\times$ magnification.

Juvenile flounder and potential crustacean predators: We used a 1 m beam trawl (3 mm mesh liner) to measure flounder distributions established at settlement but potentially modified by predation and emigration. During each trapping experiment, replicate trawl tows ($N = 3$; speed = 1 m s^{-1} , duration = 30 s) were made at the stations (Table 1). An additional trawl survey was conducted on July 5. We measured (in mm) and counted all organisms and expressed abundance as number of individuals 10 m^{-2} of tow. Densities of sand shrimp *Crangon septemspinosa* $>30 \text{ mm}$ total length (TL), and blue crabs *Callinectes sapidus*, which are potentially important predators of newly settled winter flounder ($<20 \text{ mm SL}$; Bertram & Leggett 1994, Witting 1995, Witting & Able 1995), were also measured with the beam trawls.

Habitat variation: Hourly bottom water temperatures (°C) were measured at the stations throughout the study with electronic recorders (Onset). We measured salinity (‰) with a probe (Yellow Springs Instruments) ≥ 4 times at the stations during each experiment. Depths were measured with an electronic depth finder and corrected to mean low water. We also collected replicate sediment cores (N = 3, 2.5 cm diameter) at each station (Table 1). Sieve fractionation was performed on the sediments to calculate mean grain sizes and sorting coefficients using the methods of Folk (1980). Dry sediment was incinerated at 500°C to measure organic content (% dry wt).

Analysis. Capture efficiency of settlement traps: Variability in the growth of settled fish inside the traps could have influenced capture efficiency. As a result we examined the relationship between the growth of marked winter flounder (17 to 27 mm SL; \bar{x} mm SL d⁻¹ trap⁻¹) and numbers of settlers in traps deployed throughout the NSBES in two 12 d experiments conducted from mid-May through mid-June 1999 (see Manderson et al. 2002 for details). Settler abundance in the traps was not related to the growth of marked fish in these experiments (Pearson's $r \leq 0.21$, $p \geq 0.54$).

Abundance patterns in space and time: We analyzed flounder and crustacean abundance patterns with nested ANOVA using experiment, region and sector as fixed factors and station as a random factor. Trawled flounder were divided into recently settled (≤ 20 mm SL) and juvenile (> 20 mm SL) size classes. Experiments in which animals were absent were eliminated from analyses. Levene's tests for heteroscedasticity (Wilkerson 1997) showed that variances were homogenized with $\log_e(n + 1)$ transformation. The region term was not used in analyses of juvenile flounder > 20 mm SL and blue crabs, which were rarely trawled in Sandy Hook Bay. We calculated expected mean squares (MS) to determine appropriate error MS and degrees of freedom (df) for all *F*-tests (Table 2).

Relationship between settlement and habitat variation: We explored relationships between flounder settlement and habitat variation with a generalized additive model (GAM; Hastie & Tibshirani 1990, Venables & Ripley 1997). Numbers of newly settled flounder in traps served as the dependent variable. Station depth (m), salinity (‰), sediment organic content (% by weight) and grain size (ϕ), and temperature (°C) expressed as relative degree days were considered as independent variables. Winter flounder larvae incubated at temperatures $\leq 2^\circ\text{C}$ in the laboratory fail to metamorphose (Laurence 1975). Thus, relative temperature degree days (TDD) were calculated for the stations on days of trap retrieval as the cumulative average daily temperature above 2°C from the start of the experiment on March 7.

Table 2. *Pseudopleuronectes americanus*. Nested ANOVA of the abundance of early life history stages of winter flounder and potentially important crustacean predators in the Navesink Sandy Hook Bay estuarine system

Life history stage [gear] (source of variation)	df	MS	<i>F</i>	<i>p</i>
Newly settled flounder [traps]^b				
Region	1	7.23	4.63	0.07
Sector(Region)	4	1.76	1.13	0.43
Station(Sector(Region))	6	1.56	10.71	<0.001
Experiment	4	4.77	4.44	0.007
Experiment \times Region	4	5.59	5.21	0.004
Experiment \times Sector(Region)	16	0.59	0.55	0.893
Experiment \times Station(Sector(Region))	24	1.07	7.35	<0.001
Error	210	0.15		
Total	269			
Recently settled flounder ≤ 20 mm SL [beam trawls]^b				
Region	1	0.03	0.58	0.48
Sector(Region)	4	0.19	3.57	0.08
Station(Sector(Region))	6	0.06	1.71	0.15
Experiment	4	0.11	6.14	0.002
Experiment \times Region	4	0.12	6.71	<0.001
Experiment \times Sector(Region)	16	0.04	2.28	0.032
Experiment \times Station(Sector(Region))	24	0.02	0.57	0.95
Error	210	0.03		
Total	269			
Juvenile flounder > 20 mm SL [beam trawls]^{a,c}				
Sector	2	0.16	3.36	0.105
Station(Sector)	6	0.05	2.56	0.024
Experiment	4	0.12	2.07	0.116
Experiment \times Sector	8	0.10	1.71	0.147
Experiment \times Station(Sector)	24	0.06	3.07	<0.001
Error	90	0.02		
Total	134			
Sand shrimp > 30 mm SL [beam trawls]^b				
Region	1	12.21	19.48	0.004
Sector(Region)	4	0.84	1.34	0.36
Station(Sector(Region))	6	0.63	1.28	0.27
Experiment	8	3.36	9.44	<0.001
Experiment \times Region	8	1.04	2.91	0.01
Experiment \times Sector(Region)	32	0.51	1.43	0.13
Experiment \times Station(Sector(Region))	48	0.36	0.73	0.91
Error	252	0.47		
Total	359			
Blue crabs [beam trawls]^{a,c}				
Sector	2	3.2	5.71	0.04
Station(Sector)	6	0.56	2.32	0.035
Experiment	8	0.25	0.77	0.630
Experiment \times Sector	16	0.16	0.514	0.927
Experiment \times Station(Sector)	48	0.32	1.33	0.098
Error	162	0.24		
Total	198			

^aRegion term dropped from analyses because individuals were nearly absent from the bay
(*F*-tests for sources of variation:
^bRegion and Sector(Region) tested with Station(Sector(Region)) MS and DF; Experiment, Experiment \times Region and Experiment \times Sector(Region) tested with Experiment \times Station(Sector(Region)) MS and DF; Station(Sector(Region)) and Experiment \times Station(Sector(Region)) tested with error MS and DF
^cSector tested with Station(Sector) MS and DF; Experiment and Experiment \times Sector tested with Experiment \times Station(Sector) MS and DF; Station(Sector) and Experiment \times Station(Sector) tested with error MS and DF

We constructed the GAM with manual forward step-wise selection using a cubic spline with 4 degrees of freedom, which produced moderate smoothing (S-Plus, Math-Soft; Hastie & Tibshirani 1990, Venables & Ripley 1997). The term added to the model at each step resulted in the largest significant ($p < 0.05$) reduction in residual deviance (\sim variance) when compared to the previous model using an approximate F -test in analysis of deviance (Hastie 1992). We calculated deviance explained as null deviance minus residual deviance divided by null deviance. First-order interactions between significant variables were also tested. Partial additive effects of the independent variables were plotted with ± 2 SE confidence bands.

To identify possible centers of winter flounder settlement, we used Arcview GIS software (ESRI) to project GAM based estimates of daily settlement across the estuary. For each date, a continuous surface of cumulative TDD (cell size = 500 m) was constructed using temperature records for the geo-referenced stations and Arcview's inverse distance weighted averaging algorithm. We used the same method to construct a continuous surface of sediment organic content using data from a 1997 sediment survey conducted at 84 stations throughout the NSBES (see Stoner et al. 2001). Sediment organic contents measured at stations in this study were similar to cell based estimates generated from the 1997 sediment survey (Pearson's $r = 0.85$, $p \ll 0.001$). Grid-cell values for the 2 variables were exported from Arcview and used in the GAM to estimate daily settlement patterns. These estimates were returned to Arcview for plotting.

Relationship between the supply of settlers and juvenile flounder distributions: To determine whether

spatial patterns of settlement were maintained through the early juvenile period, we used Kendall's coefficient of concordance and regression analysis to compare trawl based estimates of flounder density, with settler supply measured as the cumulative abundance of fish in traps.

RESULTS

Trap collections and patterns of settler supply

Newly settled flounder were trapped from mid-April through mid-June ($N = 299$). The fish ranged in length from 5 to 29 mm SL (median = 18 mm) and most had body depths exceeding 4 mm (median = 7 mm, 2 to 11 mm; Fig. 2a). Fish collected during the 13 d trap deployments ranged in age from 4 to 14 d post eye-migration (median = 10 d; Fig. 2b). Their growth rates averaged 1.3 mm SL d^{-1} ($SE = 0.1$).

We also trapped sand shrimp, amphipods and polychaetes. Shrimp were captured infrequently and were too small ($N = 64$; 2 to 13 mm TL) to consume newly settled winter flounder (Witting & Able 1993, 1995, Bertram & Leggett 1994).

Settlement dynamics

Flounder settlement measured with the traps was spatially dynamic (Fig. 3, Table 2). Settlement occurred earlier in the river than the bay and the trial by region interaction accounted for a large amount of variation in the ANOVA (21% of total variance [TV]).

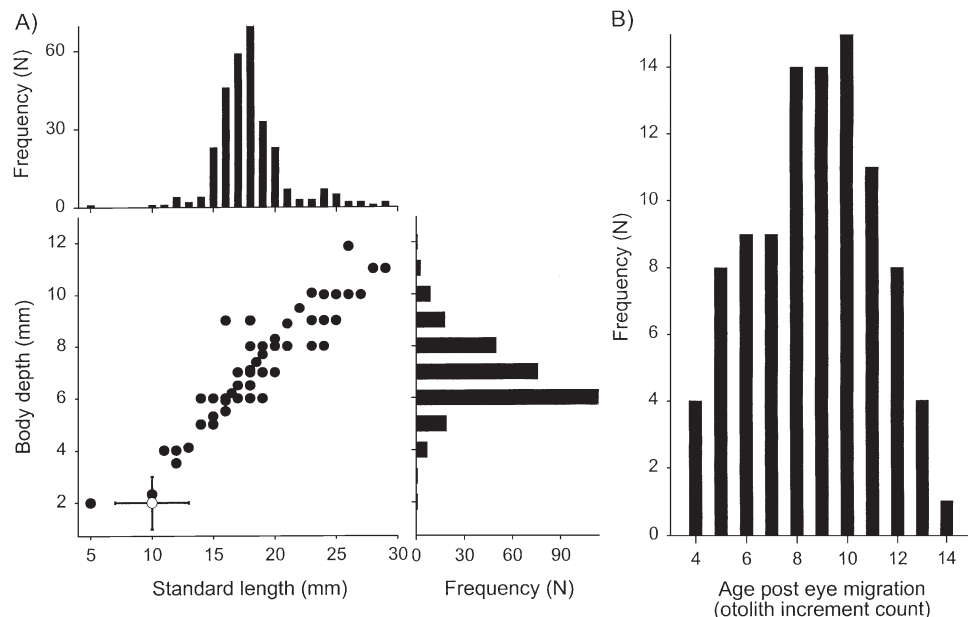


Fig. 2. *Pseudopleuronectes americanus*. Frequencies of (A) size and (B) age post-eye migration for newly settled winter flounder collected in the settlement traps ($N = 299$). Open symbol with lines in (A) indicates the range of lengths and body depths for settlement-stage fish reported by Chambers & Leggett (1987)

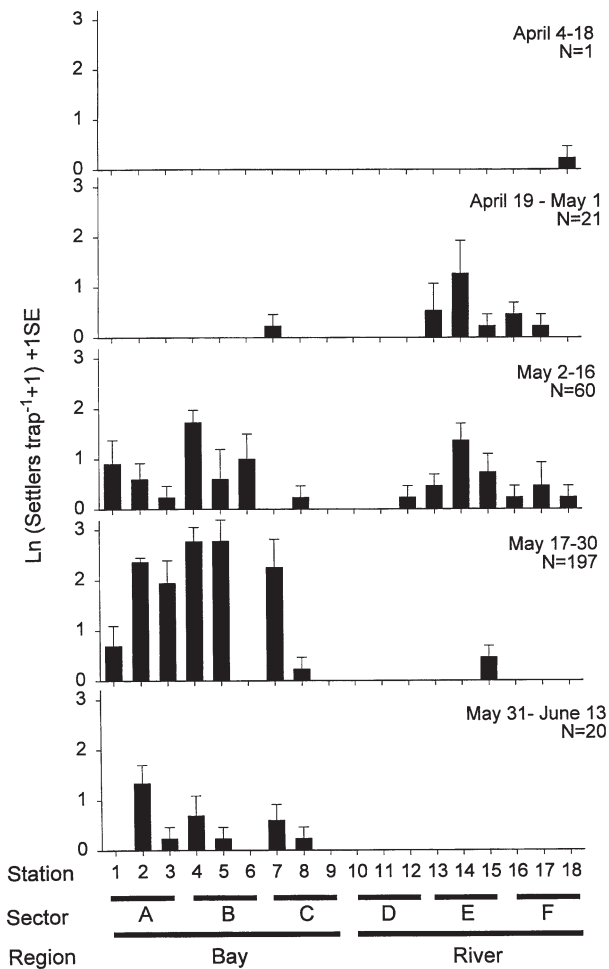


Fig. 3. *Pseudopleuronectes americanus*. Abundance of newly settled winter flounder in settlement traps, which was dynamic in time at a regional spatial scale, with earlier settlement in the Navesink River than Sandy Hook Bay (see Table 2). (Fig. 1 for station locations. Experiments in which fish were absent from traps are not included)

Newly settled fish were primarily collected in the river from April 18 through May 1. Abundance peaked in the river on May 16, when values were similar in the river and bay (river: $\bar{x} = 0.81$ fish trap⁻¹, SE = 0.26; bay: $\bar{x} = 1.41$ fish trap⁻¹, SE = 0.40). On May 30 and June 13 most fish were trapped in the bay. Settlement peaked in the bay on May 30, when abundance in the region ($\bar{x} = 7.22$ fish trap⁻¹, SE = 1.70) was nearly an order of magnitude higher than in the river on May 16.

Newly settled fish were rare in Sector D of the river, but the effects of sector within region were insignificant in the ANOVA (Fig. 3, Table 2). Settler abundance was highly variable among stations within sectors in time (40% TV).

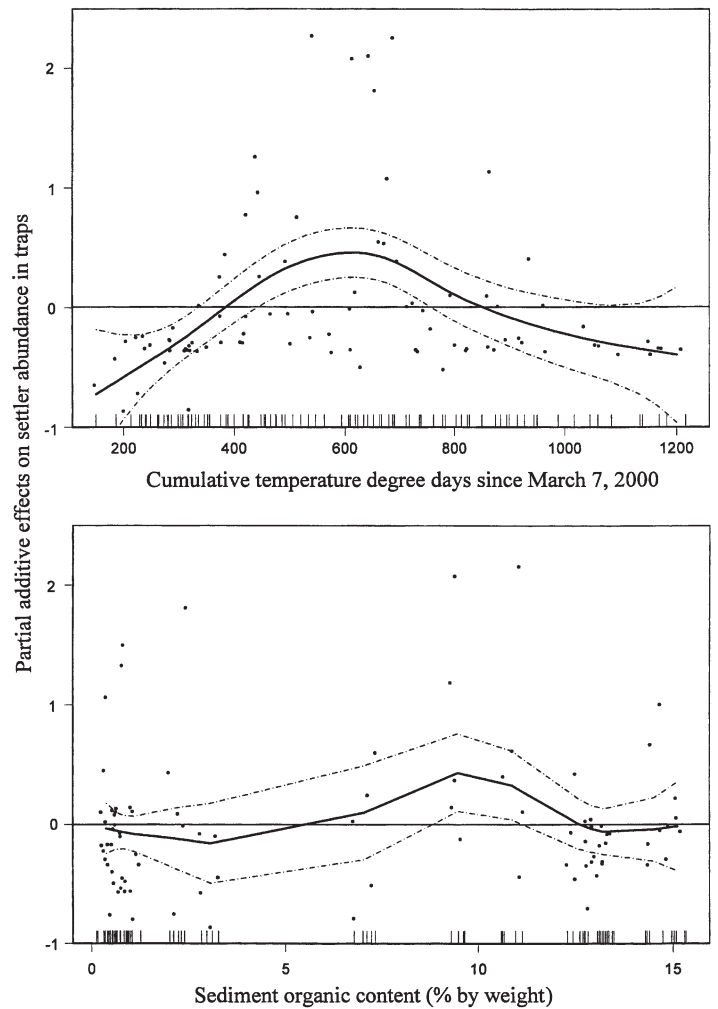


Fig. 4. *Pseudopleuronectes americanus*. Generalized additive model (GAM) based partial additive effects showing that relative temperature degree days between 350 and 850, and sediment organic contents between 5 and 12% by weight, had positive effects on the abundance of newly settled flounder in traps (see Table 3)

Dynamic habitat and likely centers of flounder settlement

Settlement was significantly related to relative TDD and sediment organic content (Table 3). Settlement showed a strong unimodal response to TDD and most fish were trapped from 350 to 875 TDD (maximum = 625 TDD; Fig. 4). Settlement was also marginally higher on organically rich substrata (5 to 12% by weight).

Rates of bottom water warming and TDD accumulation were more rapid in the river than the bay. Mean daily warming rates were positively correlated with distance upstream (Pearson's $r = 0.60$, $p = 0.01$; Fig. 5a), and degree day values within the range of positive effects in the GAM occurred 2 wk earlier in the river

Table 3. *Pseudopleuronectes americanus*. Generalized additive model showing that the abundance of newly settled winter flounder in traps was significantly related to relative temperature degree days and sediment organic content in the Navesink River/Sandy Hook Bay estuarine system (NSBES) (see Fig. 5a). The null model assumed that settlement variation was not explained by habitat parameters

Model	df	F	p	Non-parametric Deviance	Non-parametric Deviance explained (%)
Null				41.17	
Degree days since March 7	3	9.69	<<0.001	10.69	26
+ sediment organic content	3	3.61	0.016	3.69	9
Total Explained				14.20	35
Residual				26.97	65
Degree days since March 7					
+ sediment grain size	3	2.24	0.090		
+ depth	3	2.20	0.094		
+ salinity	3	1.68	0.178		

(April 21 to June 5) than the bay (May 2 to June 21). Substrata with organic contents of 5 to 12% occur in the middle and upper reaches of the river and center of the bay (Fig. 5b).

Two likely centers of flounder settlement located in the middle reach of the river and center of the bay were identified when cell-based estimates of TDD and organic carbon content were used to project the GAM across the estuary (Fig. 6). The projections showed that settlement probably began on organically rich substrata in the middle reach of the river in late April and continued there

until mid-May. High settlement probably also occurred on similar substrata in the center of the bay from mid-May through mid-June.

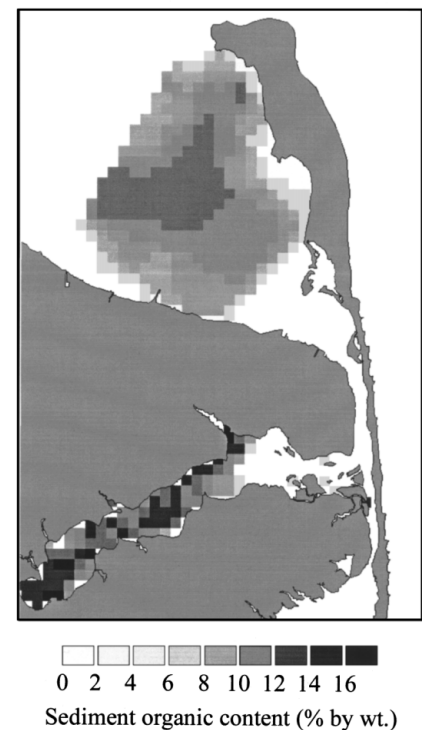
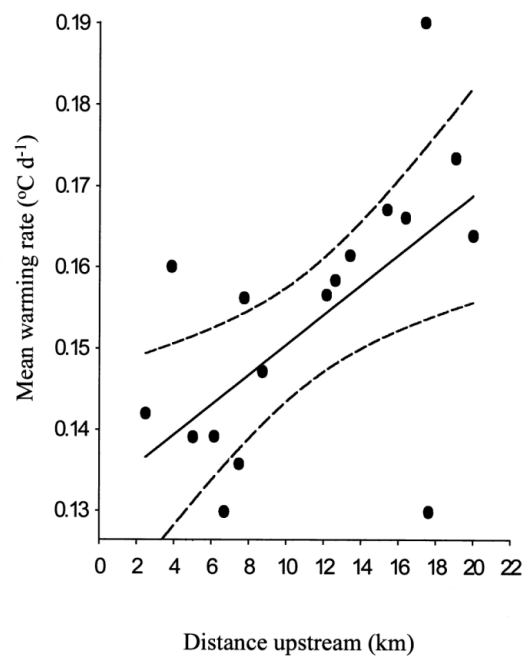
Beam trawl collections

Flounder ($N = 122$; 5 to 59 mm SL) were trawled throughout the estuary. Abundance patterns for recently settled fish ≤ 20 mm SL were spatially dynamic and broadly similar to the trapping pattern (Fig. 7a, Table 2). Newly settled fish were collected in the river from April 11 through May 23, in the bay from May 9 through June 5, and the trial \times region interaction accounted for a large portion of

explained variation in the ANOVA (9.6% TV). However, in contrast with the trapping results, peak densities of recently settled fish were similar in the 2 regions (river, April 25: $\bar{x} = 0.96$ per 10 m^2 , $SE = 0.47$; bay, May 23: $\bar{x} = 0.52$ per 10 m^2 , $SE = 0.22$). Fish ≤ 20 mm SL were rare in Sectors C in the bay and D in the river, but abundance varied among sectors within regions in time.

Juvenile flounder > 20 mm SL were commonly trawled in the river from May 9 through the last survey on July 5 (Fig. 7b). However, fish of this size were nearly absent in

Fig. 5. *Pseudopleuronectes americanus*. Variability in space and time of habitat characteristics related to settlement dynamics in the generalized additive model (GAM). (A) From March 7 through July 5, 2000, bottom temperatures warmed and degree days accumulated more rapidly upstream in the Navesink River than downstream in Sandy Hook Bay. (B) Sediment organic values are typically within the range of positive effects in the GAM (5 to 12% by weight) in the central part of the bay and the middle and upper reaches of the river



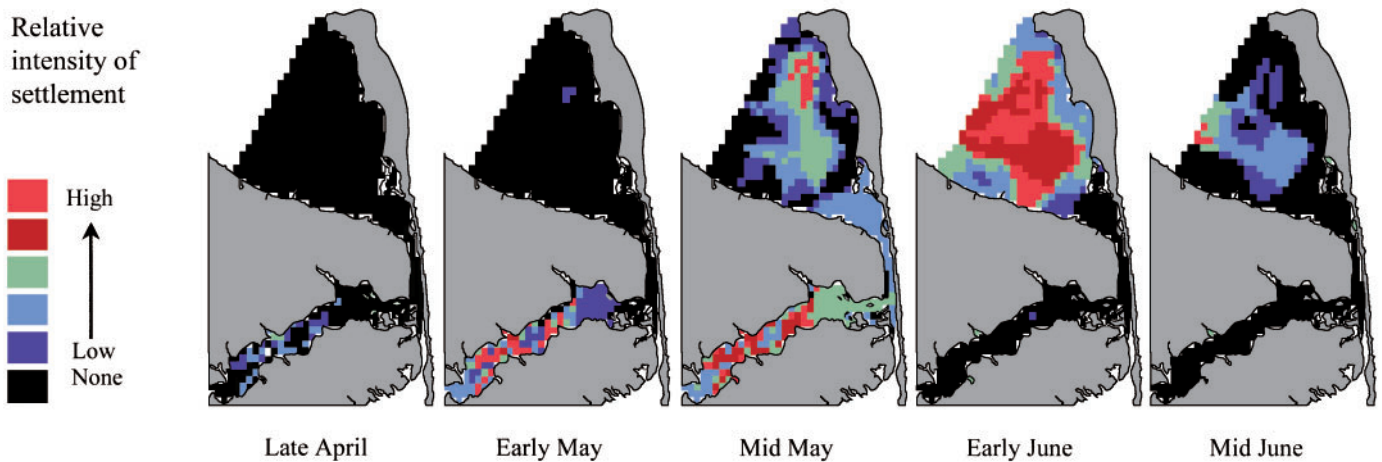


Fig. 6. *Pseudopleuronectes americanus*. Projections of the generalized additive model (GAM; see Table 3, Fig. 4) indicating that the middle reach of the Navesink River and the central portion of Sandy Hook Bay were likely centers for winter flounder settlement, but that recruitment occurred earlier in the river than the bay

the bay ($N = 2$). The abundance of fish >20 mm SL varied among stations within sectors in time in the river (Table 2).

Relationship between settler supply and juvenile distributions

Patterns of juvenile flounder abundance established at settlement appeared to be modified much more rapidly by post-settlement processes in the bay than the river. Juvenile abundance patterns were not related to settlement in the bay (Fig. 8, Table 4). In the river, however, the index of settler supply explained 95% of the variation in the average abundance of juveniles. Juvenile distributions were generally correlated with settler supply in the river from April 25 to June 5 (Table 4). When beam-trawled size classes were considered separately, estuary-wide distributions of recently settled fish ≤ 20 mm SL were related to settler supply from May through mid-June (Spearman's ρ : 0.444 – 0.822, $p < 0.04$), while densities of fish >20 mm SL and all juveniles were not (Table 4).

Crustacean predators were generally less abundant in the bay than the river and thus probably not responsible for the alteration of the settlement pattern (Fig. 9, Table 2). Blue crabs (median CW = 17 mm; range = 2 to 142) were rare in the bay. In the river, crab densities varied among sectors and increased upstream. Densities of sand shrimp (≥ 30 mm TL) capable of consuming newly settled flounder varied by region in time. During flounder settlement (April 11 to June 19), shrimp densities were slightly higher in the river than the bay, but the regional difference was significant in only 1 survey (June 19; Bonferroni multiple comparison test, $p = 0.001$).

DISCUSSION

Trapping techniques

Passive collectors have been used to measure variation in settler supply for a variety of marine invertebrates (Yund et al. 1991, Gaines & Bertness 1993, Eggleston et al. 1998, Moksnes & Wennhage 2001) and a few site-attached reef fishes (Behrens 1987, Levin 1996, Steele et al. 2002). When effective, collectors integrate densities of competent larvae and fluid flows over discrete periods of time while limiting post-settlement mortality and emigration, and thus provide a relative measure of the flux of potential settlers (Gaines & Bertness 1993). In contrast, traditional plankton sampling produces snapshots of highly variable densities of pre-competent as well as competent larvae during the dispersal phase. Although fine-mesh trawls only capture settled and thus competent individuals, they also produce snapshots of distributions that may represent settlement patterns that have been dramatically altered by post-settlement processes.

Our traps integrated fluxes of fully competent settlement-stage winter flounder over 13 d periods while limiting the effects of post-settlement mortality and emigration. The flounder we collected probably entered the traps from competency to less than about 8 d in post-metamorphic age. The fish had completed metamorphosis, which occurs when larvae reach 7 to 13 mm SL (Chambers & Leggett 1987, Able & Fahay 1998), and grew at an average of 1.3 mm SL d^{-1} inside the traps. Sogard et al. (2001) reported similar growth for settling fish collected in Sandy Hook Bay over 9 yr ($\bar{x} = 1.12$ SL mm d^{-1}). Since the 3 mm mesh excluded flounder >14 mm SL ≈ 4 mm BD from the traps, fish settling

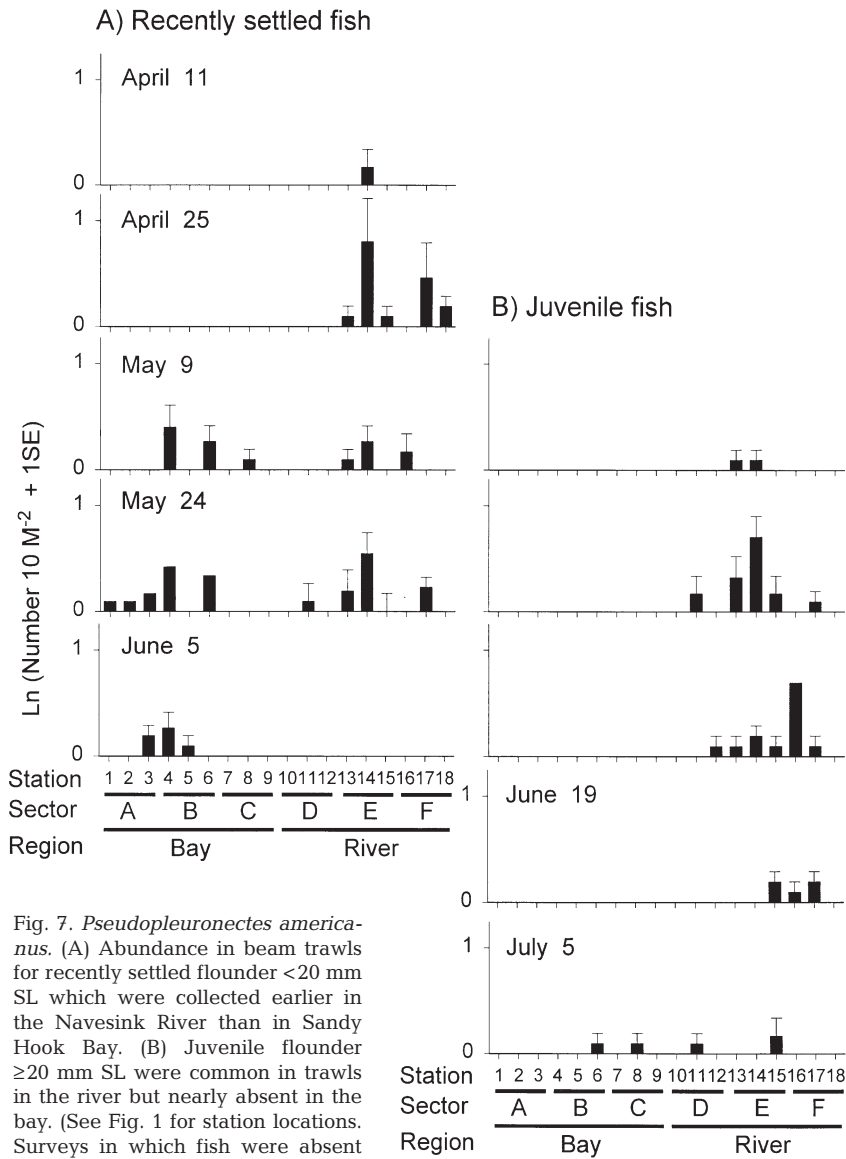


Fig. 7. *Pseudopleuronectes americanus*. (A) Abundance in beam trawls for recently settled flounder <20 mm SL which were collected earlier in the Navesink River than in Sandy Hook Bay. (B) Juvenile flounder ≥ 20 mm SL were common in trawls in the river but nearly absent in the bay. (See Fig. 1 for station locations. Surveys in which fish were absent are not included)

at the smallest size that grew 1 mm SL d^{-1} were probably unable to enter the gear 7 to 8 d after metamorphosis. This estimate is within the range of the post-metamorphic ages of the fish we trapped (4 to 14 d).

Our trap-based index of settler supply was probably not confounded by post-settlement mortality and emigration. The fine mesh traps retained fish just larger than the maximum size at settlement ($\sim 14 \text{ mm SL}$) and thus minimized emigration. Predators were also excluded by the gear. Although we trapped sand shrimp, the individuals were too small to consume newly settled winter flounder (Witting & Able 1993, 1995, Bertram & Leggett 1994).

Our estimates of settler supply also appeared to be unbiased by variations in the habitat-specific growth

or mortality of fish inside the traps, and reflected natural settlement patterns. Settler abundance was not correlated with the growth of marked fish inside the traps in the 1999 experiment. The settlement index was probably not biased by mortality, since survivorship for small flounder (16 to 28 mm SL) caged for 10 to 12 d in enclosures identical to the traps has not been related to natural habitat variation in several growth studies (Able et al. 1999, Manderson et al. 2002). Finally, correlations between the abundance of flounder in traps and trawls suggested that the traps measured natural settlement patterns. Abundance of settlers in traps and fish <20 mm SL in trawls were -statistically correlated and broadly similar. In addition, the index of settler supply derived from the traps explained 95% of the variability in the average abundance of juveniles at stations in the river where post-settlement processes appeared to modify settlement patterns relatively slowly.

Winter flounder settlement dynamics

Although flounder settled throughout the estuary, we collected large numbers of new recruits in organically rich depositional habitats. Newly settled fish were most consistently trapped and trawled at depositional sites in the river and bay, and our GAM indicated that the abundance of flounder in traps was higher on

Table 4. *Pseudopleuronectes americanus*. Rank correlation tests (Kendall's τ) showing significant relationships between juvenile flounder abundance (beam trawls) and settler supply (cumulative abundance of fish in traps) in the Navesink River (April 25, May 9, June 5) but not in Sandy Hook Bay

Sampling date	Study area		River		Bay	
	τ	p	τ	p	τ	p
April 12	-0.01	0.808	-0.028	0.720	-	-
April 25	0.399	0.007	0.500	0.039	-	-
May 9	0.333	0.019	0.556	0.011	0.1389	0.5234
May 24	0.222	0.173	0.417	0.099	0.3056	0.2254
June 5	0.275	0.082	0.638	0.009	0.4167	0.0601
June 19	-0.059	0.594	0.167	0.444	-	-
July 5	-0.163	0.186	-0.139	0.465	-0.277	0.143

organically rich substrata. Projections of the GAM described 2 likely centers of winter flounder settlement, located in the middle reach of the river and center of the bay. The locations of these centers were remarkably similar to those reported by Stoner et al. (2001) (their Fig. 6), who also found early juvenile fish (<25 mm TL) to be associated with organically rich substrata (>6% by weight) in their analysis of June trawl surveys conducted in the NSBES in earlier years. Associations of Age 0 winter flounder with depositional muddy substrates has been reported in other estuarine systems as well (Saucerman 1990, Howell et al. 1999, Meng & Powell 1999) and fish <20 mm SL actively select fine-grained muddy substrates in the laboratory (Phelan et al. 2001).

Flounder settlement occurred approximately 2 wk earlier in the Navesink River (late April through late May) than in Sandy Hook Bay (mid-May through mid-June), even though the recruitment centers were just

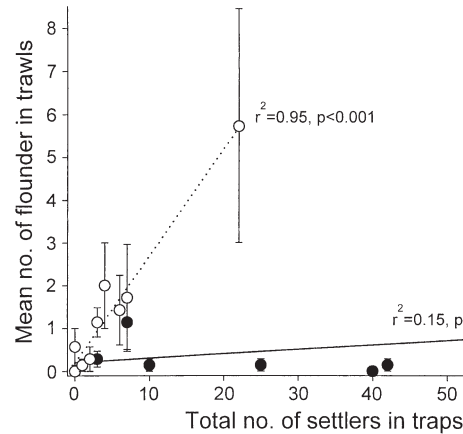
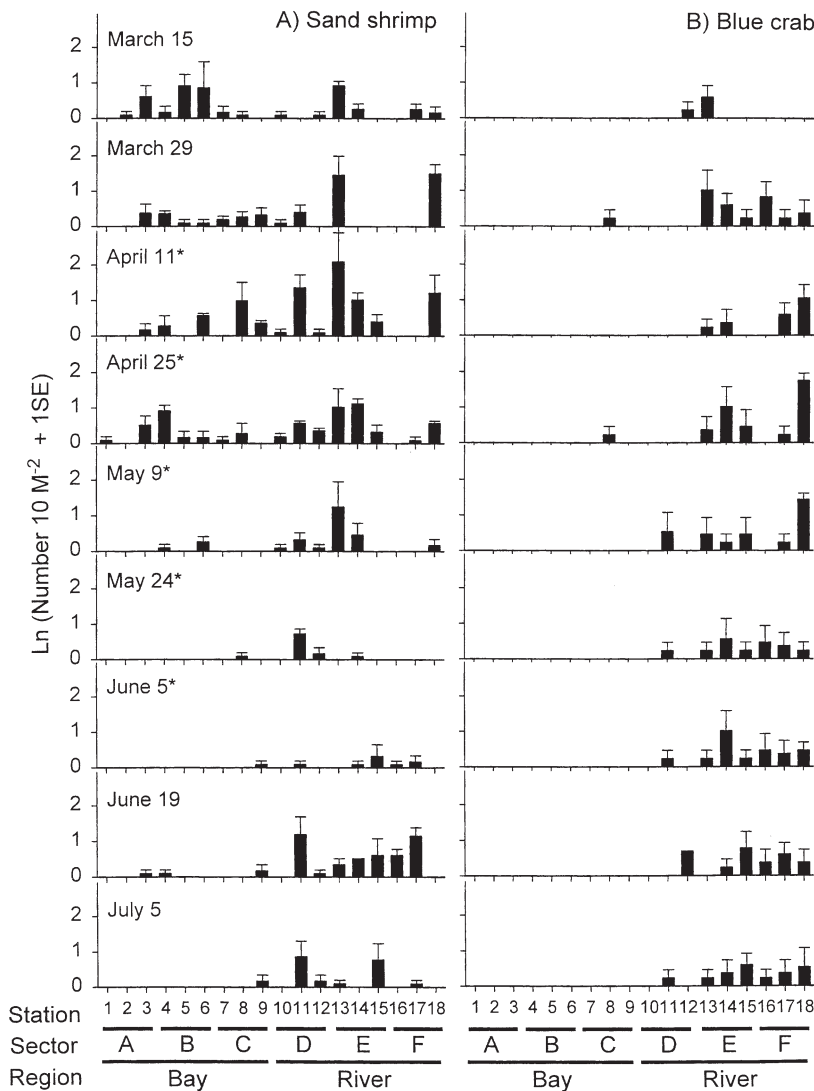


Fig. 8. *Pseudopleuronectes americanus*. Mean abundance of Age-0 flounder (trawls) was strongly correlated with total settler supply (traps) in the river (○) but not in the bay (●) indicating that settlement patterns were rapidly modified by post-settlement process in Sandy Hook Bay. Lines, r^2 and p values are results of regression analyses



15 km apart. In our analysis this fine-scale spatially dynamic settlement pattern was related to geographic variation in spring warming within the estuary. Settler abundance showed a strong unimodal response to TDD which accumulated more rapidly in the river. The importance of temperature history indexed as degree days probably reflected temperature effects on larval stage durations. Stage duration in larval fishes is inversely temperature-dependent (Houde 1989, Chambers & Leggett 1992, Benoit et al. 2000), and an increase in laboratory incubation temperature from 5 to 8°C can shorten the winter flounder larval period by 31 d (Laurence 1975).

The relationship between flounder settlement dynamics and geographic variation in spring warming with the estuary indicates that substantial numbers of larvae were probably segregated in the river and bay for long enough that regional temperature differences influenced larval stage durations. Previous studies of flounder spawning and circulation in the estuary support this hypothesis. Adult fish spawn in the middle and upper reaches of

Fig. 9. (A) Sand shrimp (TL ≥30 mm TL) and (B) blue crabs were generally more abundant in the river than in the bay and thus probably not responsible for the alteration of the winter flounder settlement pattern. *Experiments in which newly settled flounder were collected in trawls and/or settlement traps (see Fig. 1 for station locations)

the Navesink River from February through March (Phelan 1992, Stoner et al. 1999), and ripe adults are collected in Sandy Hook Bay during the same months (Chambers & Witting pers. comm.). Larvae hatching in the river are likely to be retained there because flood-dominated tidal circulation results in upstream transport to the middle reach (Chant & Stoner 2001). In Sandy Hook Bay residual tidal circulation produces a cyclonic gyre that concentrates particles and may promote larval retention near the center of the bay (Hires & Mellor 1988). Associations of early juvenile winter flounder with organically rich depositional habitats in the NSBES and other estuaries may be partially related to circulation mechanisms that maintain depositional habitats and concentrate larvae in the vicinity of them.

Flounder settlement was related to temperature and substrate characteristics in our study, but a considerable amount of the variation remained unexplained. This is not surprising since settlement can be controlled by a suite of factors not measured or considered in our analysis, including the location and timing of spawning and egg hatching; meteorological and hydrographic processes that influence larval dispersal; larval mortality, prey densities and swimming behavior; and active habitat selection by larvae competent to settle (Norcross & Shaw 1984, Breitberg et al. 1995, Dame & Allen 1996, Sponaugle & Cowen 1996, Cowen & Sponaugle 1997, Wennhage & Gibson 1998, Bradbury & Snelgrove 2001).

Modifications of settlement patterns by post-settlement processes

In our study the upstream distribution of juvenile flounder was not produced by geographic variation in the total supply of potential new recruits, but by spatial variation in the rate at which the settlement pattern was modified by post-settlement processes. Our trap data suggested that settlement was nearly an order of magnitude higher in Sandy Hook Bay than in the Navesink River. Nevertheless, flounder >20 mm SL were rarely trawled in the bay, where juvenile abundance was not correlated with settlement. In contrast, larger juveniles were common in the river, where the index of settlement explained 95% of the variation in average flounder abundance. Age 0 flounder are consistently more abundant and generally larger upstream in the Navesink River than in Sandy Hook Bay in early summer trawl surveys (Fig. 10). Age 0 fish are distributed upstream in other estuaries as well (Pearcy 1962, Armstrong 1995, Meng & Powell 1999). In the NSBES, the formation of the upstream nursery ground appears to be the result of particularly rapid modification of winter flounder settlement patterns by post-settlement processes in the bay.

We were unable to directly measure juvenile emigration and mortality and therefore identify the specific post-settlement process(es) that modified the settlement pattern. Fish may have emigrated upstream into the river or toward shallow shoreline habitats from settlement sites in the bay. Although a mark-recapture study indicated that young flounder (20 to 80 mm TL) rarely move from nursery habitats (Saucerman & Deegan 1991), Pearcy (1962) and Witting (1995) used trawl data to argue that fish emigrate rapidly from settlement sites. Pearcy (1962) suggested that fish migrate upstream following settlement because the abundance of newly settled flounder declined at sites in the lower Mystic River, Connecticut, as densities of larger fish increased upstream. Similar upstream movements are exhibited by early juveniles of a Northern European flatfish (*Platichthys flesus*; Kerstan 1991). However, upstream migration was not evident in our study since flounder densities were consistently low in the inner bay and lower river and did not increase in the river over time. Newly settled flounder may also move to shallow areas as they age and grow (Armstrong 1997, Stoner et al. 2001), and fish settling in deeper bay habitats may have emigrated more rapidly to shorelines than from shallower settlement areas in the river. Since we did not sample shallow shoreline habitats in this study, we cannot rule out the possibility that settlers emigrated to shallow areas at higher rates in the bay. However, in Stoner et al.'s (2001) spatially comprehensive study of the NSBES, juvenile winter flounder were less likely to occur in shallow bay areas than in habitats of similar depth in the river.

Predation is thought to be the leading cause of mortality for newly settled fishes (Bailey 1994, van der Veer et al. 1997, Connell 1998, Dahlgren & Eggleston 2000), and mortality rates for recently settled flounder may have been higher in the bay than the river. Shrimp of the genus *Crangon* and crabs consume newly settled flatfishes, including winter flounder, in the field and laboratory (Macer 1967, Edwards & Steele 1968, van der Veer & Bergman 1987, Seikai et al. 1993, Bertram & Leggett 1994, Witting 1995, Witting & Able 1995, Ansell et al. 1999, Fairchild & Howell 2000). In our study, however, modification of the settlement pattern was not related to density variations of shrimp and blue crabs, which were equally or more abundant in the river than the bay. Fishes are also important predators of early juvenile flatfishes on some nursery grounds (Edwards & Steele 1968, Ellis & Gibson 1995) and migratory fish including striped searobin *Prionotis evolans*, summer flounder *Paralichthys dentatus*, red hake *Urophycis regia*, striped bass *Morone saxatilis*, and bluefish *Pomatomus saltatrix* consume winter flounder (Poole 1964, Juanes et al. 1993, Manderson et al. 1999, 2000, North East Fisheries Science

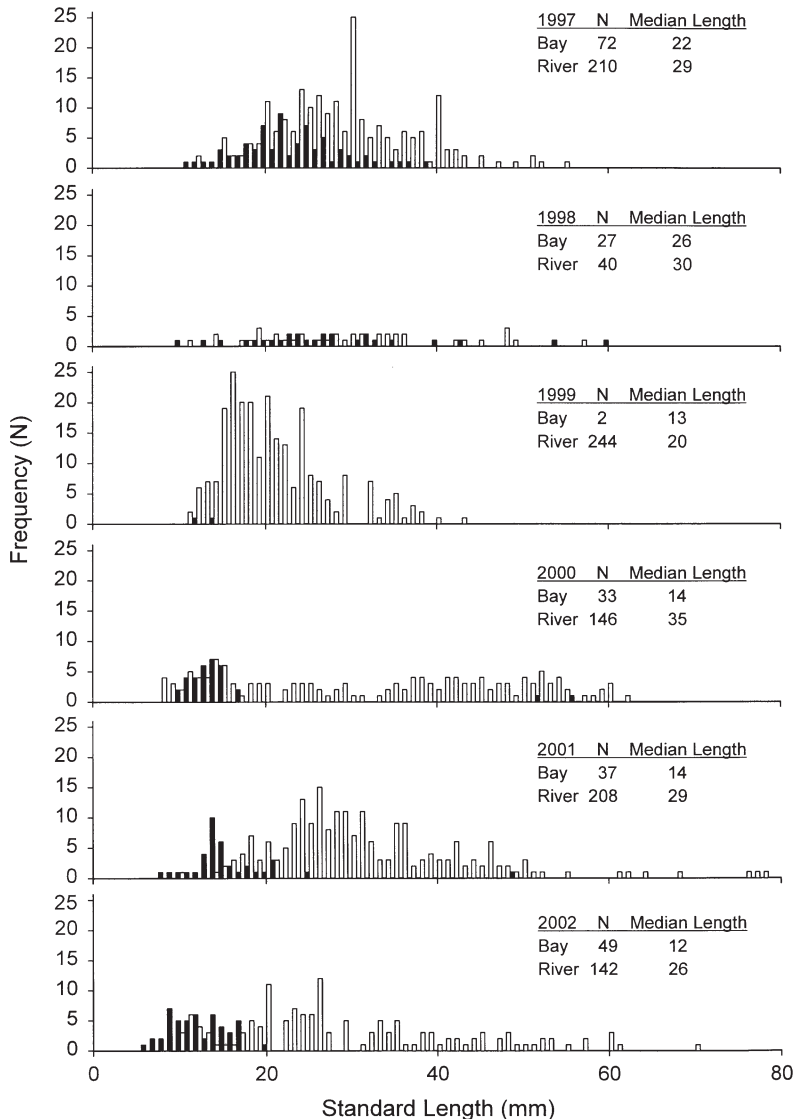


Fig. 10. *Pseudopleuronectes americanus*. From 1997 through 2002 Age 0 winter flounder were generally larger in size and more abundant in the Navesink River (white bars) than in Sandy Hook Bay (black bars) in May through early June trawl surveys of estuary

Center unpubl. data). With the exception of hake, all of these species enter the NSBES through the bay in the spring and early summer. Sea robins and hakes consume large numbers of newly settled fish (<20 mm SL) in the NSBES and are generally more abundant in the bay (Manderson et al. 1999, J.P.M. unpubl. data). Predation pressure exerted by fish could have been higher in the bay for at least a short period during and immediately following flounder settlement. However, spatial differences in the availability of structurally complex refuge habitats composed of vegetation or woody debris, which are more common in the river, could have affected survivorship independently of predator density.

CONCLUSION

Our goal in this study was to assess the relative contributions of supply side and post-settlement processes to the formation of juvenile winter flounder distributions and the primary nursery ground in a mid-Atlantic estuarine system. In our experiment, the upstream distribution of young flounder was produced by the modification of settlement patterns by post-settlement processes rather than spatial variation in the total supply of potential new recruits. However, variation in habitat characteristics that influence larval traits, including settlement timing, can strongly influence the ways in which post-settlement processes affect early juveniles. For example, juvenile survivorship for some coral reef fishes and European flatfish is related to larval characteristics including settlement timing (Al-Hossaini et al. 1989, Modin & Pihl 1996, Searcy & Sponaugle 2001, Bergegnius et al. 2002). Our study indicates that the combined effects of local heterogeneity in hydrographic retention mechanisms and temperatures on larval development rates may produce fine-scale spatial (~10 km) and temporal (wk) variability in larval settlement for winter flounder, a species that uses natal estuaries as juvenile nurseries. Specifically, fish settled earlier in a rapidly warming upstream estuarine region where juvenile distributions reflected settlement for a relatively long period of time. In an earlier study we showed that early spring warming combined with optimal salinities and prey densities promoted rapid growth in early juvenile winter flounder within this same region for a limited period during the late spring (Manderson et al. 2002). Early settlement combined with the rapid early growth in the upper estuary probably produces winter flounder body-size variations we generally observe (Fig. 10), and could strongly affect the ways in which size as well as time- and age-dependent post-settlement processes shape early juvenile distributions. Work presented here and in our earlier growth study suggests that environmental conditions in the upper reaches of estuaries may favorably affect critical supply-side and early post-settlement processes, and ultimately promote the survivorship of winter flounder through the early juvenile stage.

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