Dynamics of early juvenile winter flounder predation risk on a North West Atlantic estuarine nursery ground

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ABSTRACT: In an effort to determine the characteristics of estuarine habitats suitable for early juvenile winter flounder *Pseudopleuronectes americanus* survivorship, we examined piscivorous fish distributions and diets, and flounder predation risk along estuarine gradients in the Navesink River/Sandy Hook Bay estuarine system, New Jersey, USA. Demersal fish, striped searobin *Prionotus evolans* and summer flounder *Paralichthys dentatus*, were more important predators of winter flounder than pelagic fish (*Pomatomus saltatrix*, *Cynoscion regalis*, *Morone saxatilis*) based on diet analysis of 4 yr of gill (1998 and 1999) and trammel net (2001 and 2002) fish collections. From April through June newly settled winter flounder < 20 mm standard length (SL) were eaten by striped searobin that were common in habitats with salinities ≥ 20‰. Fish > 20 mm standard length (SL) were consumed by summer flounder in shallow habitats in June and July. In May and June tethering experiments, Age-0 winter flounder predation risk was high in habitats with salinities > 19‰ and temperatures > 20°C. In 3 yr, salinities were < 20‰ in the upstream reach of estuary which probably served as a predator refuge for settling flounder. During 2002, however, historically low freshwater discharge associated with a spring drought produced high salinities ≥20‰ in upstream habitats where searobins ate large numbers of settling winter flounder and predation risk was high. These results suggest that the volume of estuarine habitat suitable for early juvenile flounder survivorship is determined, in part, by predator and prey responses to spatially dynamic physico-chemical gradients. Because gradient dynamics are controlled by climate forcing, climate variation may cause nursery habitat volumes to contract or expand resulting in variation in the local production of Age-0 recruits.

KEY WORDS: Nursery habitat dynamics · Predation risk · Essential fish habitat

INTRODUCTION

For many demersal fish, recruitment variability is generated in early life history and population size is related to the availability of suitable nurseries (Sissenwine 1984, MacCall 1990, van der Veer et al. 2000a). Predation plays an important role in regulating nursery habitat suitability and population size (van der Veer et al. 2000b, Wennhage & Phil 2001, Webster 2002). Predation rates on tropical reef fish are highest during the first days to weeks following larval settlement and are strongly affected by habitat variation (Hixon & Jones, 2005 and references therein). Early post-settlement mortality is difficult to measure for mobile species in turbid, temperate environments but appears to regulate temperate populations (van der Veer et al. 2000a, Wennhage & Phil 2001, Manderson et al. 2003).

Predation is extremely variable but can be structured in systems with strong habitat gradients (Post et al. 1998, Overholtzer-McLeod 2004). In temperate estuaries, sea-

sonal and upstream changes in temperature and salinity are reflected in biological community variation (Jung & Houde 2003, Martino & Able 2003). Conceivably, species-specific responses to these physico-chemical gradients determine times and regions of predator–prey habitat overlap. Within regions of overlap, finer scale biological (e.g. alternative prey) and structural characteristics (e.g. habitat complexity) as well as body size constraints, further modify predation risk (Murdoch et al. 1975, Sogard 1997, Forrester & Steele 2004).

Northwest Atlantic estuaries serve as winter flounder *Pseudopleuronectes americanus* nurseries (see Pereira et al. 1999 for review). During winter and spring, adults spawn demersal eggs that hatch pelagic larvae. Larvae settle near spawning grounds in spring and early summer (Sogard et al. 2001, Manderson et al. 2003). Juveniles are generally most abundant in upstream estuarine reaches (Pearcy 1962, Armstrong 1997, Meng & Powell 1999, Stoner et al. 2001). Upstream distributions result from early post-settlement mortality and/or emigration rather than larval supply in some estuaries (Pearcy 1962, Curran & Able 2002, Manderson et al. 2003). Most studies of juvenile flounder mortality have emphasized the role of sand shrimp predators (e.g. *Crangon septemspinosa*; Bertram & Leggett 1994, Taylor & Collie 2003). However, Taylor (2005) demonstrated that shrimp predation was low in a mid-Atlantic estuary compared with New England nurseries and suggested that shrimp predation rates increase with increasing latitude. If this is the case, fish predation may be an important mechanism regulating habitat suitability and population size in the southern part of the species range. Fish are known to consume Age-0 winter flounder (reviewed in Pereira et al. 1999) but factors controlling fish predation on winter flounder nurseries have not been examined.

Our goal in this study was to describe the spatial dynamics of habitat suitability for early juvenile winter flounder survivorship on a mid-Atlantic estuarine nursery ground. We used gill net, trammel net, and beam trawl surveys to identify seasonal, spatial, and size-dependent patterns of flounder consumption by fish predators. To quantify relationships between predation risk, variations in the predator field, and estuarine gradients during flounder settlement, we conducted simultaneous tethering experiments and net surveys throughout the nursery.

MATERIALS AND METHODS

Study area. We performed this study in the Navesink River/Sandy Hook Bay estuarine system (NSBES), New Jersey, USA which is similar to many riverine estuaries in the Mid-Atlantic Bight and contributes to the winter flounder stock (present Fig. 1; Sogard et al. 2001). The NSBES connects to the Atlantic Ocean at the Sandy Hook peninsula and extends 20 km south and west to the confluence of the Navesink and Swimming Rivers. Maximum depths range from ~15 m in Sandy Hook Bay to ~3 m in the Navesink River. The Swimming River is the primary freshwater source for the Navesink and salinity can range from ~10‰ in the western Navesink to ~30‰ in the northeastern part of Sandy Hook Bay. Water temperatures can exceed 30°C in the river during summer and the tidal range averages 1.4 m (see also Stoner et al. 2001, Manderson et al. 2002, 2003).

Surveys of predators. We used gill net and trammel net surveys to identify seasonal, spatial, and size-dependent patterns of Age-0 flounder consumption by, and distributions of, piscivorous fish (Table 1, Fig. 1). Gill nets (46 m long × 2.5 m deep: 7.6 m panels of 1.3, 1.9, 2.5, 3.8, 5.1 and 7.6 cm mesh) were fished for 2 h fortnightly at 14 shallow stations from May through October 1998 and 1999. We set the nets ~1 h before high tides occurring <4 h after sunrise.

In 2001 and 2002, we used trammel nets (100 m long × 2 m deep, 5 cm inner mesh, 36 cm nylon walls) to more effectively capture important demersal predators of winter flounder identified in gill net surveys (Tables 1 & 2). The nets were fished weekly for 2 h, 2 h after sunrise during winter flounder settlement (May and June). In 2001 we continued the surveys fortnightly through mid-October. Three stations randomly selected from grids within each of 6 sectors of the NSBES were sampled in each 2001 survey (18 Stns survey^{-1}; Fig. 1). In 2002, we fished the nets at the 12 stations where we performed tethering experiments (see below).

During surveys, we measured depths with an electronic depth finder (cm), and bottom water temperatures (°C) and salinities (‰) with a probe (Yellow Springs Instruments). In 2001 and 2002 we used a 1 m beam trawl (3 mm mesh liner; tow speed = 1 m s^{-1}, duration = 30 s) to measure flounder and alternative prey densities following the recovery of each trammel net.

We counted and measured (length, mm) fish collected in gill nets, trammel nets, and beam trawls. Catch per unit effort (CPUE) was calculated as the number of individuals captured h^{-1} in nets, and 10 m^{-2} of tow in beam trawls. We removed and preserved (10% formalin) stomachs of fish collected in nets for diet analysis. Diet items were identified to species, counted, weighed (wet weight, g), and length was measured (mm) when possible.

We summarized patterns of habitat use for flounder predators collected in nets and identified in diet analysis with descriptive discriminant analysis (DA) using backward stepwise selection (Ade-4 library in R: Thioulouse et al. 2004, available at http://pbil.univ-lyon1.fr/ADE-4/adelist.html; R Development Core Team 2004). We analyzed gill net and trammel net surveys separately. Spe-
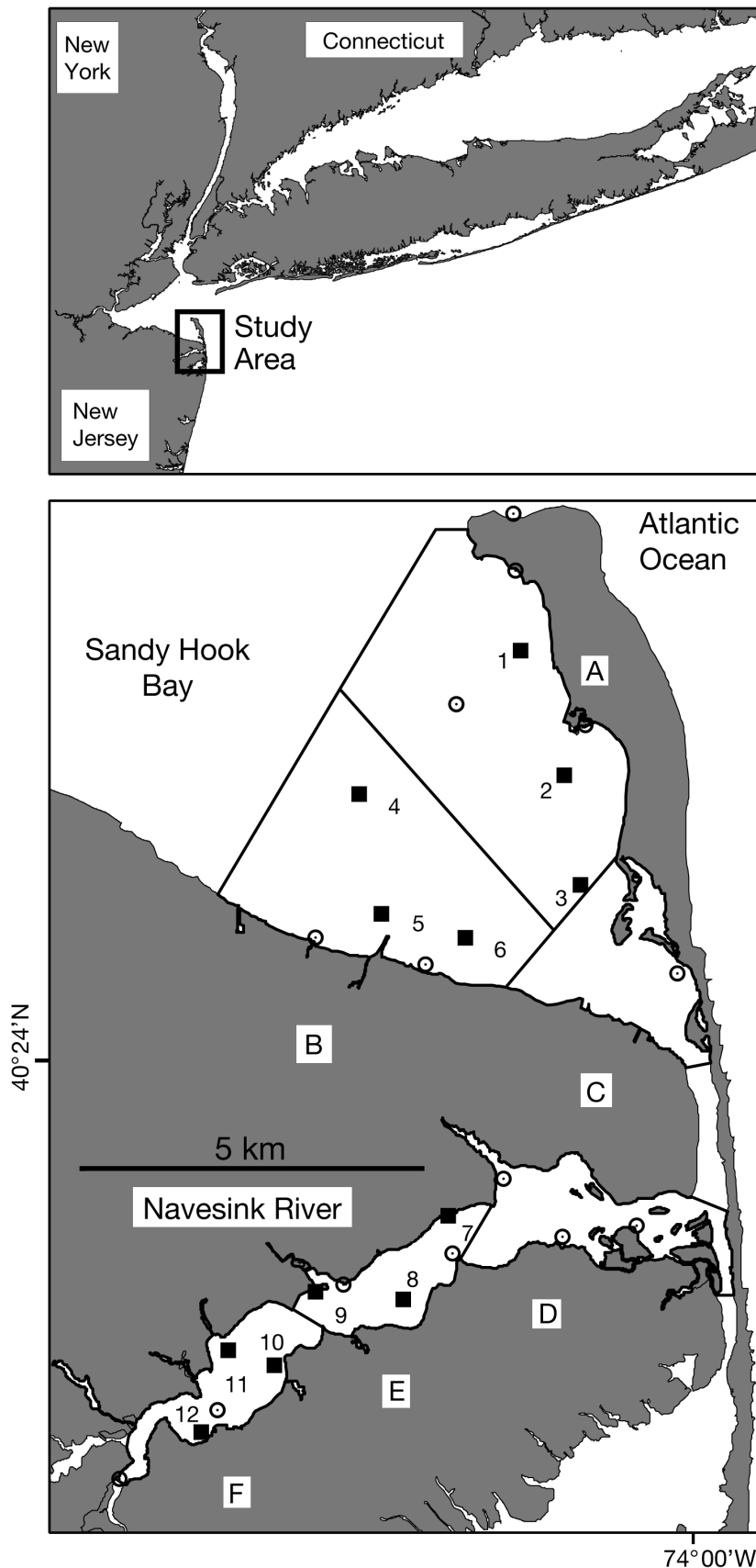
Fig. 1. Location of the study area on the Mid-Atlantic coast of the USA and of stations in the Navesink River/Sandy Hook Bay estuarine system, New Jersey, where predator surveys and tethering were performed. Gillnets were fished at 14 shallow water stations (⊙) in 1998 and 1999. Trammel nets were fished at stations selected at random within 3 sectors nested within the bay (Sectors A, B, C) and the river (Sectors D, E, F) in 2001. In 2002 trammel nets were fished at 12 fixed stations (■) where tethering was also performed

cies presence in each net served as dependent variables because most predators were schooling and individual fish were not independent. Since beam trawl collections were made with trammel net surveys, we included Age-0 winter flounder presence in trawls in the DA of 2001 and 2002 data to summarize predator-prey habitat overlap. The independent variables were year, day of the year, distance upstream (km from the tip of Sandy Hook; Fig 1), temperature (°C), and salinity (‰). We included depth in the DA of 2001 and 2002 data because a wide range of depths was sampled (Table 1). DA models were tested using Monte-Carlo tests with 1000 permutations.

We calculated probabilities of occurrence of dominant flounder predators during winter flounder settlement with respect to salinity and temperature using logistic generalized additive models (GAM; Wood & Augustin 2002, R Development Core Team 2004). Predator presence/absence in trammel nets fished from late April through June 2001 and 2002 served as dependent variables. We used trammel net data because the surveys were conducted weekly during flounder settlement and collected large numbers of demersal flounder predators (see 'Results'). Cubic spline smooths of temperature, salinity, and the interaction were included in initial models. We performed backward selection of significant terms (χ^2, $p \leq 0.05$) using analysis of deviance of nested models (Venables & Ripley 1997). We replaced smoothed terms with linear terms if nonparametric degrees of freedom were close to 1 and deviance plots indicated that dependent and independent variables were linearly related.

Table 1. Surveys used for analyses of distributions and diets of piscine predators of juvenile winter flounder *Pseudopleuronectes americanus* in the Navesink River / Sandy Hook Bay estuarine system. Fixed stations were used in all years except 2001 when stations were randomly selected within each of 6 sectors for each survey (see Fig.1). River discharge data from http://nwis.waterdata.usgs.gov/nj/nwis/monthly/?site_no=01407500&agency_cd=USGS. Mean discharge during April and May from 1923 to 2003 = 2.24 m^3 s^{-1}

Year	Gear	Stations (N)	Depth (m, range)	Swimming River discharge April–May (m^3 s^{-1})	Duration (mo/d)	Frequency	Nets set (N)
1998	Gillnet	14	2.2 (1.5–3.0)	4.98	5/8–11/6	Fortnightly	182
1999	Gillnet	14	2.2 (1.5–3.0)	1.28	5/12–11/10	Fortnightly	182
2001[a]	Trammel net	18	3.2 (0.3–8.2)	1.46	4/19–10/17	Weekly to 6/18 then fortnightly	330
2002[a,b]	Trammel net	12	4.0 (0.8–8.2)	0.26	4/22–6/21	Weekly	108

[a]1 m beam trawl collections of Age-0 winter flounder and alternative prey were also made following the recovery of each net at each station
[b]Weekly tethering experiments were performed with surveys in 2002

Table 2. Fish collected in gillnet (1998 and 1999) and trammel net (2001 and 2002) surveys and frequency of juvenile winter flounder *Pseudopleuronectes americanus* in their diets (Flounder %). Gillnet collections were dominated by pelagic bluefish and weakfish as well as striped bass that consumed flounder infrequently. Demersal striped searobin and summer flounder predators were abundant in trammel nets and frequently consumed Age-0 winter flounder. N stom. = number of stomachs examined

Scientific name	Common name	N	1998 Flounder (%) (N stom.)	N	1999 Flounder (%) (N stom.)	N	2001 Flounder (%) (N stom.)	N	2002 Flounder (%) (N stom.)
Prionotus evolans	Striped searobin	83	33.3 (75)	46	6.9 (29)	975	15.9 (482)	284	23.4 (248)
Paralichthys dentatus	Summer flounder	14	11 (9)	13	12.5 (8)	284	16.8 (173)	24	41.2 (17)
Morone saxatilis	Striped bass	68	3.8 (52)	26	4.8 (21)	2	0 (1)	0	0
Cynoscion regalis	Weakfish	136	1.0 (96)	245	0 (121)	8	33.3 (3)	1	0 (1)
Pomatomus saltatrix	Bluefish	699	0.6 (308)	1027	1.0 (395)	55	0 (25)	10	0 (2)
Scophthalmus aquosus	Windowpane flounder	0	0	3	0 (3)	83	0 (39)	4	0
Raja spp.	Skates	0	0	0	0	20	0 (18)	7	0 (7)
Pseudopleuronectes americanus	Winter flounder	0	0	0	0	27	0 (27)	0	0
Menticirrhus saxatilits	Northern kingfish	20	0 (12)	0	0	0	0	0	0
Stonglyura marina	Atlantic needlefish	2	0 (2)	16	0 (7)	0	0	0	0
Synodus foetens	Inshore lizardfish	4	0 (4)	1	0 (1)	0	0	0	0
Tautoga onitis	Tautog	1	0 (1)	1	0 (1)	5	0 (4)	1	0
Morone americana	White perch	2	0 (2)	1	0 (1)	1	0 (1)	0	0
Mustelus canis	Smooth dogfish	0	0 (2)	0	0	5	0 (5)	2	0
Centropristis striata	Black sea bass	0	0	0	0	1	0 (1)	0	0
Astroscopus guttatus	Northern stargazer	1	0 (1)	0	0	0	0	0	0
Total		1030	5.6 (562)	1379	1.4 (587)	1466	14 (779)	333	23 (277)

Tethering experiments. To measure variation in predation risk during flounder settlement we performed weekly tethering experiments from May through mid-June, 2002 using methods described in detail in Manderson et al. (2004). We selected 12 stations in sectors of the estuary (A, B, E, F) that serve as flounder settlement areas (Fig. 1, Table 1; Manderson et al. 2003). To minimize tangling artifacts we chose sites where woody and stone debris and attached vegetation were absent.

Winter flounder trawled in the NSBES were held in flow-through tanks supplied with seawater from Sandy Hook Bay <7 d before they were tethered. The tanks had 2 cm of fine sand substratum (grain diam. = 0.14 mm) and the fish were fed *Artemia* sp. nauplii and chopped clam ad libitum.

We tethered flounder 20 to 50 mm SL in the laboratory with monofilament (2.2 kg test, 75 cm long) using methods described in Manderson et al. (2004). Fish <20 mm SL were too small to tether, while those <60 mm are vulnerable to demersal fish predators in laboratory experiments (Manderson et al. 1999, 2000). The fish were tied rather than sewn to tethers to minimize tissue damage that can artificially attract predators (Curran & Able 1998). Tethered fish recovered in the laboratory for ~18 h before they were transported to the field in a cooler filled with aerated seawater.

We performed tethering on 2 consecutive days each week from May 8 through June 18 (6 stations d^{-1}). Eight tethered fish were attached to snap swivels attached at 3 m intervals to 3 mm diam. chain that was staked to the substratum at each station by a diver. We set tethers <4 h after sunrise. After 4 h we retrieved tethers and counted remaining fish. To avoid depleting predator fields, the trammel net surveys described above were performed 24 h after tethering.

We measured bottom temperatures, salinities, and depths at the stations during tether deployment and recovery. Divers collected bottom water that was measured for turbidity with a nephalometer (Hatch 2100p), and sediment samples (2.5 cm diam., n = 3) that were analyzed for grain size using sieve fractionation (Folk 1980). Divers also quantified bottom cover of habitat structures (shell, vegetation, polychaete and amphipod tubes) using replicate (n = 3) counts of 0.5 m quadrats with 25, 10 cm grid cells.

We applied analysis of deviance to nested logistic linear models to partition and test the significance (χ^2) of deviance in predation risk (~presence/absence of tethered fish) related to time, space at the 3 scales (region [~10 km], sector within region [~5 km], station within sector within region [~1 km]; see Fig. 1), and space × time interactions (Venables & Ripley 1997). Observations were weighted with the soak times of tethers which varied by ± 35 min.

To quantify the relationship between predation risk and habitat characteristics we constructed a logistic GAM with the backward selection procedure used to model predator responses to temperature and salinity (see above). Independent variables considered were salinity, temperature, sediment grain size, percent cover of habitat structures, turbidity, depth, and abundance (CPUE) of Age-0 flounder and dominant predators. We also considered 'alternative prey' calculated as the combined abundance in trawls of *Crangon septemspinosa* and *Palaemonetes* spp. which occurred at high frequencies (16 to 80%) in predators' diets.

RESULTS

Physical characteristics

Water temperatures (range = 6.8 to 28.6°C) were lowest in Sandy Hook Bay in spring (Days 100 to 153) and highest in the Navesink River in July and August (Days 183 to 245; Fig. 2). In spring and summer (Days 100 to 245) the river was typically 1 to 2°C warmer than the bay. We recorded unseasonably high temperatures in July 1999 (Days 183 to 214; 28.6°C) and late April and early May 2002 (Days 120 to 130; 18°C) when the river was ~5°C warmer than the bay. Winter 2002 was the warmest and driest in 107 yr in the North Eastern US (see www.nrcc.cornell.edu/climate/Summary_2002-Winter.html) and temperatures near the tip of Sandy Hook were 4 to 5°C above 5 yr daily averages in mid-April (1998 to 2002).

Salinity (range 9 to 31‰) was generally low in spring (Days 100 to 153) and high in late summer and fall (Days 200 to 312; Fig. 2). Salinity decreased upstream in all surveys (Spearman, rho < −0.40, p < 0.001), but bay and river salinities were typically most different during spring and early summer (Days 100 to 183; $\bar{x}$ difference = 2.0‰, 1.0 to 5.2‰). However, we measured unseasonably high salinities >18‰ throughout the river in April through mid-May 2002 (Days 110 to 136) when freshwater discharge from the Swimming River was the lowest in April and 5th lowest in May in 81 yr (Table 1; see http://nwis.waterdata.usgs.gov/nj/nwis/monthly/?site_no = 01407500&agency_cd = USGS).

General patterns of predator occurrence and winter flounder consumption

Gillnet collections (1998-9) were dominated by the pelagic fish, bluefish *Pomatomus saltatrix* (frequency of occurrence [FO] = 46.7%; median fork length [medFL] = 190 mm, 83 to 760 mm) and weakfish *Cynoscion regalis*; (FO = 23%; median total length
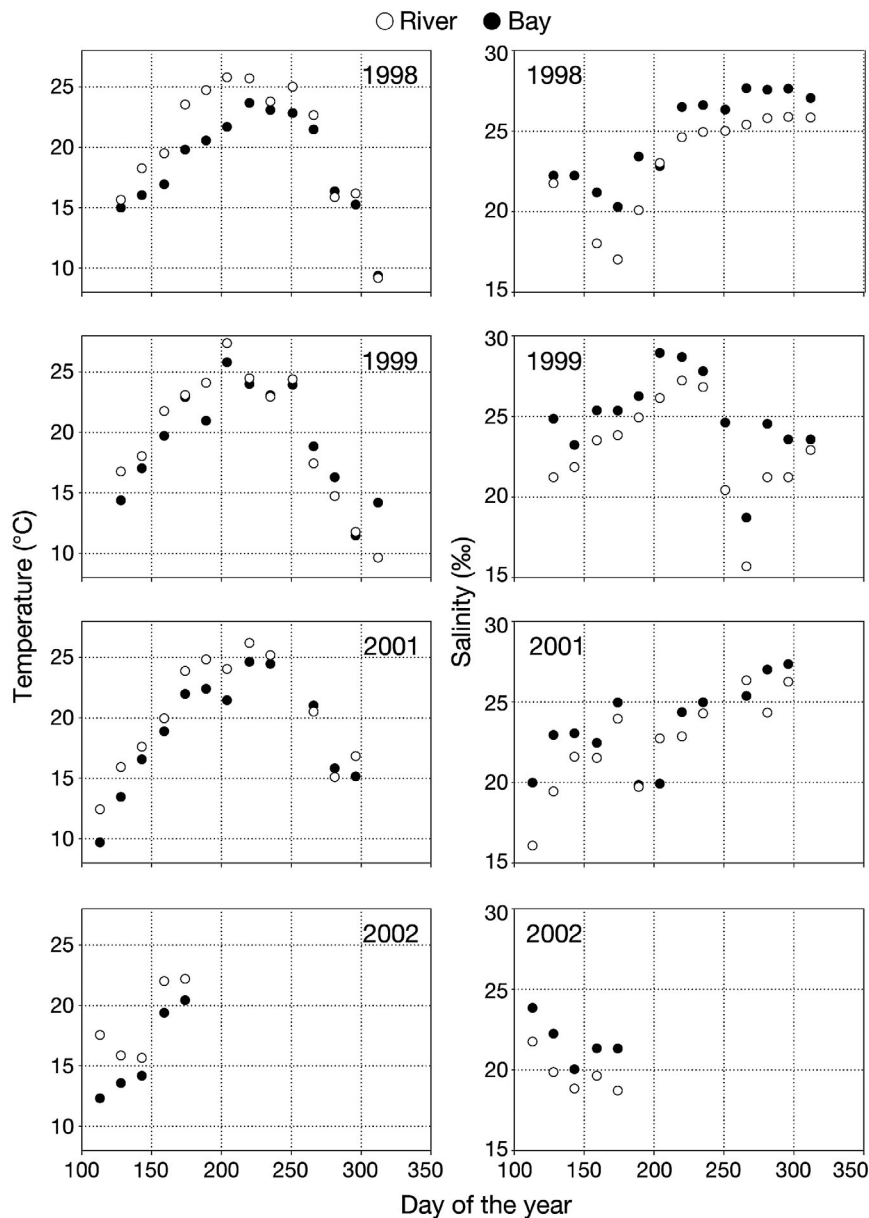
Fig. 2. Seasonal changes in mean temperatures and salinities measured in river and bay regions during gillnet (1998 and 1999) and trammel net (2001 and 2002) surveys

[medTL] = 235 mm, 95 to 654 mm; Table 2). Striped bass *Morone saxatilis* (FO = 11.5%; medFL = 502 mm, 114 to 448 mm), striped searobin *Prionotus evolans* (FO = 9.5%; medTL = 226 mm, 32 to 430 mm), and summer flounder *Paralichthys dentatus* (FO = 6.2%; medTL = 357 mm, 280 to 530 mm) were also collected. In contrast with gillnets, trammel nets (2001 and 2002) collected large numbers of the demersal fish, striped searobin (FO = 30.2%; medTL = 310 mm, 146 to 437 mm) and summer flounder (FO = 27.8%; medTL = 342 mm, 67 to 652 mm). Bluefish (FO = 5.6%; medFL = 520 mm, 170 to 835 mm), weakfish (FO = 1.9%) and

striped bass (FO = 0.5%) were relatively rare in trammel nets.

Striped searobin, summer flounder, striped bass, weakfish, and bluefish consumed Age-0 winter flounder (12 to 70 mm SL; Table 2). Winter flounder were frequent in striped searobin and summer flounder diets, particularly during the 2002 survey which ended in late June, shortly after flounder settlement. Winter flounder were rare in striped bass, bluefish, and weakfish stomachs.

Predator distributions and typical patterns of predator–prey habitat overlap

Distributions of flounder predators varied seasonally and upstream along the axis of the estuary (Fig. 3). Distance upstream, temperature, and day were included by backward selection in the DA of 1998 and 1999 gillnet data which was significantly different (p = 0.001) from randomized data in the Monte-Carlo test. The first canonical variate (CAN 1; 52% of total dispersion, TD) represented upstream estuarine gradients. Seasonal temperature variations defined the second variate (CAN 2; 40% TD). Striped bass (CPUE: $\bar{x}$ = 0.14 h^{-1}, max. = 7.5 h^{-1}) and searobins (CPUE: $\bar{x}$ = 0.19 h^{-1}, max. = 13.5 h^{-1}) were abundant in late spring (May to early June) when temperatures were cool and thus had high CAN 2 scores. Striped bass were most abundant upstream in the river and had a low CAN 1 score. Searobins were primarily collected downstream in the bay and thus had the highest CAN 1 score. Only a few searobins occurred in the river from late July through September 1999. Summer flounder (CPUE: $\bar{x}$ = 0.04 h^{-1}, max. = 1.5 h^{-1}) were present from late June through August in the inner bay and lower river. As a result, the predator had a low CAN 2 score and relatively high CAN 1 score. Bluefish (CPUE: $\bar{x}$ = 2.55 h^{-1}, max = 36.5 h^{-1}) and weakfish (CPUE: $\bar{x}$ = 0.57 h^{-1}, max = 20.5 h^{-1}) were common from July through early September in the river and had low scores on both variates.

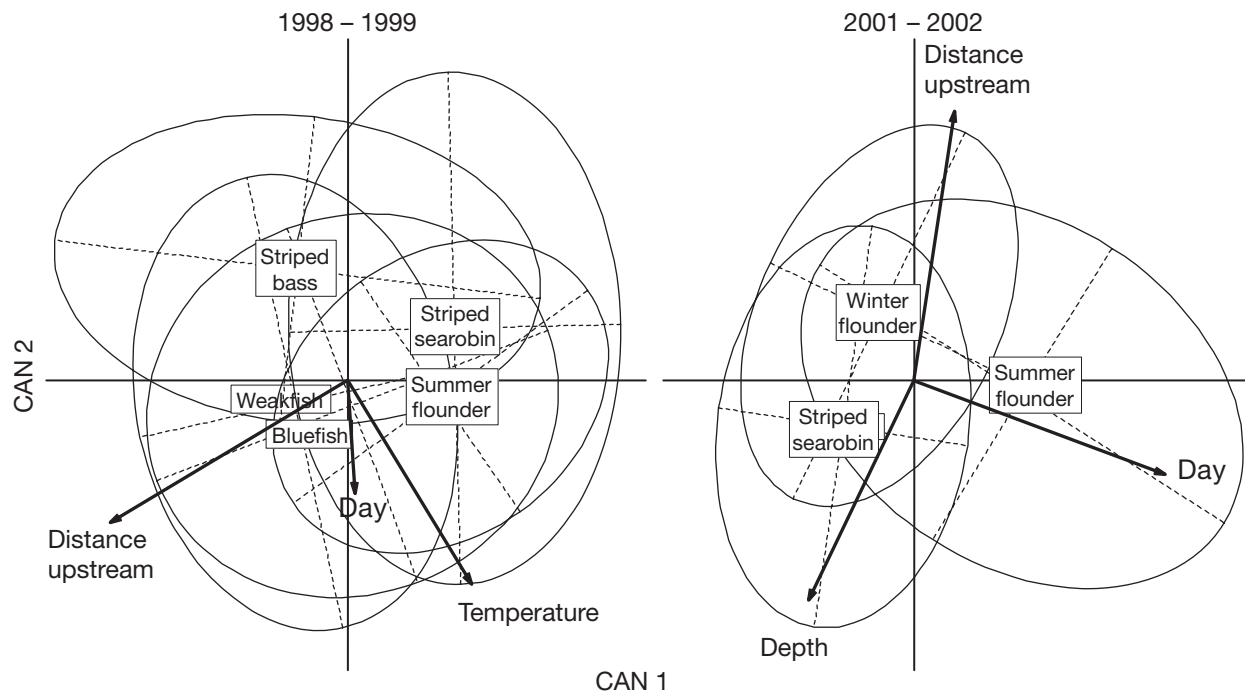The DA of 2001 and 2002 trammel net and beam trawl data indicated that Age-0 winter flounder were

Fig. 3. Species centroids with inertia ellipses and cosines of canonical scores for independent variables (arrows) significant in stepwise discriminant analysis of winter flounder predators collected in gillnets in 1998 and 1999 and in trammel nets in 2001 and 2002, and winter flounder prey collected in beam trawls in 2001 and 2002. Searobin and summer flounder were generally more abundant in the lower estuary; thus, the upper estuary probably served as a spatial predator refuge for early juvenile winter flounder during most years. CAN = canonical axis

most likely to co-occur with searobins in deep bay habitats during the settlement period and with summer flounder later in the season in shallow habitats in the middle of the estuary (Fig. 3). Bluefish (CPUE: $\bar{x}$ = 0.1 h^{-1}, max. = 9 h^{-1}; FO = 5.6%) and weakfish (CPUE: $\bar{x}$ = 0.01 h^{-1}, max. = 1 h^{-1}; FO = 1.9%) were rare in trammel nets and analyses of 2001 and 2002 data were similar. As a result, we combined the 2 years to provide a summary of habitat overlap between searobin, summer flounder, and Age-0 winter flounder. Backward selection included day, distance upstream, and depth in the DA which was significantly different (p = 0.001) from randomized data in the Monte-Carlo test. The first canonical variate (CAN 1; 79% TD) was strongly related to day while the second variate (CAN 2; 21% TD) reflected upstream variations in habitat characteristics including depth. Searobins (CPUE: $\bar{x}$ = 1.8 h^{-1}, max. = 62.5 h^{-1}) were collected during the first surveys in early May 2001 and late April 2002. The species reached peak abundance in mid-May during both years and had the lowest CAN 1 score. The predator was most abundant at deep sites in Sandy Hook Bay and had the lowest CAN 2 score. Searobins rarely occurred in the river in May and June 2001. In May 2002, however the predator was common in the river. Searobins appeared to occur in large groups as 21% of trammel nets containing the predator collected 10 or

more individuals and 12% collected 20 or more. Summer flounder (CPUE: $\bar{x}$ = 0.4 h^{-1}, max. = 10 h^{-1}) were abundant later in the season (mid-June to mid-July) further upstream than searobins and had the highest CAN 1 and a low CAN 2 score. The predator was common in shallow habitats in the middle of the estuary. Summer flounder were not collected in large groups as only 15% of nets captured 5 or more individuals. Age-0 winter flounder (n = 308, median SL = 20 mm, 6 to 143; $\bar{x}$ CPUE = 0.24 10 m^{-2}, max. = 8 10 m^{-2}) reached peak abundance in early May and thus, like searobins, had a low CAN 1 score. Newly settled fish < 20 mm SL were present in May and June 2001, and from late April through mid-June 2002. Winter flounder were most abundant in the river ($\bar{x}$ CPUE ± SE; 2001: river 0.30 ± 0.07, bay 0.06 ± 0.01; 2002: river 0.61 ± 0.11, bay 0.20 ± 0.01) and had the lowest CAN 2 score.

Distributions of dominant predators in relation to salinity and temperature

Striped searobins were most likely to occur (probability > 0.5) at salinities > 20‰ and temperatures of 12 to 22°C, while summer flounder were common at temperatures > 24°C in the GAMs of trammel net collections made during flounder settlement (Fig 4; Table 3).
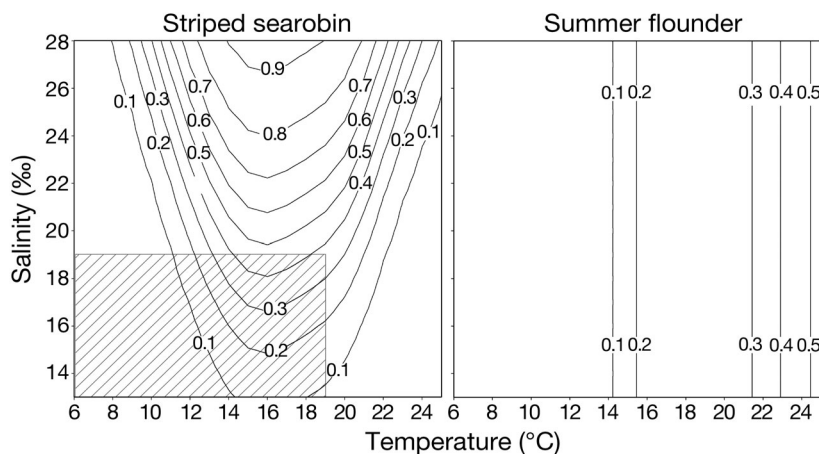
Fig. 4. *Prionotus evolans* and *Paralichthys dentatus*. Probabilities of occurrence for dominant demersal predators in relation to temperature and salinity during winter flounder settlement (late April to June) based on logistic generalized additive models (GAM) of trammel net collections in 2001 and 2002. Searobins were more likely to occur at cool temperatures and high salinities typically measured in the Sandy Hook Bay, while summer flounder were most likely to occur at warm temperatures (see Table 4). Hatched area on searobin plot indicates temperature and salinity combinations at which the survivorship of tethered winter flounder *Pseudopleuronectes americanus* was relatively high, based on the GAM of tethering data (see Table 4b, Fig. 8)

Table 3. *Prionotus evolans* and *Paralichthys dentatus*. Logistic generalized additive models of relationships between the occurrence of demersal predators and temperature and salinity during winter flounder *Pseudopleuronectes americanus* settlement from late April through June 2001 and 2002. Striped searobin were most likely to occur at high salinities and cool temperatures while summer flounder were most likely to occur at relatively high temperatures (see Fig. 4). Temperature term included in final model using a cubic spline smoother; otherwise the term was included as a linear term. p < 0.001 in all cases

Species Term	df	Nonparametric χ^2	t-ratio	Coefficient
Striped searobin				
Intercept	1		–4.92	–6.98
Salinity	1		4.64	0.30
Temperature	3.87	38.1		
% total deviance explained	20.3			
Summer flounder				
Intercept	1		–5.07	–1.95
Temperature	3.76	19.7		
% total deviance explained	14.2			

Temperature × salinity interactions were not significant (p > 0.05) for either species, and summer flounder distributions were not related to salinity.

Seasonal, spatial and size-dependent patterns of winter flounder consumption

Winter flounder prey body sizes reflected seasonal patterns of predator occurrence and consumption (Fig. 5). Searobins fed on large numbers of newly settled winter flounder (median SL = 17 mm, 7 to 70 mm, n = 369, max. = 13 prey stomach^{-1}) in spring and early summer. This pattern was strong in early May 2001 and 2002 when many prey <20 mm SL were eaten by searobins. During these years, searobin consumption of flounder peaked before the peak abundance of winter flounder in trawls. However, sizes of flounder in searobin diets were smaller than fish trawled indicating trawl bias toward larger sizes (2 sample Kolmogorov-Smirnov test [*D*] = 0.28, p << 0.001). Searobins occasionally consumed flounder >20 mm SL through mid-August. Striped bass consumed relatively large flounder (25 to 38 mm SL, n = 3) infrequently in May.

Summer flounder consumed larger winter flounder (*D* = 0.57, p << 0.001; median SL = 32 mm, 15 to 60 mm, n = 69, max = 9 prey stomach^{-1}) later in the season than searobins (Fig. 5). Winter flounder first appeared in summer flounder diets in late May and most prey were >20 mm SL. Summer flounder continued to eat the prey through August. Bluefish and weakfish ate relatively large flounder (median SL mm = 48, 25 to 56; n = 19) infrequently in July and August.

Spatial patterns of winter flounder consumption generally reflected predator distributions (Fig. 6). In 1998 and 1999 and 2001 most flounder were eaten by searobins downstream in the bay. In May 2002, however, many prey were eaten by searobins collected in the middle and upper river. Summer flounder ate winter flounder in the inner bay and lower river. Striped bass, bluefish, and weakfish fed infrequently on the prey throughout the estuary.

Tethering assessment of winter flounder predation risk

The survival of tethered flounder (total n = 666) averaged 57% and ranged from 25 to 87% in 7 experiments performed during the 2002 winter flounder settlement period. The median size of fish tethered was 36 mm SL and similar in most experiments. However, fish used in the 5th and 7th experiments were slightly larger (median SL mm = 39 and 38; ANOVA, df = 6.679, *F* = 19.8, p < 0.001: Tukey pairwise test, p ≤ 0.007).
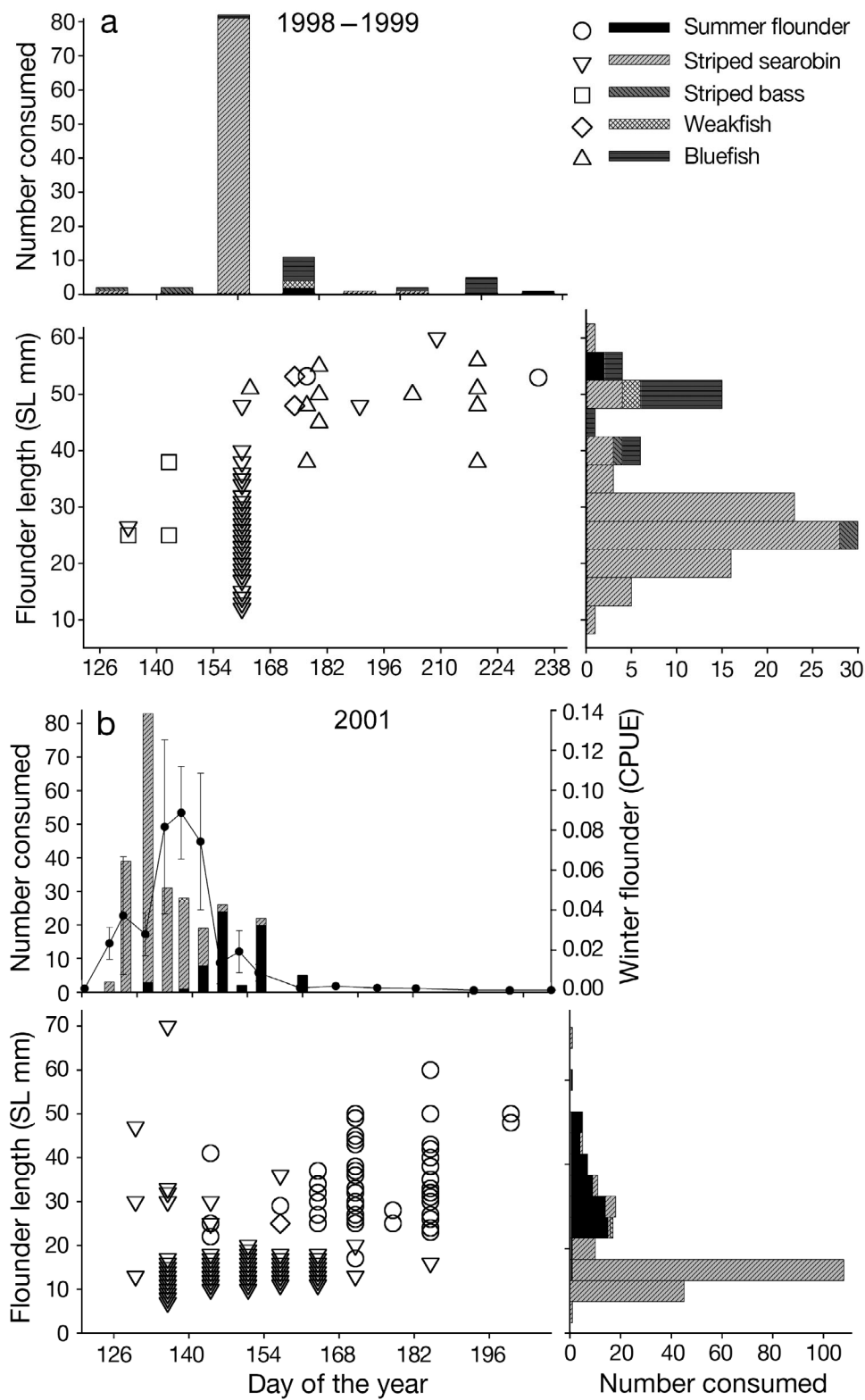
Fig. 5. (Above and overleaf) *Pseudopleuronectes americanus.* Seasonal and size-dependent patterns of winter flounder consumption by predators collected in (a) gillnets in 1998 and 1999, and in trammel nets in (b) 2001 and (c) 2002. Striped searobins consumed small recently settled flounder <20 mm SL during May and early June, while summer flounder consumed post-settlement winter flounder >20 mm SL in June and July. Striped bass, bluefish and weakfish ate post-settlement winter flounder >20 mm SL infrequently. Temporal patterns of Age-0 winter flounder abundance measured in beam trawls are overlaid on upper panels in (b) and (c)
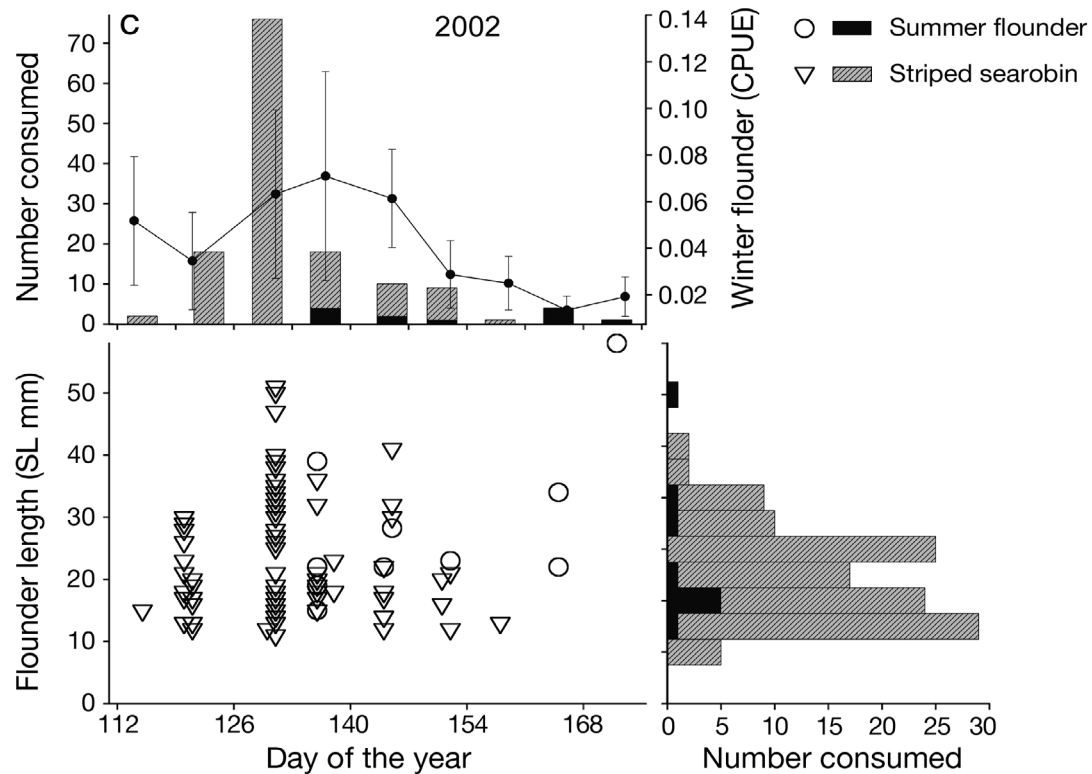
Fig. 5 (continued)

The survival of tethered fish was higher in the bay (p = 0.69 ± 0.07) than in the river (p = 0.44 ± 0.07; Table 4a, Fig. 7). Survivorship varied significantly among regions, and differences were nearly significant (p = 0.06) among sectors within regions. Survival was high in the western part of the bay (Sector B: p = 0.87 ± 0.08) and low in the upper river (Sector F: p = 0.41 ± 0.11) where searobins with many flounder in their diets were collected (Fig. 6).

Survivorship was high at times and sites with moderate shell cover (10 to 30%), salinities <19‰, temperatures <20°C, and low sector-wide predator densities (Table 4b, Fig. 8). The cover of other habitat structures, turbidity, sediment grain size, and alternative prey densities did not affect survival (p > 0.05). Survival increased significantly with winter flounder abundance in trawls (χ^2 = 13.55, p = 0.003). However, we removed this variable from the final model because high flounder densities may have been an effect rather than a cause of high survivorship. Few tethered fish survived at Station 11 in

Table 4. *Pseudopleuronectes americanus*. (a) Analysis of deviance of nested general linear logistic models showing that tethered winter flounder survivorship varied significantly (p < 0.05) between regions and that variation was nearly significant between sectors within regions (see Fig. 7). (b) Logistic generalized additive model showing that patterns of tethered winter flounder survivorship were related to variations in shell cover, salinity, temperature and the abundance of searobin and summer flounder predators at the sector scale (see Fig. 8). All terms used cubic spline smoothers. Npar chi: non-parametric Chi-square

| (a) Term	df	Deviance	p (chi)	
Null model (includes intercept)	665	116.57		
Experiment	1	0.078	0.779	
Region	1	5.548	0.019	
Sector(Region)	2	5.736	0.057	
Station(Sector[Region])	4	1.549	0.818	
Experiment × Region	1	0.070	0.791	
Experiment × Sector(Region)	2	0.424	0.809	
Experiment × Station(Sector[Region])	4	0.787	0.940	
Residual	650	102.38		
(b) Term	df	Npar chi	p	Deviance
Shell	2.9	39.24	<<0.001	41.25
Salinity	3.0	16.13	0.001	17.10
Temperature	3.0	11.99	0.007	21.52
Predator abundance (sector)	2.8	9.96	0.016	20.55
Independent effects				100.42
Intercorrelated effects				38.13
Total				138.55
Residual	649.3			772.52
Null	655			911.07
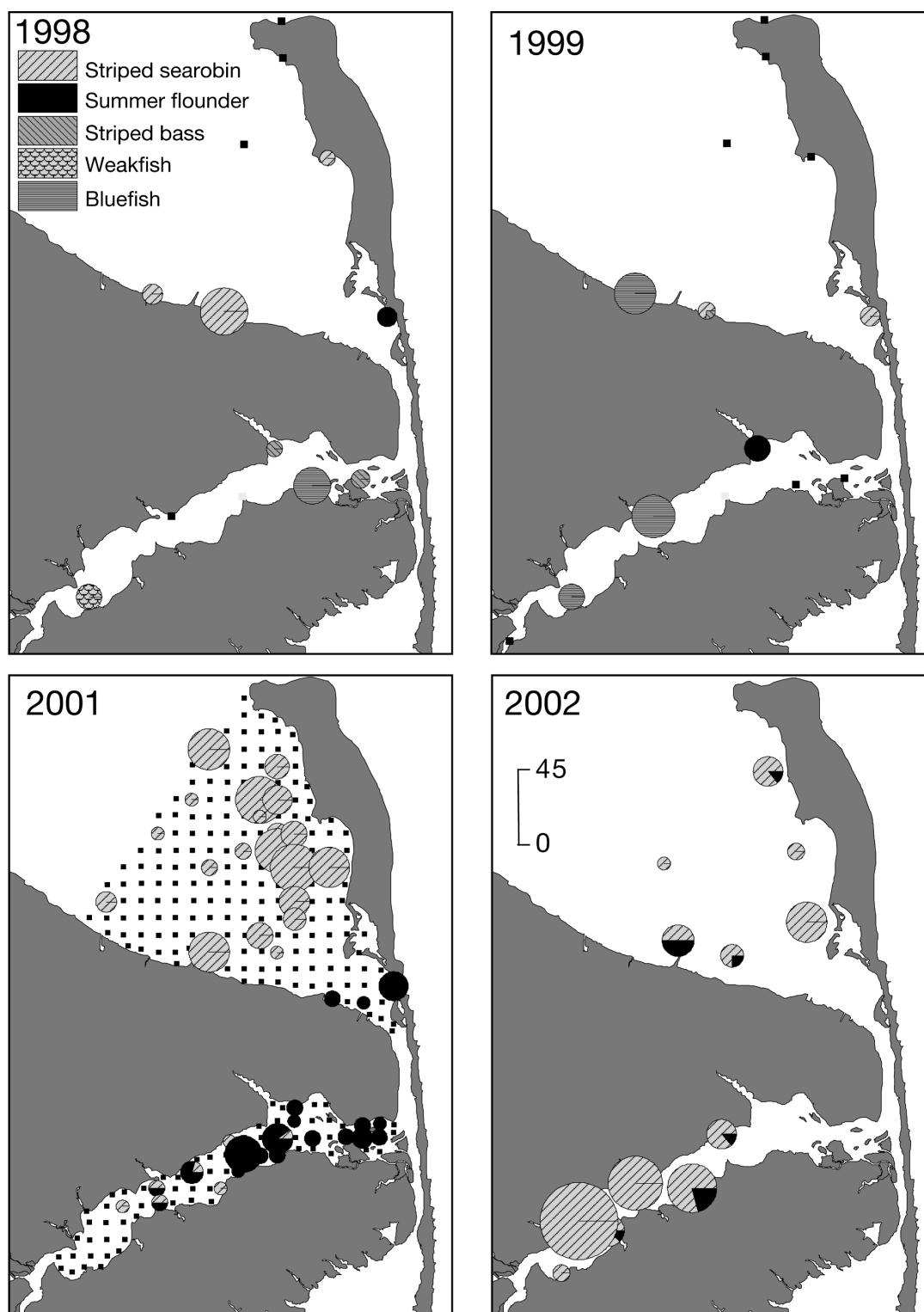
Fig. 6. *Pseudopleuronectes americanus*. Spatial patterns in numbers of juvenile winter flounder consumed by fish predators. Striped searobin generally consumed large numbers of recently settled winter flounder <20 mm SL in Sandy Hook Bay, except in 2002 when many prey were eaten in the Navesink River. Summer flounder that fed on post-settlement winter flounder >20 mm SL were primarily collected in the middle of the estuary, while weakfish, bluefish and striped bass ate the prey infrequently throughout the system. Symbol diameters represent the number of winter flounder and are scaled in the lower right panel. (■) Stations where predators with flounder in diets were not collected
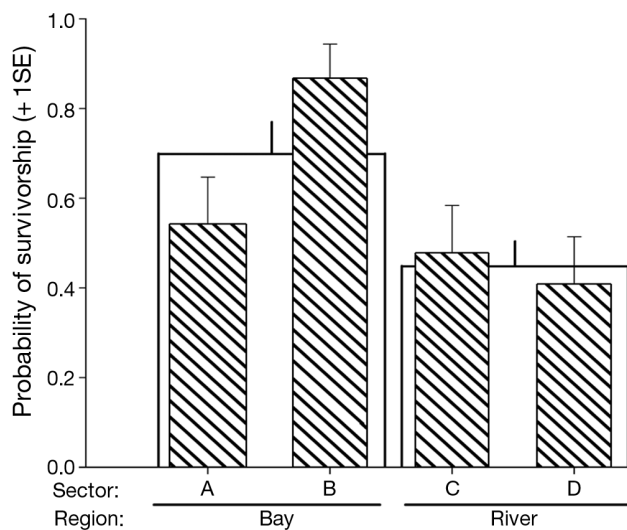
Fig. 7. *Pseudopleuronectes americanus*. Survivorship of teth-ered winter flounder. This was significantly higher (p = 0.019) in the bay than the river and differences were nearly signifi-cant among sectors within the 2 regions in 2002 (see Table 4a). Consistently low survivorship was measured in the west-ern part of the Navesink River where searobins with large numbers of recently settled winter flounder in diets were also collected in trammel nets (see Fig. 6)
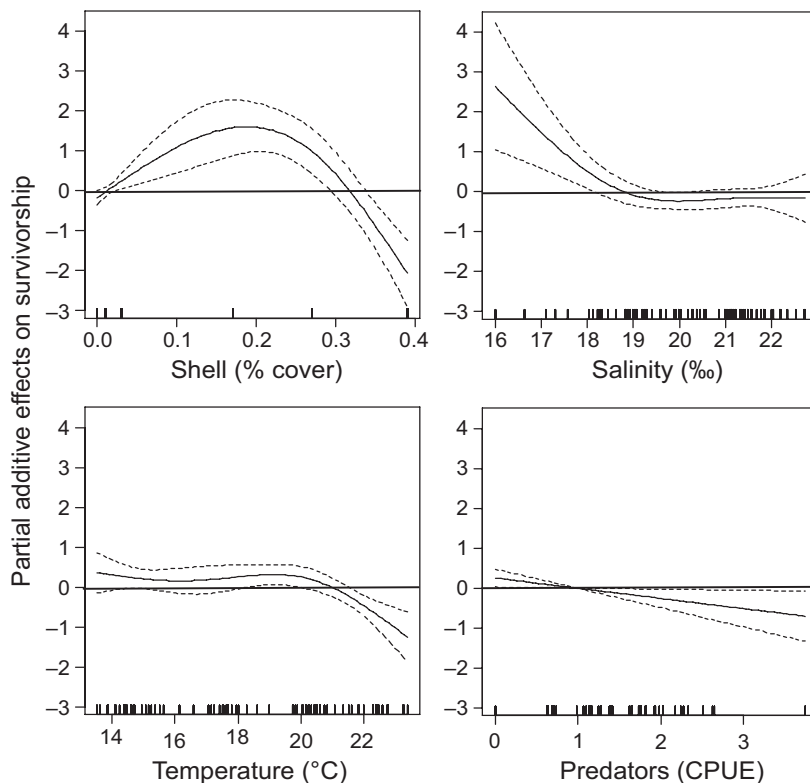

Fig. 8. *Pseudopleuronectes americanus*. Deviance plots derived from general-ized additive model (GAM) indicating that the survivorship of tethered winter flounder was higher in habitats with moderate shell cover (%), salinities <19‰, temperatures <21°C and in sectors where the abundance of predators (striped searobin and summer flounder) was relatively low (see Table 4b). 'Tick' marks on *x*-axis show the distribution of values for each independent variable

the upper river where shell cover was high (>30%), but searobins were abundant and consumed many floun-der (Figs. 1 & 6).

DISCUSSION

Populations of demersal fish, including flatfish, can be strongly regulated by mortality during the early post-settlement period when it is estimated that 30 to 85% of settlers are consumed by predators (van der Veer et al. 2000a, Almany & Webster 2006). Most stud-ies of early juvenile flatfish mortality have emphasized the role of crustacean predators (van der Veer et al. 2000a and references therein). Our study indicates that demersal fish, specifically striped searobin and summer flounder, may be important early juvenile winter floun-der predators in an estuarine system where crustacean predation is low (Manderson et al. 2003, Taylor 2005).

Striped searobins fed upon large numbers of rec-ently settled winter flounder <20 mm SL from April through June, while summer flounder primarily con-sumed post-settlement stage fish >20 mm in June and July. These seasonal and size depen-dent consumption patterns reflected differences in the timing of estuarine ingress of the 2 predators with respect to the timing of flounder settlement. Winter flounder larvae settle to benthic habitats in Mid-Atlantic Bight (MAB) estuaries including the NSBES from late April through June (Sogard et al. 2001, Manderson et al. 2003). Striped searobin migrate in the spring to MAB estuaries where they spawn beginning in May (Wilk et al. 1990, McBride 2002). Searobins occurred in our sur-veys in April and reached peak abun-dance in May when they fed upon large numbers of newly settled winter flounder. In contrast, summer flounder were abundant in the NSBES in late June and July when they fed on post-settlement staged prey. Summer floun-der are generally most abundant in MAB estuaries in July and August when temperatures are warm (Packer et al. 1999 and references therein).

Although temporal differences in predator-prey habitat overlap primarily determined sizes of winter flounder consumed by striped searobins and summer flounder, sensory mechanisms used for prey detection may also have influenced size selection. Summer

flounder rely on vision to detect prey, and winter floun-
der vulnerability to the predator increases linearly with
increasing prey body size from 15 to 80 mm SL (Olla et
al. 1972, Manderson et al. 2000). Searobins use pec-
toral finrays equipped with tactile and chemosensory
receptors to search for and flush prey from sediments,
and feed on smaller flounder (Silver & Finger 1984,
Manderson et al. 1999). Encounter rates of individual
searobins with small flounder (30 to 40 mm SL) are also
elevated when groups of predators use finrays to
search for and flush prey from laboratory substrata
(J. P. Manderson unpubl. data). Searobins appeared to
aggregate in the field in May, when individual tram-
mel nets frequently captured large numbers of
searobins. Groups of foraging searobins could cause
exceptionally high winter flounder mortality in habi-
tats where the predator and prey co-occur.

Pelagic fish were abundant in the NSBES particu-
larly in gillnet surveys, but we caught only a few
pelagic predators with flounder >25 mm SL in their
diets. Flounder were probably rare in pelagic fish diets
as a result of seasonal and vertical differences in habi-
tat use. Bluefish and weakfish move into mid-Atlantic
estuaries in large numbers in late June and July fol-
lowing flounder settlement and thus most newly set-
tled winter flounder probably have a temporal refuge
from the 2 predators (Able et al. 2003, Jung & Houde
2003, Sharf et al. 2004, this study). Weakfish and blue-
fish also primarily feed upon pelagic prey including
Brevoortia tyrannus, *Menidia menida*, *Anchoa
mitchilli* and mysids (Hartman & Brandt 1995, Lank-
ford & Targett 1997, Juanes et al. 2001, Buckel & McK-
own 2002, Nemerson & Able 2004) which are more
abundant than juvenile flounder in the NSBES (Sharf
et al. 2004, J. P. Manderson unpubl. data). Encounters
of the predators with flounder are probably relatively
rare irrespective of differences in vertical habitat use
of pelagic predators, preferred pelagic prey and dem-
ersal flatfish prey. Although striped bass feed on dem-
ersal estuarine prey during spring and early summer
(Buckel & McKown 2002, Jordan et al. 2003), we col-
lected just a few striped bass that had eaten flounder ≥
25 mm SL in May when smaller newly settled winter
flounder are much abundant (Stoner et al. 2001, Man-
derson et al. 2003, this study). Newly settled winter
flounder may be relatively invulnerable to striped bass
which, as visual predators, select larger prey (Scharf et
al. 2003).

Most predators collected in gill and trammel nets
were >80 mm TL and >230 mm TL, respectively, and
smaller fish could also be important winter flounder
predators. We did not capture juvenile spotted hake
Urophycis regia (47 to 209 mm) that occur in spring
trawl surveys of Sandy Hook Bay and consume floun-
der 12 to 20 mm SL (J. P. Manderson unpubl. data).

Grubby sculpin *Myoxocephalus aenaeus*, oyster toad-
fish *Opsanus tau*, and windowpane flounder *Scoph-
thalmus aquosus* are reported to feed on winter floun-
der, but we have not found the prey in these species
diets in the NSBES (Pereira et al. 1999, this study,
J. P. Manderson unpubl. data).

Our analyses of predator distributions and diets indi-
cate that searobin predation pressure is usually high in
winter flounder settlement habitats located down-
stream in Sandy Hook Bay, while summer flounder are
probably an important source of mortality for post-
settlement winter flounder in shallower habitats in the
middle of the estuary. Searobins were usually most
abundant in the bay, where they consumed the great-
est numbers of newly settled winter flounder during
most years. The predator was associated with rela-
tively high salinities and cool temperatures normally
found in deeper downstream areas in May and June
which is consistent with observations in other estuaries
(Pearcy & Richards 1962, Martino & Able 2003). Sum-
mer flounder are abundant in shallow sandy coastal
habitats (see Packer et al. 1999 for review) and were
relatively common in shallow areas in the inner part of
Sandy Hook Bay and lower reach of the Navesink
where they ate Age-0 winter flounder in June and July.
These observations suggest that the upper estuary
serves as a spatial refuge for settling flounder during
most years. This conclusion is consistent with an earlier
finding that mortality (and/or emigration) caused
densities of settling flounder to decline at much lower
rates in the Navesink River than in Sandy Hook Bay
during the first few weeks following larval settlement
(Manderson et al. 2003). Age-0 winter flounder are
generally most abundant in upstream estuarine re-
gions that, in some systems, have characteristics
promoting early larval settlement and rapid early juve-
nile growth (Pearcy 1962, Armstrong 1997, Meng &
Powell 1999, Meng et al. 2001, Manderson et al. 2002,
2003). Our study indicates that habitat suitability for
early juvenile winter flounder survivorship may also be
high in upstream areas with specific environmental
conditions.

The extent of an upstream predation refuge for win-
ter flounder settling in the NSBES appeared to be con-
trolled by the spatial structure of salinity, and to a lesser
extent temperature, gradients in the estuary. From
April through June, flounder predation risk and pro-
bability of searobin occurrence were both low at sites
and times when salinities were ≤20‰ in independent
GAMs of tethered fish survivorship and predator distri-
butions. During springs with average to high freshwa-
ter discharge from the Swimming River, bottom salini-
ties range from 14 to 16‰ in the middle and upper
Navesink River during slack after flood tide when max-
imum salinities are recorded (Fugate & Chant 2005,

their Fig. 7). These conditions probably exclude searobins from the middle and upper river (Fig. 9). Flounder predation risk was also relatively low at cool temperatures <20°C. While searobins preferred cool temperatures, summer flounder were more likely to occur at warmer temperatures. During most years bottom temperatures in the river rarely exceed 15°C during the beginning of flounder settlement in April and early May (Manderson et al. 2003, this study, J. P. Manderson unpubl. data). Thus, in years of sufficient discharge and average spring warming, gradients in salinity, and to a lesser extent temperature, probably exclude both predators from the upper reaches of the estuary. This hypothesis is consistent with predator distributions and diets measured in 1998, 1999, and 2001 (in this study), spring trawl surveys (J. P. Manderson unpubl. data), and an earlier study of settlement and early post-settlement processes affecting winter flounder distributions in the NSBES (Manderson et al. 2003). In 2002, however, a severe spring drought and warm temperatures resulted in historically low freshwater discharge into the Navesink where salinities exceeded 18‰ and temperatures exceeded 18°C from late April through mid-

May. During this year winter flounder predation risk was high in the upper estuary where demersal predators, particularly searobins, were abundant and consumed many newly settled flounder. Historically low discharge produced a weak salinity gradient in the estuary during the 2002 winter flounder settlement period which appeared to result in a contraction of the upstream predation refuge (Fig. 9). Similar changes in fish distributions in response to changes in salinity gradient structure and freshwater discharge are common in estuaries (Jung & Houde 2003, Hurst et al. 2004).

Predator and prey responses to dynamic temperature and salinity gradients in the estuary appeared to produce coarse scale gradients of predation risk and a region of low predation risk that may serve as a spatial refuge for newly settled winter flounder during most years. However within times and regions of predator-prey overlap fine scale structural habitat characteristics, such as depth and biogenic structure, including shell cover, that are nested within coarse scale gradients may modify encounter rates, predator attack success, and overall predation risk (Manderson et al. 2000, 2004, Stoner & Titgen 2003). This appears to have been
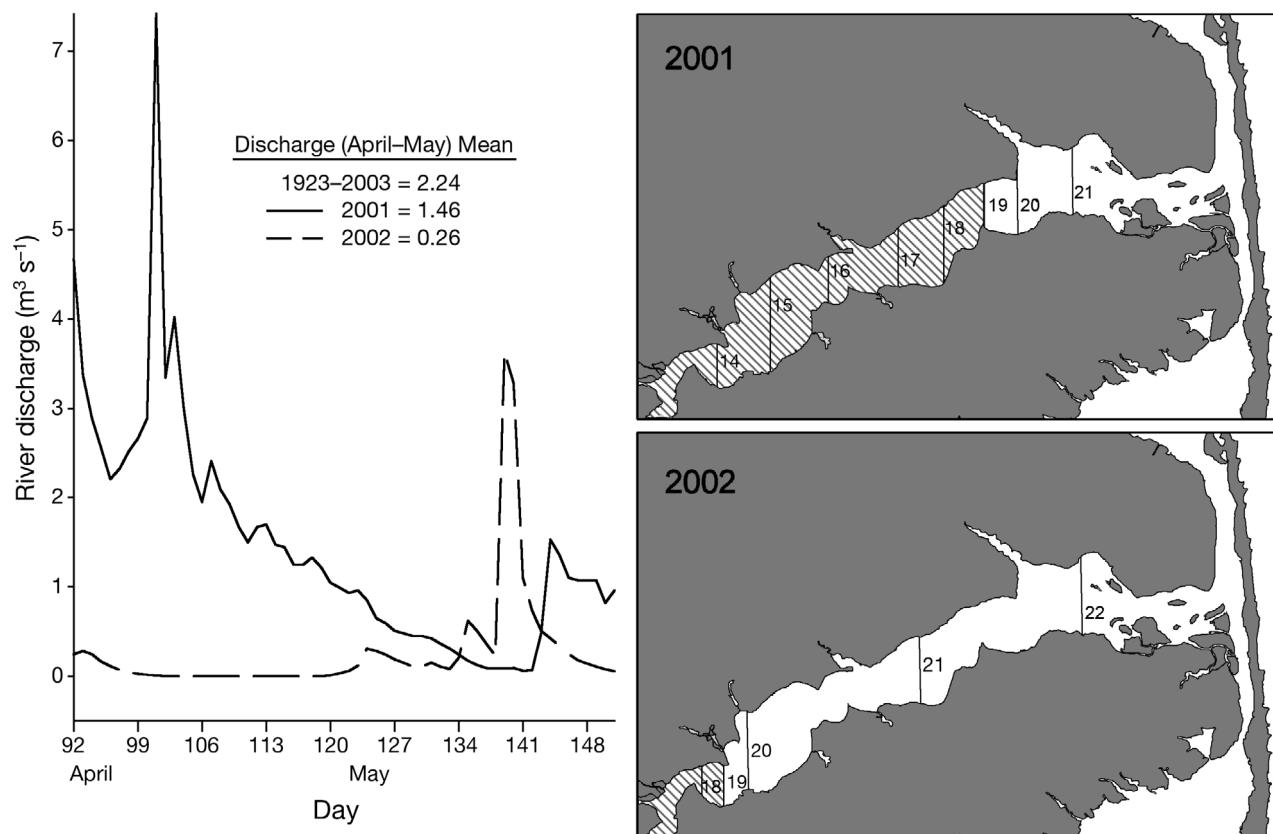

Fig. 9. *Pseudopleuronectes americanus*. Surface area of nursery habitat suitable for the survival of newly settled winter flounder (hatched area). This was probably much larger in 2001 than 2002 based on analysis of tethering experiments (Fig. 8), searobin occurrence (Fig. 4), Swimming River discharge (left panel) and the approximate spatial structure of the salinity gradient (numbered values) in the Navesink River (right panels)

the case in our tethering experiments, as shell cover accounted for a significant portion of the deviation in winter flounder predation risk.

There are several potential artifacts associated with the timing of sampling and tethering that could have confounded our results. Piscivorous fish feeding and prey mortality show diel variations and are generally higher during dawn and dusk than day and night (Linehan et al. 2001, Holbrook & Schmitt 2002, Clark et al. 2003). Summer flounder feed during the day and searobin predation on Age-0 winter flounder is higher during the day than at night in the laboratory (Olla et al. 1972, Manderson et al. 1999). It is possible that we would have observed different patterns in tethered fish mortality and predator consumption patterns if we had sampled at dusk. However, we believe our near dawn sampling occurred when predation rates on winter flounder are probably representative. There are also potential artifacts associated with tethering (addressed in detail in Manderson et al. 2004). However, unique to this study was our use of relatively large individuals to assess patterns of relative predation risk during flounder settlement when smaller fish are common. We were unable to successfully tether fish <20 mm SL and acknowledge that survivorship patterns of small newly settled individuals may be somewhat different from those observed. However we selectively tethered flounder that fell within the size range of prey highly vulnerable to the dominant predators species (Manderson et al. 1999, 2000).

CONCLUSIONS

In a previous study, we demonstrated that winter flounder settled earlier in depositional habitats upstream in the Navesink River than in downstream Sandy Hook Bay habitats as a result of the combined effects of spatial variation in spring warming, circulation and substrate characteristics (Manderson et al. 2003). Recently settled juveniles also grew rapidly upstream for a limited period following settlement in response to dynamic temperature and salinity gradients as well as fine scale variations in prey density and dissolved oxygen (Manderson et al. 2002). The typical spring phenology and spatial structures of important habitat gradients appear to promote early larval settlement, rapid early juvenile growth and high early juvenile survivorship in the upstream reach of the estuary during most years. However, the present study suggests that variability in spring climatology which ultimately controls the spatial structures of physico-chemical gradients may cause the volume of suitable winter flounder nursery habitat to contract or expand. Interannual variation in recruitment is associated with sim-

ilar changes in nursery habitat volumes for several species including white perch *Morone americana* (Kraus & Secor 2005). Changes in the volume of suitable nursery habitat defined by rate regulating and spatially dynamic habitat characteristics could produce interannual variations in the production of winter flounder recruits.

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