



Predator–prey relations between age-1 + summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes

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Received 7 December 1999; received in revised form 18 February 2000; accepted 10 March 2000

Abstract

Laboratory experiments and weekly trammel net surveys in the Navesink River, New Jersey (USA) were used to examine the predator–prey interaction between age-1 + summer flounder (*Paralichthys dentatus*) and age-0 winter flounder (*Pseudopleuronectes americanus*). Winter flounder (24–67 mm TL) were the dominant piscine prey of summer flounder ($n = 95$, 252–648 mm TL) collected in trammel nets. We observed a temporal shift in summer flounder diets from sand shrimp (*Crangon septemspinosa*) and winter flounder, dominant during June and early July, to blue crabs (*Callinectes sapidus*) and other fishes (primarily Atlantic silversides, *Menidia menidia* and Atlantic menhaden, *Brevortia tyrannus*) later in the summer. Variations in prey selection appeared to be related to changes in the spatial distribution of predators and spatio-temporal variation in prey availability. In laboratory experiments, summer flounder (271–345 mm total length, TL) preferred demersal winter flounder to a pelagic fish (Atlantic silversides) and a benthic invertebrate (sand shrimp) prey, and the vulnerability of winter flounder increased with increasing prey body size from 20 to 90 mm TL. Experiments testing habitat effects showed that mortality of winter flounder in three different size classes (20–29, 40–49, 60–69 mm TL) was not influenced by sediment grain sizes permitting differential burial of the prey. However, vegetation enhanced survival, with fish suffering lower mortality in eelgrass (*Zostera marina*, $15 \pm 0.04\%$) than in sea lettuce (*Ulva lactuca*, $38 \pm 0.04\%$) or bare sand ($70 \pm 0.07\%$) when the macrophytes were planted to produce similar leaf surface areas ($5000 \text{ cm}^2 \text{ m}^{-2}$). Prey vulnerability appeared to be related to the role of vision in the predator's attack strategy and prey activity levels. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Flatfish predator; Prey choice; Prey size selection; Burial; Sea grass; Sea lettuce

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1. Introduction

Estuaries function as nurseries for a variety of important resource species and are particularly vulnerable to impacts associated with human use and development. Consequently, there is a need for investigations of the functional significance of estuarine habitats that can provide information for the development of sound conservation practices (Langton et al., 1996; Able, 1999). A number of studies have examined the effects of estuarine habitat characteristics on the growth of juvenile western Atlantic flatfishes (Sogard, 1992; Guindon and Miller, 1995; Able et al., 1999; Phelan et al., 2000), but only a few have investigated habitat effects on predation (Witting, 1995; Witting and Able, 1995; Manderson et al., 1999). Predation is thought to be the primary cause of juvenile flatfish mortality (Pihl and van der Veer, 1992; Bailey, 1994; Gibson, 1994) and prey vulnerability is a function of probabilities of encounter with and capabilities of specific predators, as well as prey behavior. Furthermore, habitat structure can modify predator and prey behaviors and thus interaction strengths (Savino and Stein, 1982, 1989; Mattila, 1992; Lindholm et al., 1999).

Summer flounder (*Paralichthys dentatus*, Linnaeus) range from Nova Scotia to Florida but are most abundant in the Mid-Atlantic Bight (MAB) from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. In the MAB, age-1 + fish migrate from the outer continental shelf in April through May to shallow coastal waters where they remain until October or November (Able and Kaiser, 1994; Packer and Hoff, 1999). Within estuaries, summer flounder feed on small, locally abundant fishes and caridean shrimp (Smith and Daiber, 1977; Powell and Schwartz, 1979; Rountree and Able, 1992). During the summer months, summer flounder co-occur with juvenile winter flounder (*Pseudopleuronectes americanus*, Walbaum) which settle to benthic habitats in MAB estuaries from April through June (Witting, 1995; Able and Fahay, 1998; Sogard et al., in review). As a result, summer flounder predation could be an important source of age-0 winter flounder mortality within estuarine nurseries.

Although age-0 winter flounder have been classified as habitat generalists (Able and Fahay, 1998), distribution patterns are often related to sediment characteristics and/or proximity to macrophytes (Saucerman, 1990; Sogard and Able, 1991; Howell et al., 1999; Goldberg et al., in review). Models of winter flounder habitat association in the Navesink River/Sandy Hook Bay Estuarine System, New Jersey, show that small age-0 fish (< 55 mm total length) are associated with fine-grained organically rich sediments (Stoner et al., in review). However, sediment characteristics are less important to larger individuals (55–130 mm TL), that frequently occur in vegetated habitats (primarily sea lettuce, *Ulva lactuca*; Stoner et al., in review). These habitat associations could be related, in part, to the importance of soft sediments and macrophytes as refugia.

In this study, we integrated field surveys and laboratory experiments to investigate the predator–prey interaction between age-1 + summer flounder and age-0 winter flounder. We performed weekly trammel net surveys to examine temporal and spatial variation in the distribution and diet of summer flounder in the Navesink River, New Jersey, which serves as a spawning ground and nursery for winter flounder (Phelan, 1992; Scarlett and Allen, 1992; Stoner et al., 1999, in review; Goldberg et al., in review). In the laboratory,

we measured summer flounder prey selection using age-0 winter flounder and an alternative pelagic fish (Atlantic silversides, *Menidia menidia*) and benthic invertebrate (sand shrimp, *Crangon septemspinosa*) prey, as well as the influence of prey body size on winter flounder survival. We also examined the effects of habitat structure, specifically sediment grain size and the presence of eelgrass (*Zostera marina*) and sea lettuce (*Ulva lactuca*), on winter flounder mortality.

2. Materials and methods

2.1. Field studies

2.1.1. Summer flounder distribution and abundance

Summer flounder were collected in the Navesink River, New Jersey (Fig. 1). The river has one primary freshwater source and a partially dredged channel (4 m at mean low water, MLW) along its axis. A weak salinity gradient (range, 10–27‰) extends eastward from the river head. The range of semidiurnal tide in the system averages 1.4 m and tidal currents attenuate in the upper river which is generally deeper (\bar{x} depth, $D = 1.5$ m at MLW), has finer grained sediments, and more vegetation (Sea lettuce, *Gracilaria*

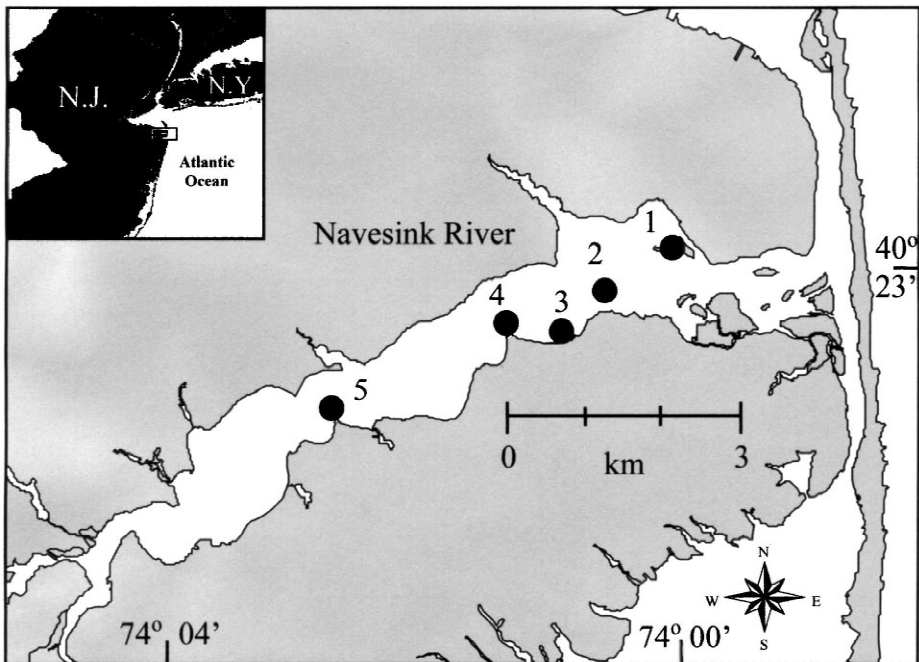


Fig. 1. Location of five stations in the Navesink River, New Jersey where weekly trammel net surveys were performed in 1999. Inset shows the study area in the Mid-Atlantic Bight.

spp.) than the lower river ($\bar{x} D = 1.0$ m at MLW). In the lower river, channels are flanked by sandbars and coves vegetated with sea lettuce and eelgrass.

Fixed stations ($n=5$) were established throughout the river (Fig. 1) for surveys with trammel nets (100 m long \times 2 m deep, 5-cm nylon inner mesh, 36-cm nylon walls). The nets, set perpendicular to sandbar and beach habitats ($D < 2$ m at MLW), were fished weekly for 2 h during the morning (08:00–10:00 EST) from the beginning of June to the end of August 1999. The catch data was standardized as number of fish collected h^{-1} . During each sampling, bottom water temperature ($^{\circ}C$) and salinity (‰) were measured with a YSI™ probe, and depth (cm) was measured with a fathometer.

2.1.2. Stomach content analysis

Summer flounder collected in trammel nets were measured (total length, TL, mm) and their stomachs were excised for dietary analysis. Diet items were identified to species when possible, counted, and percent stomach volume for each taxon was estimated visually. Prey lengths (mm) were also measured. Winter flounder TL (mm) were estimated from standard lengths (SL mm) using the equation:

$$TL = 1.213(SL) - 0.447 \quad (\text{Able and Fahay, 1998}).$$

Predator–prey body size relationships were estimated with quantile regression (Stata; StataCorp, 1995) using the rule $n > 10/q$ to determine quantiles (q) reflecting trends in maximum and minimum prey sizes given sample size (n) (Scharf et al., 1998).

Gape sizes of freshly killed summer flounder ($n=61$, 252–473 mm TL) were measured to determine the possible morphological constraint on maximum prey size. Mouth height (MH) and width (MW) were measured (mm) with vernier calipers as the distance between the maxillary bones in the mouth interior. To measure esophagus width (EW), predators were decapitated at the cliethrum and calipers were inserted into the esophagus, which was stretched by applying consistent pressure to the calipers.

Linear regression was used to relate gape size (MH, MW, EW) to predator TL (mm). Because body depth determines vulnerability for flatfish prey (Ellis and Gibson, 1995, 1997; Manderson et al., 1999), the following regression relating winter flounder body depth (BD mm, maximum dorso-ventral distance) to total length (TL mm) was used to examine the relationship between predator gape size and prey size:

$$TL \text{ mm} = 6.792 + 2.856 (BD \text{ mm}), r^2 = 0.93 \quad (\text{Manderson et al., 1999})$$

2.2. Laboratory studies

2.2.1. Collection and maintenance of experimental animals

Summer flounder were collected with barbless hook and line, and winter flounder, sand shrimp, and Atlantic silversides were collected with haul seines, in the Navesink River. Animals were transported to the James J. Howard Marine Sciences Laboratory, Highlands, NJ, and maintained in continuous flow-through tanks (2.5 m diam. \times 5 m deep) supplied with ambient seawater pumped from Sandy Hook Bay (temperature, 16–25 $^{\circ}C$; salinity, 21–25 ‰). Simulated seasonal changes in photoperiod were maintained in all laboratories with computerized lighting systems. The bottoms of tanks were

covered with 2–3 cm of washed sand (\bar{x} grain diam., GD=0.5 mm). Summer flounder ranging from 262 to 350 mm TL ($n=30$, \bar{x} wt.=220 g, range=153–402 g) were fed live killifish (*Fundulus heteroclitus*) or frozen Atlantic menhaden (*Brevoortia tyrannus*) ad libitum between experiments. Prey were also fed ad libitum (winter flounder with live *Artemia* and chopped clam, shrimp with frozen fish, and Atlantic silverside with commercial fish pellets).

2.2.2. General experimental procedures

Except where indicated below, randomly selected and satiated summer flounder were introduced individually into experimental tanks (2.5 m diam.×0.5 m deep) for a 24-h starvation period. The bottoms of the tanks were covered with 2–3 cm of fine sand (\bar{x} GD=0.14 mm, S.D.=0.02) except in experiments examining the effects of sediment grain size on prey vulnerability. Prior to the start of each experiment, predators were isolated within the tanks in opaque PVC cylinders (0.7 m diam.×0.6 m deep). Prey were measured (TL mm) and immediately introduced to the area outside the cylinders. The predators were released after 1 h and allowed to feed for 24 h. All experiments were started at ~12:00 EST. At the end of experiments, summer flounder were removed from experimental tanks and weighed and measured. The tanks were drained and sediment raked to recover surviving prey. In the choice experiments using winter flounder and sand shrimp prey and in the macrophyte experiments, survivors were recovered by sieving all sediments through 3-mm mesh. In all experiments, except for the test of prey body size effects, six replicates of each treatment were performed (Table 1). Ten replicates of each treatment were performed in the prey body size experiment.

2.2.3. Prey choice

We examined summer flounder selectivity for demersal winter flounder and alternative benthic invertebrate (sand shrimp) and pelagic fish (Atlantic silverside) prey at three relative densities (5:15, 10:10, 15:5; Table 1). Two prey combinations were used; winter flounder/Atlantic silverside, and winter flounder/sand shrimp. Prey sizes were similar within each species pair. Chesson's α_i with food depletion (Chesson, 1983) was used as the prey selectivity index. The null hypothesis of no selection ($\alpha_i = \alpha_j = 0.5$) was tested for each prey combination and ratio using a *t*-test with a Bonferroni correction.

2.2.4. Relationship between prey size and winter flounder vulnerability

The relationship between winter flounder body size and vulnerability to summer flounder predation was examined by offering individual prey in 10-mm size classes from 20 to 90 mm TL to individual predators in a narrow size range (Table 1). Trials were performed to provide 10 replicates for each prey size class which was randomly selected for each predator. Logistic regression was used to parameterize the relationship between mortality (response frequencies; dead versus alive) and prey body size.

2.2.5. Effects of sediment grain size and macrophytes on prey vulnerability

We investigated the role of sediment as refuge for winter flounder by presenting the prey ($n=10$) to individual summer flounder in experimental tanks covered with 2 cm of (1) gravel (\bar{x} GD=18 mm, S.D.=19.8), (2) coarse sand (\bar{x} GD=1.55 mm, S.D.=

Table 1

Design of laboratory experiments performed to examine interactions between summer flounder predators and winter flounder, sand shrimp and Atlantic silversides prey

Experiment	\bar{x} Total length mm (range)		Temperature (°C) range	Treatments	No. replicates treatment ⁻¹
	Predator	Prey			
Prey choice	295 (271–345)		20–22		
Winter flounder vs. Atlantic silversides		51 (35–60) 48 (35–70)		Three prey ratios (5:15, 10:10, 15:5)	6×3 prey ratios
Winter flounder vs. Sand shrimp		41 (28–52) 27 (16–39)		Three prey ratios (5:15, 10:10, 15:5)	6×3 prey ratios
Winter flounder body size	291 (282–305)	(20–90)	16–18	Seven in 10-mm size classes	10×7 size classes
Sediment effects	291 (262–346)		18–20	All prey sizes tested in	
Small winter flounder		26 (20–30)		Gravel	6×3 prey sizes
Medium winter flounder		45 (40–49)		Coarse sand	6×3 prey sizes
Large winter flounder		64 (60–74)		Fine sand	6×3 prey sizes
Effects of macrophytes	302 (274–350)	45 (34–59)	21–22	Eelgrass	6
				Sea lettuce	6
				Bare fine sand	6
Prey behavior					
Winter flounder		44 (40–55)	21–22		4
Sand shrimp		35 (30–44)			4
Interaction					4
Predator–prey behavior					
Summer flounder winter flounder interaction	332(310–355)	44 (30–60)	17–19		3

0.191), or (3) fine sand (\bar{x} GD=0.137 mm, S.D.=0.017) (Table 1). Because body size determines the burial capabilities of flatfishes (Gibson and Robb, 1992) and thus may influence their vulnerability, three size classes of winter flounder (20–29, 40–49, 60–69 mm TL) were offered separately to predators on each substratum. Preliminary experiments were performed with individual winter flounder in each size class on each substratum to measure size-dependent burial capability. The extent of burial was scored for each replicate fish ($n=4$ substrate type⁻¹), 15 min, 30 min, 45 min, and 1 h following their introduction to containers (35 cm diam.×15 cm deep) provided with 2 cm of sediment. Burial was scored as (0) 0–25%, (1) 25–50%, (2) 50–75% and (3) 75–100% of the body covered with sediment. Maximum burial scores for each replicate fish were analyzed.

The effects of macrophytes on prey vulnerability were examined by exposing winter flounder ($n=10$) to individual predators for 24 h in tanks (2.5 m diam×0.3 m deep) with eelgrass (*Zostera marina*), sea lettuce (*Ulva lactuca*), and bare sand (Table 1). Average leaf surface areas for eelgrass shoots (50 cm² shoot⁻¹) and sea lettuce leaves (78 cm² g⁻¹ wet weight) freshly collected in the Navesink River were measured. Shoot densities of 100 m⁻² were established in the eelgrass treatment producing a leaf surface area of ~5000 cm² m⁻². Sea lettuce (64 g m⁻²; ≈9 fronds m⁻²) provided a similar leaf surface area. Eelgrass rhizomes and tips of algal fronds were buried in the sediment to hold the plants on the bottom. Starved predators were placed in PVC cylinders and prey were immediately introduced to the area outside the cylinders. The predators were released after 1 h.

Proportions of winter flounder surviving in the sediment and macrophyte experiments were arcsine transformed and preliminary analyses of covariance using predator weight (g) as the covariate were performed. Because the covariate was never significant ($P>0.11$), we used two-way ANOVAs to test for the effects of: (1) prey size (20–29, 40–49, 60–69 mm) and sediment grain size (fine sand, coarse sand, gravel); and (2) trial and vegetation type (eelgrass, sea lettuce, and bare sand) on prey mortality. Trial was not included as a factor in the analysis of the sediment experiment because all prey sizes were not available for each trial ($n=6$ over 16 days) and thus trial and prey size were partially confounded.

2.2.6. Predator and prey behavior

Predator and prey behaviors were examined in two additional experiments because the small sizes of cryptic prey and sensitivity of predators to observers made it impossible to monitor behaviors in the large experimental tanks. Interspecific differences in winter flounder and sand shrimp activity were videotaped in the absence of predators (Table 1). Satiated winter flounder ($n=2$) and shrimp ($n=2$) of similar size were introduced into separate glass-fronted tanks (61 cm wide×32 cm high×15 cm deep). Two individuals of each species were also combined in a third tank to observe interspecific interactions. The tanks were videotaped for 5 min every hour for 24 h. Percent time active (= % of time moving) and percent time swimming in the water column (upper half of tank) were quantified for each 5-min period.

Videotaped observations of summer flounder feeding on winter flounder were made during the daytime in a glass-front rectangular tanks (2.5 m long×0.8 m wide×0.5 m

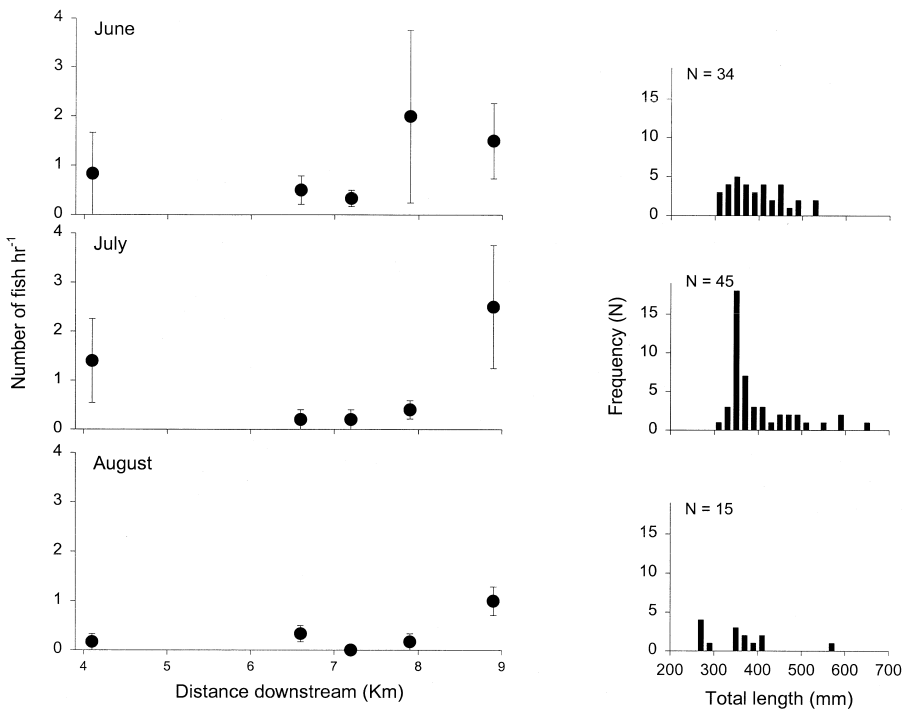


Fig. 2. Spatial and temporal patterns of summer flounder catch per unit effort in trammel nets (0 CPUE=no fish $\text{h}^{-1} \pm \text{S.E.}$), and size distribution in the Navesink River. Station numbers are indicated on the abscissa.

deep) (Table 1). Predators were isolated and prey acclimated within the tanks as described above. Ten prey were exposed to each predator for 4 h and the trials were videotaped continuously. Each 4 h videotape was analyzed to quantify: (1) the number of attacks; (2) method of attack (lie-in-wait or active stalking); (3) whether prey were visible and unburied and/or; (4) moving prior to the attack; and (5) location of attacks (bottom or water column).

3. Results

3.1. Field studies

3.1.1. Summer flounder size and distribution

Summer flounder collected in trammel nets ranged in size from 252 to 648 mm TL (Fig. 2). The size distributions of fish were similar in June and July ($n=80$, Median TL=359 mm; two sample Kolmogorov–Smirnov test, $KS=0.23$, $P=0.21$). Although too few individuals were collected in August to permit analysis, the size distribution also appeared to be similar ($n=15$, Median TL=336, 252–556 mm). Summer flounder were consistently abundant at the easternmost station (Sta. 1; Fig. 2). Although fish were also

Table 2

Contribution to total prey volume (% by vol.) and occurrence (%) for prey of summer flounder collected in the Navesink river containing stomach contents ($n=55$)

Prey species	\bar{x} 0% by vol. (S.E.)	% Occurrence (n)
Sand shrimp	30.4±5.7	45 (25)
<i>Crangon septemspinosa</i>		
Winter flounder	21.5±5.1	27 (15)
<i>Pseudopleuronectes americanus</i>		
Blue crab	19.3±5.2	22 (12)
<i>Callinectes sapidus</i>		
Mysids	5.4±3.0	11 (6)
Atlantic silversides	5.0±2.7	7 (4)
<i>Menidia menidia</i>		
Grass shrimp	2.7±1.9	11 (6)
<i>Palaemonetes</i> spp		
Unidentified fish	4.3±2.3	5 (4)
Atlantic menhaden	4.7±2.7	5 (3)
<i>Brevortia tyrannus</i>		
Lady crab	3.6±2.5	4 (2)
<i>Ovalipes ocellatus</i>		
Northern pipefish	0.8±1.2	4 (2)
<i>Syngnathus fuscus</i>		
Other	0.3±0.6	(1)

collected at stations upstream (Sta. 3–5), catches were lower and relatively few fish were collected in the upper river in August.

3.1.2. Dietary patterns

Fifty-eight percent of the summer flounder collected ($n=95$) contained prey and stomach fullness was not correlated with environmental variables (Spearman's ρ , $P>0.05$). Sand shrimp and winter flounder were the dominant prey (Table 2). Individual predators consumed as many as 27 shrimp ($\bar{x}=5.3$) and 11 winter flounder ($\bar{x}=2.7$). Blue crabs (*Callinectes sapidus*), mysids, and grass shrimp (*Palaemonetes* spp.) were also relatively common. Most of the prey were consumed whole.

The diets of the predators changed through time (Fig. 3). Sand shrimp and winter flounder were important in June and July, but absent from diets in August. Other fishes (*Menidia menidia*, *Brevoortia tyrannus*, *Syngnathus fuscus* and *Gobiosoma* spp.) and blue crabs were dominant prey in August.

Spatial variation in dietary composition only occurred with respect to sand shrimp prey (River km versus shrimp percent of stomach volume, SV: Spearman's $\rho = -0.36$, $P<0.01$). Frequency of occurrence (F) and percent stomach volume for shrimp were higher for predators collected in the upper river (Sta. 4–6; \bar{x} SV $\geq 64\%$, $F \geq 77\%$, $n=16$) than in the lower river (Sta. 1 and 2; \bar{x} SV $\leq 37\%$, $F \leq 54\%$, $n=21$).

3.1.3. Prey size and predator gape size

Predators consumed sand shrimp ranging from 9 to 48 mm TL ($n=109$; 2.4–14.4% of predator TL) and winter flounder from 24 to 67 mm TL ($n=60$, median TL = 32, 6–19%

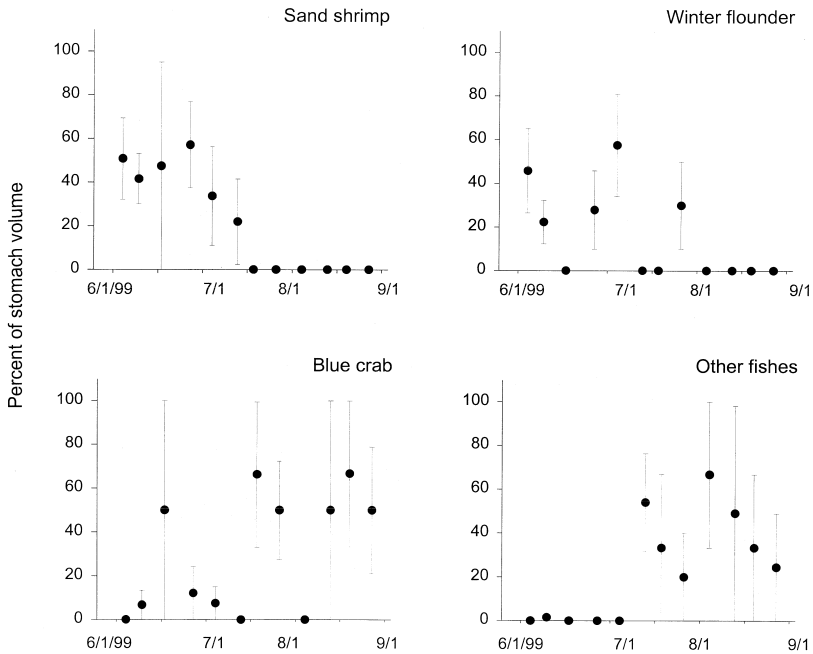


Fig. 3. Temporal patterns in mean percent stomach volume (\pm S.E.) for important prey consumed by summer flounder in the Navesink River.

of predator TL). We found no evidence for significant predator–prey body size relationships as the slopes of quantile regressions estimating maximum, minimum, and median prey size were not different from 0 ($P > 0.34$; quantiles: winter flounder; 20th, 80th and 50th; sand shrimp, 90th, 10th and 50th). Winter flounder consumed in the field were smaller than maxima defined by summer flounder gape dimensions (Fig. 4 and Table 3).

3.2. Laboratory experiments

3.2.1. Prey selection

Summer flounder consistently selected demersal winter flounder over pelagic fish (Atlantic silversides) and benthic invertebrate (sand shrimp) prey at all ratios (Fig. 5 and Table 4). Chesson's α values for winter flounder were significantly greater than 0.5 ($P \leq 0.02$) in five of six prey type/prey ratio combinations (Table 4). Selection for winter flounder was not statistically significant when Atlantic silversides were offered in equal numbers (i.e., 10:10). However, Chesson's α for winter flounder averaged 0.82 (S.E. = 0.13) in the treatment, and predators consumed more silversides in only one replicate.

3.2.2. Winter flounder body size and prey vulnerability

Winter flounder vulnerability to the predators increased significantly ($\chi^2 = 9.20$, $P = 0.002$) with increasing prey body size from 37% (S.E. = 0.06) for 20–30 mm fish

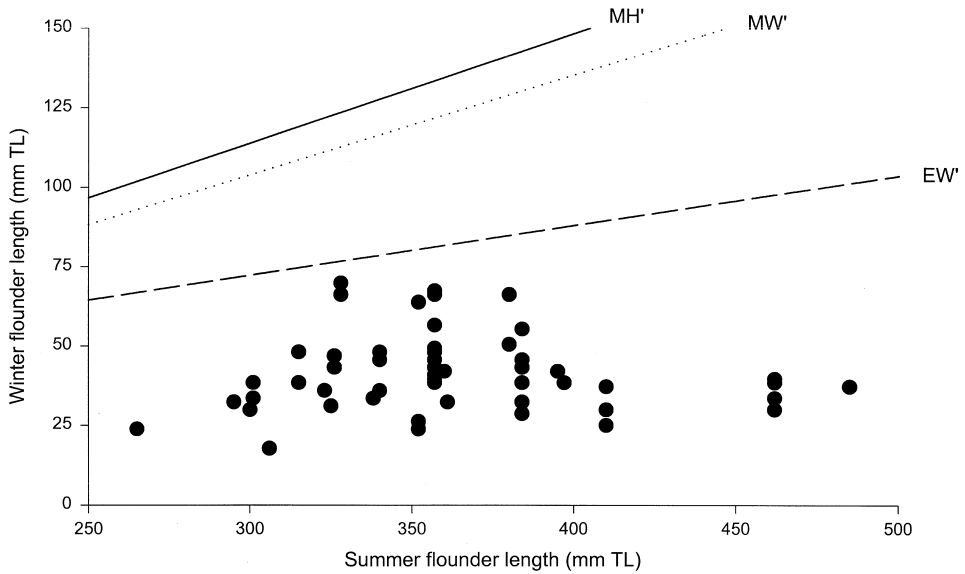


Fig. 4. Scatterplot of body size relationships between summer flounder collected in the field and winter flounder found in their stomachs. Lines indicate estimated winter flounder TL (mm) if predator mouth height (MH'), mouth width (MW') and esophageal width (EW') determine maximum prey size. Estimates were developed from regressions for summer flounder gape (Table 3) and the winter flounder total length/body depth relationship (see Section 2).

(10% of predator length) to 88% (S.E.=0.03) for the 80–90 mm size class (29% of predator length; Fig. 6).

3.2.3. Effects of sediment grain size and macrophytes on prey vulnerability

Winter flounder mortality resulting from summer flounder predation was not influenced by sediment grain size. In the preliminary size-dependent burial experiment, all three sizes of winter flounder buried completely in fine sand (mean maximum burial score (\bar{x} max. B) > 2.25) but could not bury in gravel (\bar{x} max. B = 0). In coarse sand, the largest fish were capable of complete burial (\bar{x} max. B = 2, S.E. = 0.58), the 40–49 mm fish capable of partial burial (25–50% of body covered; \bar{x} max. B = 1, S.E. = 0), and the smallest fish were incapable of burying (\bar{x} max. B = 0). However, neither sediment grain

Table 3

Regressions to determine the relationship between summer flounder total length (mm) (n = 61, 252–473 mm TL) and gape dimensions (mm)

Dependent variable	Effect	Coefficient (S.E.)	T	P	R^2
Mouth height (MH)	Intercept	1.359 (4.190)	0.324	0.747	0.517
	Total length	0.121 (0.011)	10.35	<0.001	
Mouth width (MW)	Intercept	1.069 (6.373)	0.168	0.867	0.315
	Total length	0.110 (0.018)	6.238	<0.001	
Esophageal width (EW)	Intercept	6.477 (2.644)	2.450	0.018	0.432
	Total length	0.055 (0.042)	7.507	<0.001	

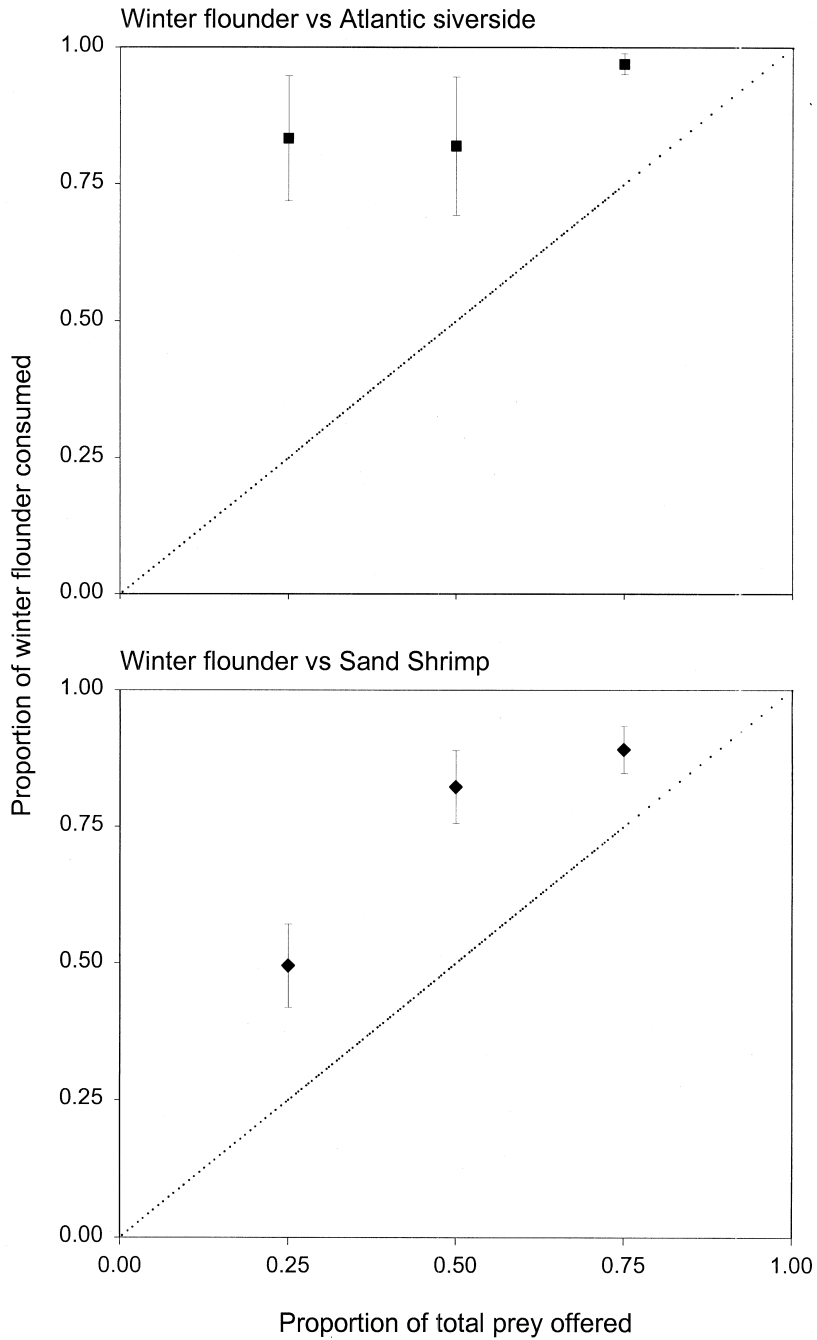


Fig. 5. Proportion of winter flounder consumed by summer flounder in choice experiments in relation to the proportion of total prey offered (see Table 4).

Table 4
Results of summer flounder prey selection experiments^a

Prey combination Prey ratio	Degrees of freedom	Chesson's α (Winter flounder) $\bar{x} \pm \text{S.E.}$	T	P
<i>Winter flounder:Atlantic silversides</i>				
5:15	5	0.947±0.039	11.465	0.000
10:10	5	0.818±0.129	2.463	0.057
15:5	5	0.944±0.036	12.467	0.000
<i>Winter flounder:sand shrimp</i>				
5:15	4	0.777±0.071	3.742	0.020
10:10	3	0.932±0.054	7.928	0.004
15:5	3	0.838±0.057	5.952	0.009

^a Only Chesson's α values for winter flounder are reported. $\alpha=0.5$ indicate no selection.

size nor prey body size influenced winter flounder vulnerability to summer flounder predators (Fig. 7 and Table 5a).

The presence of macrophytes decreased the vulnerability of winter flounder to summer flounder predators (Fig. 8, Table 5b). Although prey mortality differed between trials ($F=4.71$, $P=0.048$; Table 5b), the trial×treatment interaction was insignificant

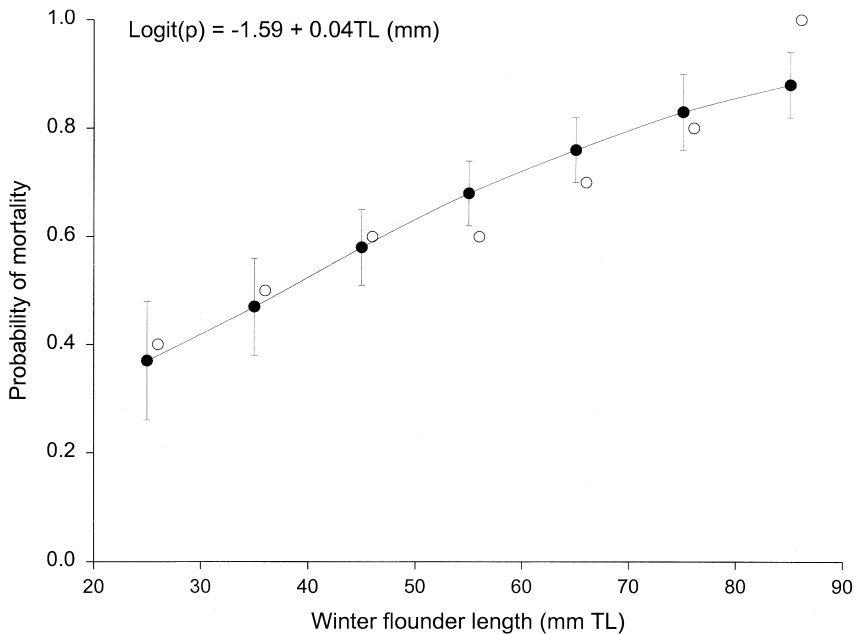


Fig. 6. Mortality probabilities (± 2 S.E., closed circles) for winter flounder of different body sizes from summer flounder predation. Open circles indicate proportion of total prey consumed in the size classes offered. Individual prey were offered at random to individual predators and 10 replicates for each prey size class were performed.

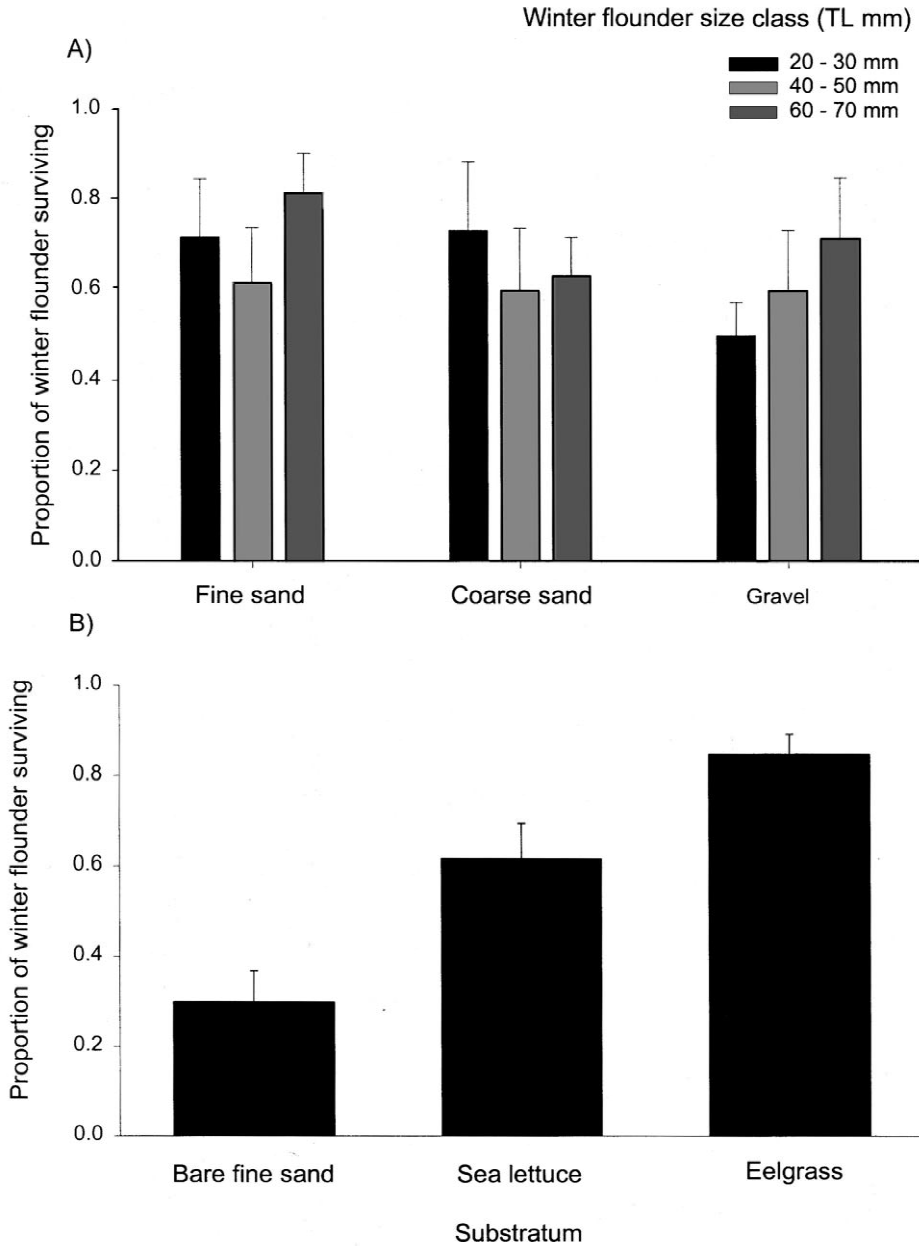


Fig. 7. Proportion of prey surviving (0 ± 1 S.E.) in experiments testing for the effects of (a) sediment grain size and prey body size and (b) macrophytes on winter flounder vulnerability to summer flounder predation. Treatments were not significantly different ($P > 0.05$) in the sediment experiment, but were significantly different ($P \leq 0.01$, Fishers LSD test) in the macrophyte experiment.

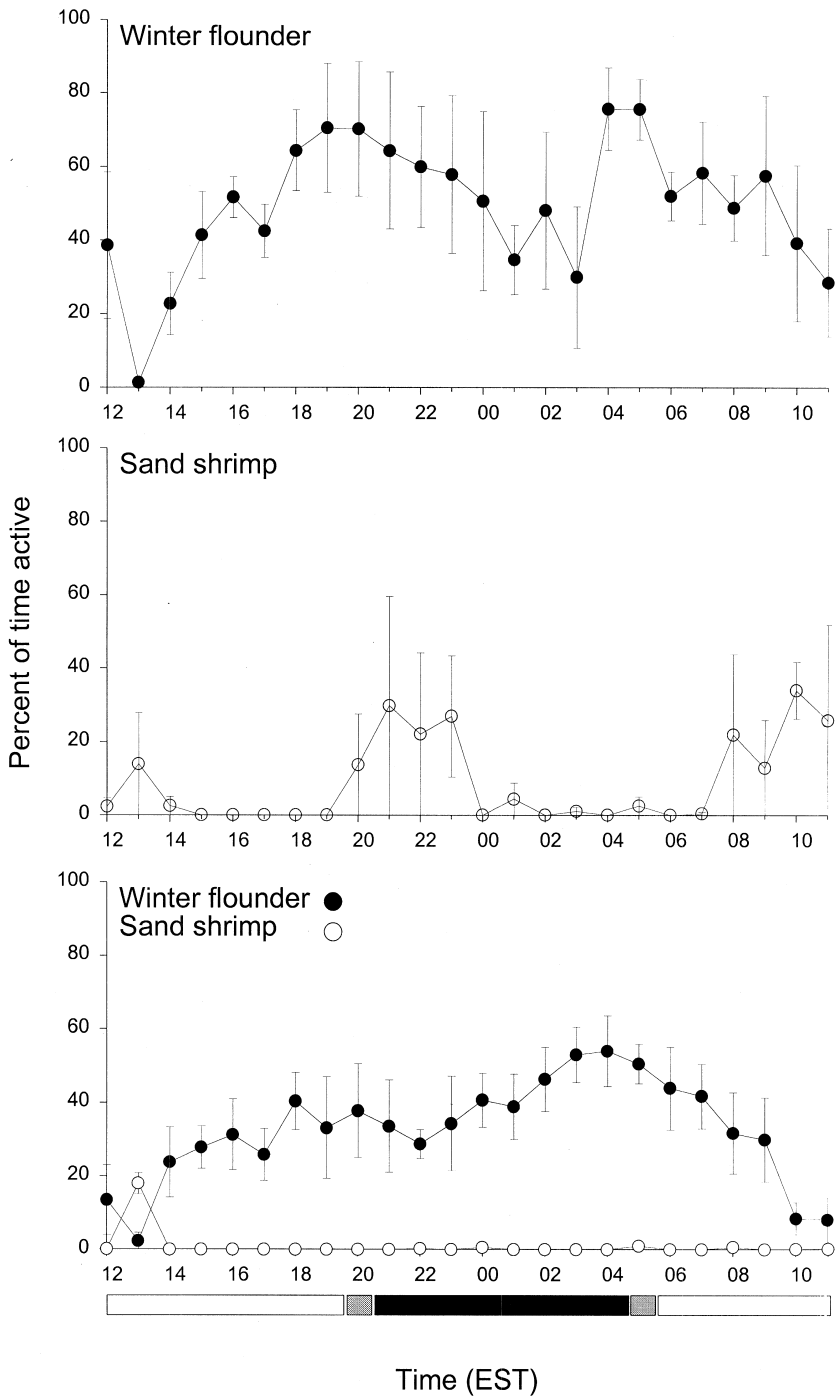


Fig. 8. Percent of time active (0 ± 1 S.E.) for winter flounder and sand shrimp in 24-h experiments. Bars below abscissa indicate simulated light levels (open, daylight; grey, sunrise or sunset; closed, night).

Table 5

Analysis of variance tests for the effects of (a) prey size (total length mm) and sediment grain size and (b) vegetation type on the vulnerability of juvenile winter flounder to summer flounder predation^a

Source of variation	Degrees of freedom	Mean square	F ratio	P
(a)				
Sediment grain size	2	0.152	0.832	0.391
Prey size	2	0.160	1.003	0.375
Interaction	4	0.094	0.590	0.672
Error	45	0.154		
(b)				
Trial	1	0.147	4.710	0.048
Vegetation type	2	0.626	29.903	<0.001
Error	14	0.031		

^a Proportions of prey surviving were arcsine transformed prior to analysis. (In macrophyte experiment, the trial \times vegetation type interaction was not significant ($F=0.451$, $df=2$, $P=0.65$) and dropped from the final analysis.)

($F=0.451$, $df=2$, $P=0.65$) and excluded from the final analysis. Prey survival was significantly higher in eelgrass ($\bar{x}=85\%$, $S.E.=0.04$) than in sea lettuce ($P=0.010$, $\bar{x}=62\%$, $S.E.=0.08$) or sand ($P<0.001$, $\bar{x}=30\%$, $S.E.=0.07$; Fishers LSD test). Survival was also higher in sea lettuce than on sand ($P=0.005$).

3.2.4. Predator and prey behavior

Winter flounder were substantially more active (\bar{x} time active, \bar{x} TA = 50%, $S.E.=2.7$) than sand shrimp (\bar{x} TA = 8.9%, $S.E.=2.7$; Fig. 8). Flounder activity was highest at sunset and sunrise and the prey spent more time swimming in the water column during night hours (day $\bar{x}=22\%$, $S.E.=3.3$; night $\bar{x}=40\%$, $S.E.=2.7$). Although shrimp showed maximum activity following sunset and sunrise, most individuals remained buried during the day and night (day \bar{x} TA = 8.5%, $S.E.=2.6$; night \bar{x} TA = 9.6%, $S.E.=4.2$) and rarely swam in the water column. In the presence of flounder, shrimp remained buried (\bar{x} TA = 0.5%, $S.E.=0.3$). Although flounder activity was slightly depressed in the presence of shrimp (\bar{x} TA = 33%, $S.E.=1.9$), diel patterns were similar to those observed when shrimp were absent.

Summer flounder attacked exposed and active winter flounder. Of the 33 attacks observed on videotape, most involved prey visible on the sediment surface prior to attacks ($\bar{x}=79\%$, $S.E.=14$), and many of the prey had been actively moving along the substratum ($\bar{x}=33\%$, $S.E.=17$). The predators never used a lie-in-wait attack strategy on bare sand, but stalked winter flounder, which were primarily attacked while on the bottom (80%, $S.E.=2.4\%$).

4. Discussion

Our dietary analysis suggests that age-0 winter flounder are important prey for summer flounder in the Navesink River. Young winter flounder (14–130 mm TL) are the most abundant demersal fish in the study area, which has been identified as a spawning

and nursery ground for the species (Phelan, 1992; Scarlett and Allen, 1992; Stoner et al., 1999, in review; Goldberg et al., in review). Summer flounder diets are typically dominated by locally abundant fishes and crustaceans (Smith and Daiber, 1977; Powell and Schwartz, 1979; Lascara, 1981; Rountree and Able, 1992) and Poole (1964) also identified young winter flounder as important prey in Great South Bay, New York.

The temporal shift in summer flounder diets that we observed was probably related to spatio-temporal variation in the distribution of predators and prey. Juvenile winter flounder were consumed by predators in June and early July and were abundant in concurrent beam trawl surveys of the study area (Northeast Fisheries Science Center, NEFSC, unpublished data). By mid July, the prey were absent from beam trawl collections and probably unavailable to predators. Prey availability probably also determined the size spectrum of winter flounder consumed by summer flounder. Summer flounder consume winter flounder 30–40% of their body length (Curran and Able, 1998) and we have observed predators (378 mm TL) eating prey as large as 140 mm TL. Winter flounder collected in the study area ($n=174$, median TL=32; range=12–71 mm; NEFSC, unpublished data) and consumed by predators (median TL=32, range=24–67 mm) were similar in size and not large enough to challenge gape limitations.

The seasonal decline in the importance of sand shrimp prey was probably also related to spatial variation in shrimp abundance as well as temporal changes in summer flounder distribution. During the early summer, the predators were commonly collected in the middle reach of the river (Sta. 4 and 5) where shrimp densities average 5.0 m^{-2} (max.= 21.5 m^{-2} ; NEFSC, unpublished data). These fish consumed large numbers of shrimp more frequently than those collected in the lower river (Sta. 1 and 2) where shrimp abundance was nearly an order of magnitude lower (\bar{x} CPUE= 0.60 m^{-2} , max.= 3.7 m^{-2}). During August, shrimp prey were rarely found in the stomachs of predators which were primarily confined to the lower river.

Although prey availability determined selection in the field, summer flounder clearly preferred winter flounder to alternative pelagic fish (Atlantic silversides) and benthic invertebrate (sand shrimp) prey in the laboratory. Our results on prey selectivity are consistent with field studies showing that summer flounder prefer demersal prey, although pelagic fishes including Atlantic silversides and juvenile weakfish (*Cynoscion regalis*) are also consumed (Smith and Daiber, 1977; Powell and Schwartz, 1979; Rountree and Able, 1992; this study). Unless demersal prey are rare or the prey types co-occur in shallow habitats, summer flounder are likely to encounter demersal prey more frequently than pelagic prey as a result of the predator's affinity for benthic habitats.

Summer flounder preference for winter flounder over sand shrimp in the laboratory was probably related to interspecific differences in prey locomotor activity. Vision is the primary sensory mode used by bothids in prey selection (De Groot, 1971; Olla et al., 1972; Lascara, 1981), and most attacks we observed involved prey visible on the sediment surface or moving and presumably detected visually by predators. In the absence of the predator, winter flounder spent less time buried and were far more active than sand shrimp, whose activity was suppressed in the presence of winter flounder. Similar variations in prey activity have been invoked to explain both inter- and intraspecific differences in prey vulnerability to other visual predators (Sih, 1987; Lima and Dill, 1990; Werner and Anholt, 1993).

Selection for winter flounder appears to conflict with reports of the importance of shrimp prey to summer flounder in the field (Poole, 1964; Smith and Daiber, 1977; Powell and Schwartz, 1979; Lascara, 1981; Rountree and Able, 1992; this study). However, differences in the relative densities of the two prey in the field can greatly exceed those used in our choice experiments. In Navesink River habitats in which the prey co-occur, the median ratio of sand shrimp to age-0 winter flounder is ~100:1 and can exceed 1000:1 (Manderson, unpublished data). Thus, encounter rates of summer flounder with shrimp are likely to be much higher in some habitats than for winter flounder.

The selectivity of predators and vulnerability of prey are strongly influenced by relative body sizes (Werner and Gilliam, 1984; Fuiman, 1994). It is generally assumed that vulnerability decreases with increasing prey body size (Sissenwine, 1984; Anderson, 1988; Sogard, 1997), but vulnerability curves may also be dome-shaped when visual predators use raptorial attack strategies (Gerritsen and Strickler, 1977; Bailey and Houde, 1989; Lundvall et al., 1999). Because small prey are more difficult for visual predators to detect (Breck and Gitter, 1983; Howick and O'Brien, 1983), they can be less vulnerable until larger prey approach handling and gape limitations. In our laboratory study, the vulnerability of winter flounder to summer flounder increased with increasing prey size from 20 to 90 mm TL. Although we were unable to offer prey to summer flounder which challenged their handling and gape limitations, winter flounder vulnerability curves are probably dome-shaped for summer flounder predators. The size-specific vulnerability of winter flounder to striped searobin (*Prionotis evolans*) predators is also dome-shaped (Manderson et al., 1999) and spot (*Leiostomus xanthurus*) show a similar pattern of size selective mortality when exposed to southern flounder (*Paralichthys lethostigmata*; Rice et al., 1993a).

Winter flounder are probably vulnerable to summer flounder predation throughout their first year. In our size-selective mortality experiment, prey with size ratios of 30% were eaten by relatively small summer flounder (Table 1) and in another study the predators consumed winter flounder prey 30–40% of predator length (Curran and Able, 1998). Using a conservative maximum prey size ratio of 35%, summer flounder in the Navesink River (median TL=360 mm) can probably consume winter flounder as large as 126 mm. Typically only 1% of winter flounder collected in July and 5% collected in November surveys of the study area are larger in size (Stoner et al., in review).

Although morphology, predator and prey behaviors, and broad scale distributional patterns determine encounter probabilities and capture success, predator–prey interaction strength can be further modified by variations in habitat structure. Flatfish preferences for soft sediments are well known (Gibson, 1994; Keefe and Able, 1994; Moles and Norcross, 1995; Neuman and Able, 1998) and have often been related to the refuge these substrata provide to the fish which exhibit size-dependent burial (Gibson and Robb, 1992). In our laboratory experiments, winter flounder mortality was not influenced by sediments that permitted differential burial for several size classes of the prey. Our result is consistent with previous laboratory experiments with benthic fish and invertebrate predators showing that the presence of soft sediments does not enhance age-0 flatfish survival (Ansell and Gibson, 1993; Manderson et al., 1999). Caution is needed when extrapolating these laboratory results to the field, however, because small arena size and

long experimental duration produce artificially high encounter rates in the laboratory. Predation threat is likely to be transitory in the field and flatfish could conceivably use burial to effectively evade visual predators in more expansive natural settings.

The importance of macrophytes as predator refugia for small fish and invertebrates is also well known (Stoner, 1982; Wilson et al., 1987, 1990; Rozas and Odum, 1988; Levin and Haye, 1996; among others). In our studies, winter flounder mortality was significantly lower in macrophytes than on bare sand. This result differs from those finding similar mortality in artificial eelgrass and bare substrata for pelagic prey (spot, Atlantic silversides) exposed to summer and southern flounder (Lascara, 1981; McCullum, 1996). These authors attributed their results to the efficiency of a lie-in-wait attack strategy adopted in structurally complex habitats (see also Coen et al., 1981; James and Heck, 1994). Summer flounder never used a lie-in-wait strategy to capture winter flounder on bare sand in our study (see also De Groot, 1971; Olla et al., 1972). This suggests that bothids may shift from an active search to a lie-in-wait strategy with increasing habitat complexity. The efficiency of each strategy may be strongly dependent on prey lifestyles. The lie-in-wait strategy may be effective for capturing pelagic prey positioned above a motionless and camouflaged predator, but less so for demersal prey hidden within the stems of vegetation. Shifts in summer flounder attack strategy with habitat complexity along with differences in prey lifestyles could result in important habitat-specific shifts in prey selectivity (Murdock et al., 1975; Buckel and Stoner, 2000).

Eelgrass provided greater refuge for winter flounder than sea lettuce when the macrophytes were planted to produce similar leaf surface areas. In our experiments, the treatments differed most dramatically in structural complexity as defined by the number of spaces between plants (*sensu* Nelson and Bondsdorff, 1990; Carr, 1994). The sea lettuce treatment (9 fronds m^{-2}) had a few large corridors of bare sediment between fronds when compared with eelgrass (100 shoots m^{-2}). Prey vulnerability generally decreases with increasing structural complexity (Nelson and Bondsdorff, 1990), which may restrict the vision and/or movement of predators (Savino and Stein, 1982; Stoner, 1982; Ryer, 1988). The vision of summer flounder was probably obscured to a greater degree in eelgrass than in the sea lettuce, where prey were presumably detected as they moved in the large open spaces between sea lettuce leaves. Sea lettuce is an important source of habitat structure, providing refuge for fish and macroinvertebrates in many mid-Atlantic estuaries (Wilson et al., 1990; Timmons, 1995). In the Navesink River, large age-0 winter flounder (50–130 mm TL) were strongly associated with habitats vegetated with sea lettuce exceeding 7 g m^{-2} (Stoner et al., *in review*). Dense beds of sea lettuce with higher structural complexity could offer winter flounder more effective refuge. However, anoxic events are associated with high sea lettuce biomass (Valiela et al., 1997), and the species avoids high densities of the macrophyte in the laboratory (Timmons, 1995).

Our results support Percy's (1962) speculation that summer flounder could be an important source of winter flounder mortality within estuarine nurseries. Encounter probabilities and capture success in the field are probably determined by responses of predators and the prey to large scale estuarine gradients (e.g., temperature) that may produce spatial refugia that vary in location and extent, and by the body morphologies of

the interacting species. Within regions of species overlap, predator–prey interaction strengths are probably further influenced by the availability of alternative prey and of structurally complex habitats, like macroalgae beds, which also reduce prey mortality rates.

Acknowledgements

The authors would like to thank Allen Bejda, Linda Stehlik, Carol Meise, John Rosendale, Jeff Buckel, Fred Scharf, Frank Morello, Peter Clarke, Carl Osterlund and Rich Nouotng, as well as numerous volunteers from Brookdale Community College and Rutgers University for help in the laboratory and field. Particular thanks go to Jeff Pessutti who contributed to all aspects of the study [SS].

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