Seasonal and ontogenetic changes in distribution and abundance of smooth flounder, *Pleuronectes putnami,* and winter flounder, *Pleuronectes americanus,* along estuarine depth and salinity gradients

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Abstract.—The distribution and abundance of two potentially competing flatfish species, smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, were examined along salinity and depth gradients in upper Great Bay Estuary, New Hampshire. Both species were abundant in the estuary but exhibited differential use of habitats along both gradients. Smooth flounder were most abundant at the mesohaline, riverine habitat, whereas winter flounder were most abundant at the polyhaline, open-bay habitat. Both species exhibited a generalized up-river movement as salinity increased with the seasons. Smooth flounder showed ontogenetic changes in distribution along the depth gradient, with smallest individuals occupying shallowest depths. Intertidal mudflats were an important nursery area for young-of-the-year smooth flounder. Winter flounder showed little separation by size along the depth gradient, and few were found in the intertidal mudflat habitat. The potential for competition between these two species is lessened by their partial segregation along the gradients examined.

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Smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, are dominant members of fish communities in estuaries along the east coast of North America, co-occurring from Newfoundland, Canada, to Massachusetts Bay, USA. These morphologically similar species are sympatric over much of their geographic ranges. However, little is known of their spatial overlap within specific estuaries. Winter flounder use estuaries primarily as nursery grounds, whereas adults spend most of their lives in coastal waters (Bigelow and Schroeder, 1953; Pearcy, 1962; Scott and Scott, 1988). In contrast, smooth flounder complete their entire life cycle within estuaries.

Smooth flounder prefer softer bottom substrata than winter flounder (Bigelow and Schroeder, 1953), and Jackson (1922) noted they were most abundant in the low-salinity regions within Great Bay Estuary, New Hampshire. Little else is known of their intraestuarine habitat preferences. Several studies have examined movements and habitat use of juvenile winter flounder in estuaries south of Cape Cod (e.g. Pearcy, 1962; Saucerman 1991). However, because many northern estuaries differ considerably from those south of Cape Cod, most obviously in their temperature regimes, it is possible that juvenile winter flounder use northern estuaries differently from ones to the south, as has been shown to be the case for adults (Hanson and Courtenay, 1996).

The purpose of this study was to provide a quantitative comparison of the occurrence of smooth and winter flounder in various habitats in upper Great Bay Estuary, New Hampshire. The habitats comprised gradients defined by depth or salinity. Comparative studies along habitat gradients can define which habitats are important to a species, especially in relation to different life history stages; such analyses can also be used to study the relative importance of physical and biotic factors in limiting species distributions (Connor and Bowers, 1987). Examination of the shape of species-abundance curves along a gradient can provide inferences into whether competition or physiological limitations are important in setting distributions (Terborgh, 1971) and can lead to the generation of testable hypotheses.

Methods

Study area

Great Bay Estuary (Fig. 1) is a complex embayment comprising the Piscataqua River, Little Bay, and Great Bay. It is a tidally dominated system and is at the confluence of seven major rivers and several small creeks, as well as the water from the Gulf of Maine (Short, 1992). Great Bay Estuary is a drowned river valley, with high tidal energy and deep channels with fringing mud flats. The main habitat types within the estuary are mudflat, eelgrass, salt marsh, channel bottom, and rocky intertidal. This study was conducted in the upper estuary, referred to as Great Bay, although preliminary sampling took place in the lower estuary also. Great Bay is a large, shallow embayment having an average depth of 2.7 m, with deeper channels extending to 17.7 m (Short, 1992) and a tidal range of about 2 m. The water surface of Great Bay covers 23 km^2 at mean high water and 11 km^2 at mean low water (Turgeon, 1976). Greater than 50% of the sediment surface of Great Bay is exposed mud or eelgrass flat at low tide. The Squamscott and Lamprey Rivers are major sources of freshwater to Great Bay. River flow varies considerably on a seasonal basis but is generally highest during spring runoff. Vertical stratification of Great Bay is rare because of strong tide- and wind-induced currents, although partial stratification may occur during periods of high freshwater runoff, particularly at the upper tidal reaches of rivers (Short, 1992).

Smooth and winter flounder were sampled monthly, May 1989 through September 1991, at five sites in upper Great Bay Estuary (Fig. 1). Ice cover prevented sampling from December through March in all study years. A 4.8-m otter trawl of 38-mm stretch mesh, with a 25-mm stretch mesh codend and a 6-mm codend liner, was used for sampling. Preliminary studies indicated that the net retained flounder as small as 25-mm total length (TL). A sample consisted of all flounder collected in one 10-minute tow at approximately 2.5 knots. Four samples were taken at each site from April to November. Two samples were taken within two hours (±) of low slack tide, one tow with the tidal current and one tow against, and two samples were taken similarly around high slack tide. All flounder collected were measured to the nearest mm TL. Bottom temperature and salinity were measured after each tow with a Beckman Model 510 temperature, conductivity, and salinity meter.

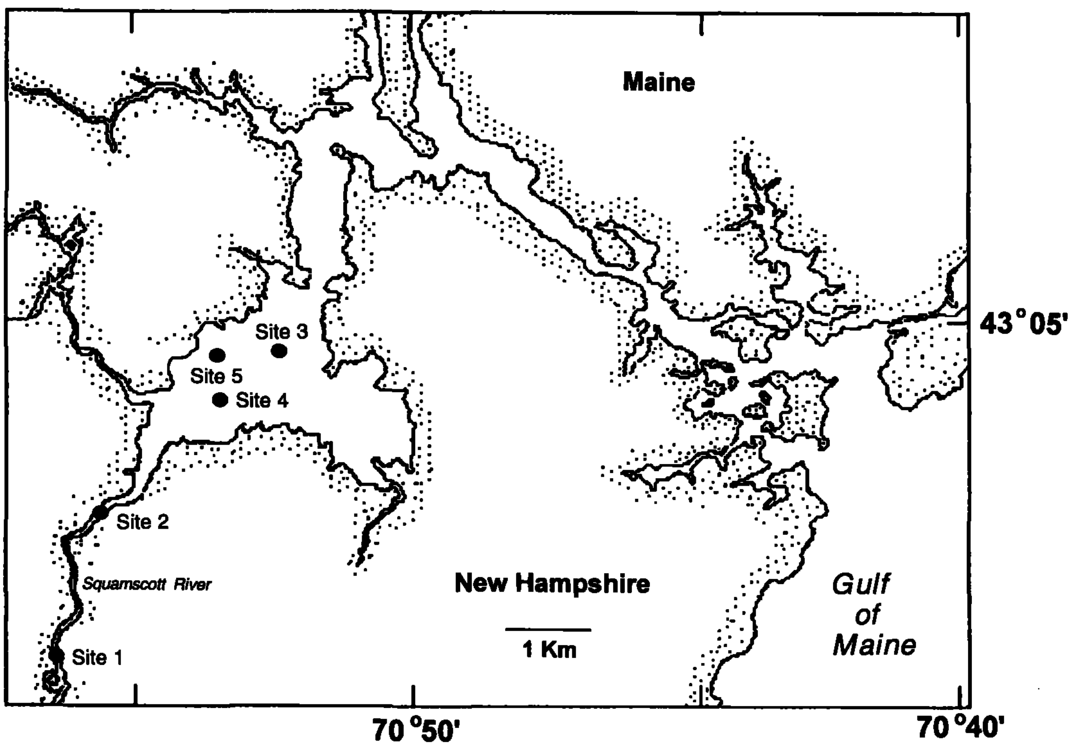

Figure 1
Study area. Survey sites were all located in Great Bay Estuary, New Hampshire, as indicated.

Site 1 (low salinity, Squamscott River at Route 51), site 2 (medium salinity, Squamscott River at Route 108), and site 3 (high salinity, middle of Great Bay) were located along a salinity gradient formed by Great Bay Estuary and one of its major tributaries (Fig. 1). The mean salinity value at each site varied considerably on a seasonal basis, but a salinity gradient always persisted along these sites. Table 1 summarizes some physical characteristics of these locations. Site 1 was located in the Squamscott River about 4 km above the mouth. Although the river is still tidal in this area, the water is often fresh or extremely low in salinity. Site 2 is also located in the Squamscott River but only 0.5 km above the mouth. Salinity at this site is highly variable but intermediate between the other two sites. Site 3, the site with greatest salinity, was located in the middle of Great Bay proper. The depth and bottom substratum were similar at all three stations (Table 1).

Sites 3 and 4 (high salinity, shallow Great Bay) and site 5 (high salinity, Great Bay intertidal flats) were located along a depth gradient in a contiguous area in the middle of Great Bay. Site 3 was the deepest site sampled along the depth gradient. Site 4 represented the intermediate depth, and site 5 was located on intertidal mudflats and therefore sampled only on high tides. All three sites had similar bottom substratum, silty mud, and owing to their proximity, experienced nearly identical salinities (Table 1).

Monthly length frequencies at each site were pooled over all study years. The Kolmogorov-Smirnov test was used to test for differences in length-frequency distributions among sites. One-way analysis of variance (ANOVA) was used to test for significant differences in catches among the three sites that made up each of the two gradients. To reduce the number of ANOVA's performed and to increase the power of the tests by increasing sample sizes, the monthly data were grouped into three seasons: spring, summer, and autumn. Months of April, May, and June were considered spring; July and August were considered summer; and September, October, and November were considered autumn. Because many months contained zero catches and, in some cases, the variances were proportionate to the means, the data were transformed by using a square-root transformation (square root(X+1)). The Kolmogorov-Smirnov test with the Lilliefors modification and probability plots of residuals indicated no significant deviations from normality, and Levene's test indicated homogeneity of variances after the transformation. Where a significant difference in catches was detected among sites, the sites were compared by using Tukey's HSD test (Zar, 1984).

Results

A total of 8,333 smooth flounder and 2,105 winter flounder were captured during the study period. Both juvenile and adult smooth flounder were abundant in the study area in contrast to winter flounder, which were abundant only as juveniles. However, length frequencies of the two flounders were similar because adult smooth flounder are about the same size as juvenile winter flounder. Smooth flounder were captured from many different year classes, whereas winter flounder were primarily age 0^+, 1^+, and 2^+, based on length frequencies.

Salinity followed a typical boreal estuarine seasonal pattern (Figs. 2 and 3). The general trend at all stations was for salinity to be lowest in April, to increase over the late spring and summer months reaching the highest levels during August and September, and to decline during autumn. These seasonal patterns were especially pronounced at site 1 and site 2. Salinities in spring of 1991 were higher at all sites than in the other two years, a result of an uncharacteristically dry spring and limited spring runoff. Another salinity anomaly occurring in 1991

Table 1

Physical characteristics of the sampling sites. Sites 1, 2, and 3 make up the salinity gradient, whereas sites 4, 5, and 3 form the depth gradient.

Site number and habitat type	Salinity (ppt)		Temperature (°C)		Depth (m)		Bottom type
	Mean	Range	Mean	Range	Mean	Range	
1 (low salinity)	4.2	0.0–22.4	19.4	4.7–25.7	2.7	1.9–4.0	silty mud
2 (medium salinity)	10.9	0.4–24.0	17.1	0.0–27.8	3.7	1.8–4.3	silty mud
3 (high salinity, greatest depth)	20.3	6.5–29.9	15.4	1.8–23.9	6.2	4.9–7.9	silty mud
4 (intermediate depth)	20.9	6.5–29.5	16.4	2.3–24.9	2.1	1.5–4.4	silty mud
5 (intertidal flats)	19.8	11.0–28.5	15.2	0.2–24.2	1.5	1.1–2.2	silty mud

was a sudden decrease in salinity in September caused by dilution from the heavy rains with Hurricane Bob in late August of that year. Sites comprising the depth gradient had similar patterns of salinity in all years of the study.

Salinity gradient

Both species were unevenly distributed along the salinity gradient, and their distributions changed seasonally (Table 2). The timing of peak abundance of smooth flounder at site 1 varied from year to year. In 1989 and 1990 smooth flounder were abundant in mid to late summer (Fig. 4). The influx of smooth flounder was associated with seasonal changes in the salinity regime from fresh to oligohaline (Fig. 2). In 1991, smooth flounder were present at site 1 in all months sampled. In this year, salinity was higher than that during the two previous years (Fig. 2). Length frequencies of smooth flounder at site 1 (Fig. 5) were significantly different ($P<0.0001$ in all monthly K-S tests, May–October) from those at site 2 (Fig. 6), although the difference appears to be less in the autumn than in the spring. Larger fish (>100 mm) made up a higher proportion of the catch at site 1 in comparison with site 2, indicating differential migration among size classes. Winter flounder were rarely collected at site 1 (Fig. 7). They were found there only on a few occasions in September and October when salinity was at a seasonal high.

Smooth flounder were abundant at site 2 during all months, and their average abundance at this site exceeded that of all other sites. Their abundance was generally high in the spring, lower in late summer to early autumn, and high again in mid to late autumn (Fig. 4). This trend was opposite to that observed for site 1. Correlation analysis of catches of smooth flounder at sites 1 and 2 indicated a weak but significant negative relationship ($P=0.032$, $r=-0.48$). When catches were large at site 1, they tended to be small at site 2. This finding suggests that the same population of smooth flounder was migrating between the stations, although the length frequencies show that a greater proportion of larger smooth flounder than smaller smooth flounder travel the 3 km between the sites.

Winter flounder were abundant at site 2 only during autumn (Fig. 7), although even during these periods of abundance, the catches of winter flounder were always lower than those for smooth flounder. The movement of winter flounder into site 2 from Great Bay proper was associated with relatively high salinities (Fig. 2) and with low abundances of smooth flounder (Fig. 4). The length frequencies of winter flounder collected from site 2 (Fig. 6) and site 3 (Fig. 8) were similar.

Smooth flounder occurred at site 3 in relative abundance only in April, May, and June (Fig. 4). Catches of smooth flounder decreased significantly after June in all years. Winter flounder were most abundant at this site than at the other two sites comprising the salinity

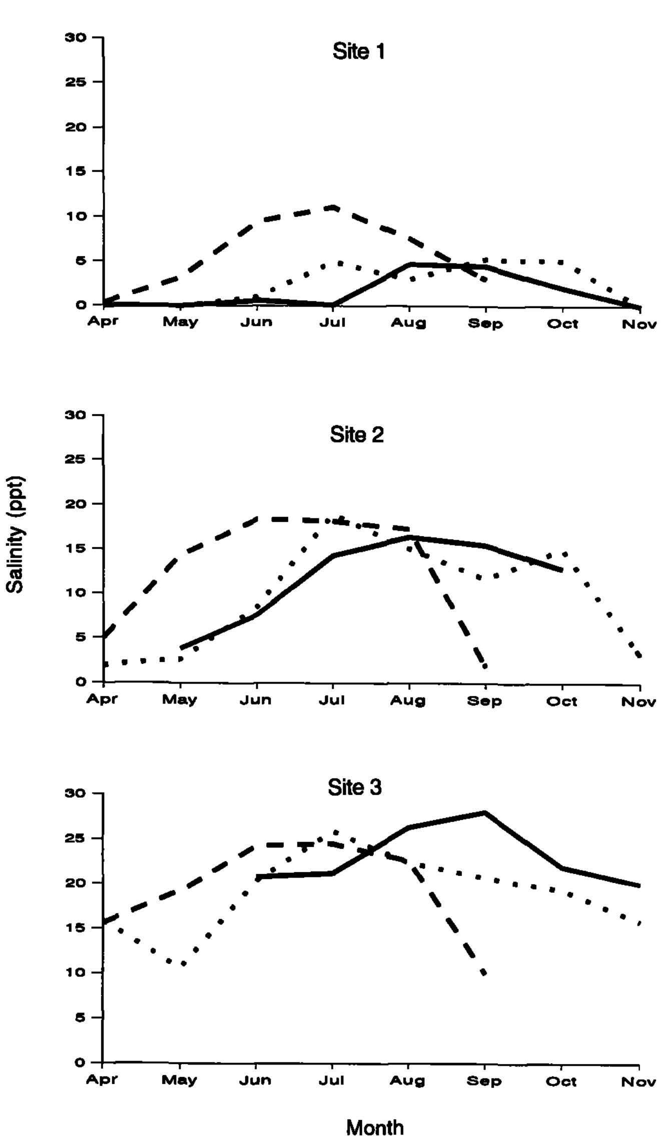

Figure 2

Salinity at three sites sampled along a salinity gradient in Great Bay Estuary, New Hampshire. Mean salinity was highest at site 3 (20.3 ppt) followed by site 2 (10.9 ppt) and then site 1 (4.2 ppt). Solid line = 1989; dotted line = 1990; dashed line = 1991.

gradient (Fig. 7). They were present in relatively large numbers during all months. There were no significant differences in catches of winter flounder among months for all study years.

Depth gradient

The two species of flounder showed a differential use of the three sites that comprised the depth gradient. There were also differences in the sizes of flounder that used the three sites. Seasonal changes in distribution were less pronounced than those exhibited along the salinity gradient.

A broad size range of smooth flounder used site 3 (Fig. 8). However, their abundance dropped off sharply after June of each year, as previously discussed (Fig. 9). Winter flounder showed few seasonal trends in abundance at this station (Fig. 10). A broad size range of juvenile winter flounder was found here. A distinct influx of young-of-the-year winter flounder could be seen at site 3 from August through November of each year (Fig. 8).

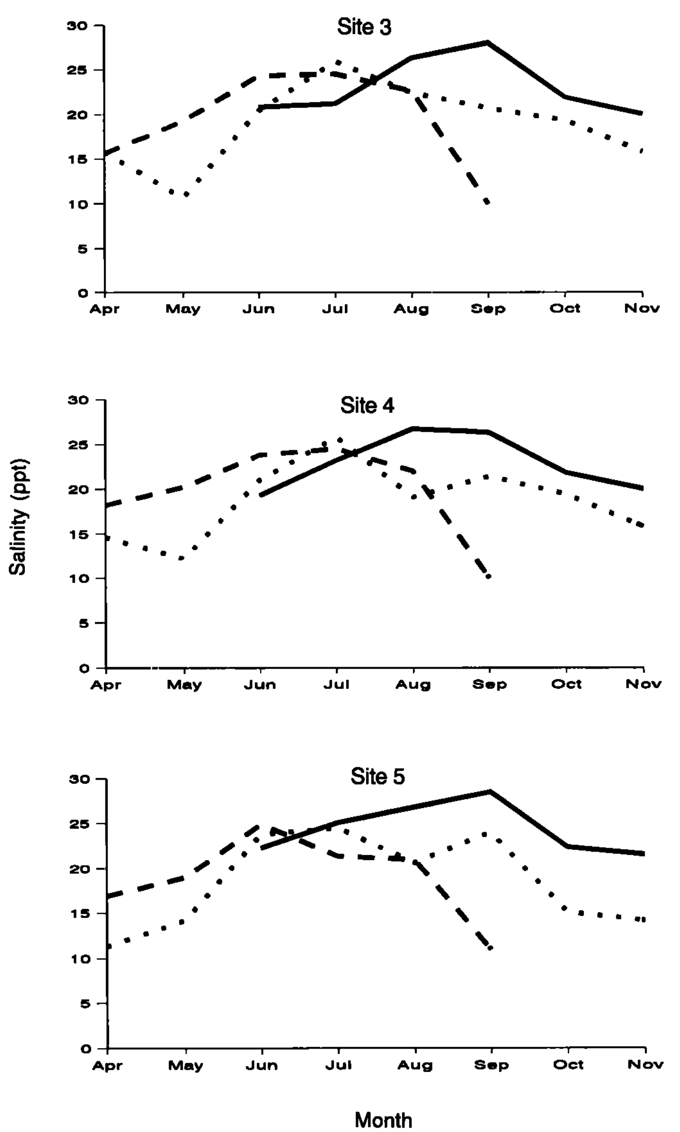

Figure 3

Salinity at three sites sampled along a depth gradient in Great Bay Estuary, New Hampshire. Mean depth was greatest at site 3 (mean = 6.2 m) followed by site 4 (2.1 m) and then site 5 (1.5 m). Solid line = 1989; dotted line = 1990; dashed line = 1991.

At site 4, smooth flounder showed little seasonal change in abundance (Fig. 9), although there was a trend for catches to be lowest in late summer and early autumn. Length frequencies differed between site 3 and site 4. At site 4, few larger smooth flounder were present during any season (Fig. 11), whereas young-of-the-year, which were absent from site 3, were collected at most times. Abundance of winter flounder at site 4 was lowest in all years in early summer (Fig. 10), and catches were always smaller than those at site 3. Length frequencies indicated that smaller winter flounder made up a greater proportion of the catch at site 4 (Fig. 11) as compared to site 3 (Fig. 8).

Catches at site 5 were very variable for both species and showed no clear seasonal patterns (Figs. 9 and 10). Smooth flounder catches at site 5 were dominated by young-of-the-year. Few larger (>100 mm TL) individuals were ever caught at this site (Fig. 12), in contrast to site 3 (Fig. 8) but similar to site 4 (Fig. 11). Winter flounder occurred at site 5 sporadically and in very low numbers (Fig. 10). Catches of winter flounder were a mix of different sizes of juveniles.

Discussion

A variety of habitats are available to smooth and winter flounder in upper Great Bay Estuary. It was the purpose of this study to quantify the occurrence of these two species in various habitats. Although the species ranges of smooth and winter flounder overlap broadly, the evidence presented here indicates that they use habitats within the estuaries differently and that their habitat use is subject to seasonal variations.

Salinity gradient

In general, smooth flounder were most abundant at site 2, the mesohaline river mouth

Table 2

Results of ANOVA's testing for differences in catches of smooth and winter flounder among three sites along the salinity gradient (sites 1, 2, and 3) and three sites along the depth gradient (5, 4, and 3). If there was a significant difference ($P<0.05$) in catches among sites, the results of Tukey's HSD test are listed from lowest to highest. See Table 1 for a description of the sites. ns = not significant.

Year and season	Smooth flounder		Winter flounder	
	Salinity gradient	(F-value; df)	Salinity gradient	(F-value; df)
1989				
Spring	site 1<site 3<site 2	(25.80; 2,20)	site 1=site 2<site 3	(46.64; 2,20)
Summer	site 3<site 1=site 2	(6.13; 2,27)	site 1=site 2<site 3	(38.11; 2,27)
Autumn	site 3<site 1=site 2	(20.29; 2,23)	site 1<site 3<site 2	(12.62; 2,27)
1990				
Spring	site 3=site 1<site 2	(36.42; 2,22)	site 1=site 2<site 3	(8.24; 2,22)
Summer	site 3<site 1=site 2	(13.88; 2,20)	site 1<site 2=site 3	(12.99; 2,20)
Autumn	site 3<site 2=site 1	(9.69; 2,23)	ns	(0.56; 2,23)
1991				
Spring	site 3<site 2=site 1	(9.52; 2,29)	site 1=site 2<site 3	(11.56; 2,29)
Summer	site 3<site 2=site 1	(4.80; 2,21)	site 1=site 2<site 3	(7.07; 2,21)
Autumn	site 3<site 1<site 2	(121.79; 2,5)	site 1<site 3<site 2	(21.26; 2,5)

Year and season	Smooth flounder		Winter flounder	
	Depth gradient	(F-value; df)	Depth gradient	(F-value: df)
1989				
Spring	ns	(2.53; 2,11)	site 5<site 4<site 3	(17.15; 2,11)
Summer	ns	(0.28; 2,21)	site 4=site 5<site 3	(16.62; 2,21)
Autumn	site 3=site 5<site 4	(3.73; 2,23)	site 5<site 4=site 3	(7.02; 2,29)
1990				
Spring	ns	(0.13; 2,28)	site 5<site 4=site 3	(10.87; 2,28)
Summer	site 3<site 5=site 4	(4.41; 2,20)	site 5=site 4<site 3	(14.03; 2,20)
Autumn	site 3=site 4<site 5	(5.63; 2,29)	site 5=site 4<site 3	(7.96; 2,29)
1991				
Spring	ns	(1.08; 2,29)	site 5=site 4<site 3	(13.45; 2,29)
Summer	site 3=site 4<site 5	(14.19; 2,17)	site 5=site 4<site 3	(5.87; 2,17)
Autumn	site 3=site 4<site 5	(162.99; 2,5)	site 5=site 4<site 3	(5.82; 2,5)

habitat. Seasonal movements were seen into and out of the oligohaline riverine station (site 1) and the polyhaline station in Great Bay proper (site 3). In all years, there was an up-estuary movement of smooth flounder associated with increasing salinity in summer and early autumn. This movement was most pronounced for larger smooth flounder. Greater movement by larger individuals is probably related to their superior locomotive abilities due simply to their larger body size. This trend towards increasing range of movement with increasing body size has also been found in the hogchoker, *Trinectes maculatus*, a flatfish that is similar in general size to smooth flounders and that is also found in estuarine rivers (Dovel et al., 1969; Smith, 1986).

There is little information available on the distribution of smooth flounder along salinity gradients. Targett and McCleave (1974) found smooth flounder to be abundant in the Sheepscott River–Back Bay River estuary, Maine, in salinities of 17.3–24.7 ppt. Fried (1973), studying the same estuary, found that smooth flounder were not present above 28.5 ppt, whereas winter flounder occurred throughout the salinity range sampled (12.5 to 32.5 ppt). Gordon and Dadswell (1984) found the greatest abundance of smooth flounder in "warm, turbid, low-salinity water" in the upper reaches of the Bay of Fundy. Smooth flounder larvae were most abundant in the low-salinity portion of the St. Lawrence River estuary (Powles et al., 1984). The conclusion of the present study, that the center of greatest abundance for smooth flounder is in the mesohaline part of the estuary, is in agreement with these previous studies.

Site 3 was the site of greatest abundance for winter flounder. Movements into site 2 were seen in late summer or early autumn in all years. Little information is available concerning the response of juvenile winter flounder to salinity gradients. Most studies on the distribution of winter flounder have considered only temperature or light as important abiotic factors that influence seasonal or short-term movements (McCracken, 1963; Oviatt and Nixon, 1973, Casterlin and Reynolds, 1982). Pearcy (1962) found a relatively homogeneous distribution of age-1 winter flounder throughout a salinity gradient in Mystic River Estuary, Connecticut, that was maintained through all seasons. However, his lowest salinity station was higher in salinity than both site 1 and site 2; therefore he did not sample habitats that might be only seasonably available. Pearcy (1962) also documented movement of young-of-the-year winter flounder from the lower estuary to the upper estuary during the summer months. Indirect evidence for similar movement by young-of-the-year winter flounder in Great Bay Estuary is presented here. No young-of-the-year winter flounder were caught in upper Great Bay until late summer and early autumn (Figs. 8 and 11), indicating an influx from the lower estuary. The lack of small winter flounder during the early part of the year was not an artifact of gear selectivity because young-of-the-year smooth flounder as small as 25 mm TL were caught, indicating that small young-of-the-year winter flounder would have been caught also if they had been present. Winter flounder spawn in the middle and lower portions of Great Bay Estuary and adjacent to the estuary in shallow coastal waters. Young-of-the-year winter flounder show little movement for a few months after metamorphosis (Saucerman, 1991); therefore it is not until they reach a larger size (30–50 mm TL) that they begin to move into the upper estuary.

Salinity is considered one of the most important factors affecting habitat use by estuarine fishes. The distributions and movements of several flatfish species including *Solea solea* (Coggan and Dando, 1988; Dorel et al., 1991), *Pleuronectes platessa* (Poxton and Nasir, 1985), and *Platichthys flesus* (Riley et al., 1981; Kerstan, 1991) have been correlated with salinity. A natural estuarine salinity gradient, in which habitats are categorized from benign to harsh in relation to tolerance by species, may serve as part of a continuum of physiological stress (Peterson and Ross, 1991). Species seeking to maximize growth must

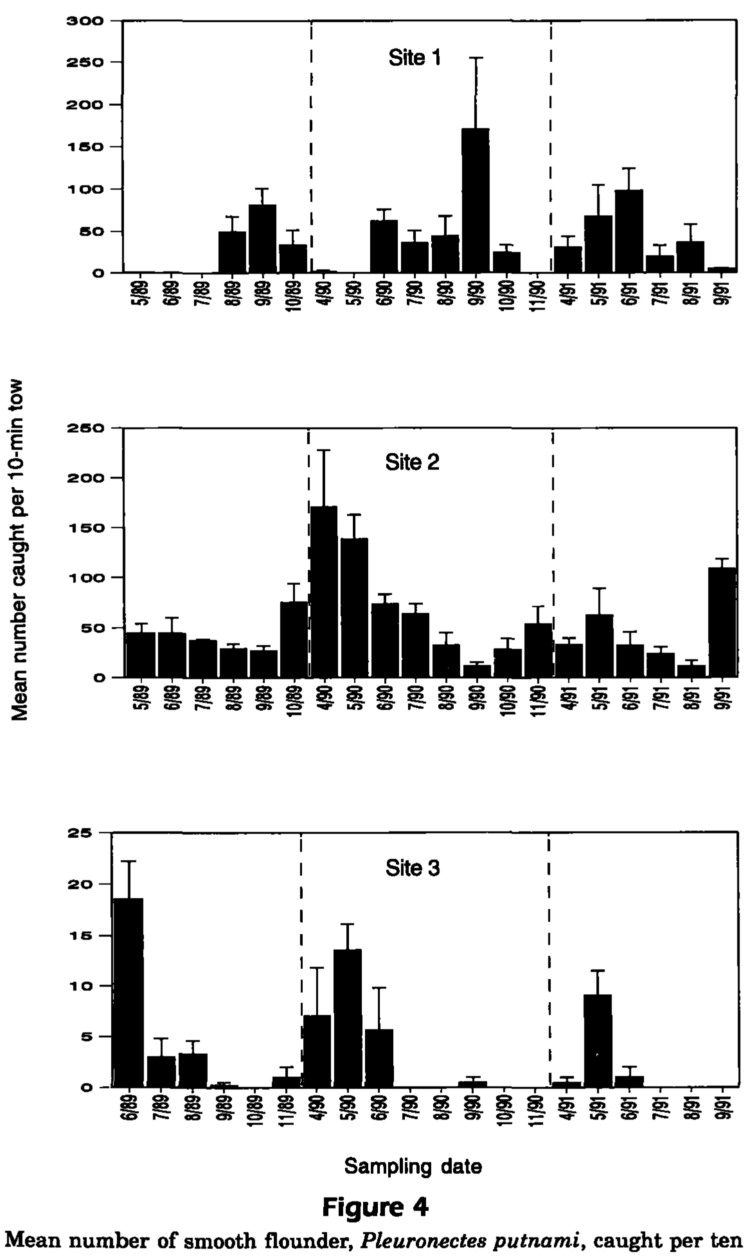

Figure 4

Mean number of smooth flounder, *Pleuronectes putnami*, caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire, May 1989–September 1991. Site 1 = oligohaline; site 2 = mesohaline; site 3 = polyhaline. Error bars are one standard error of the mean.

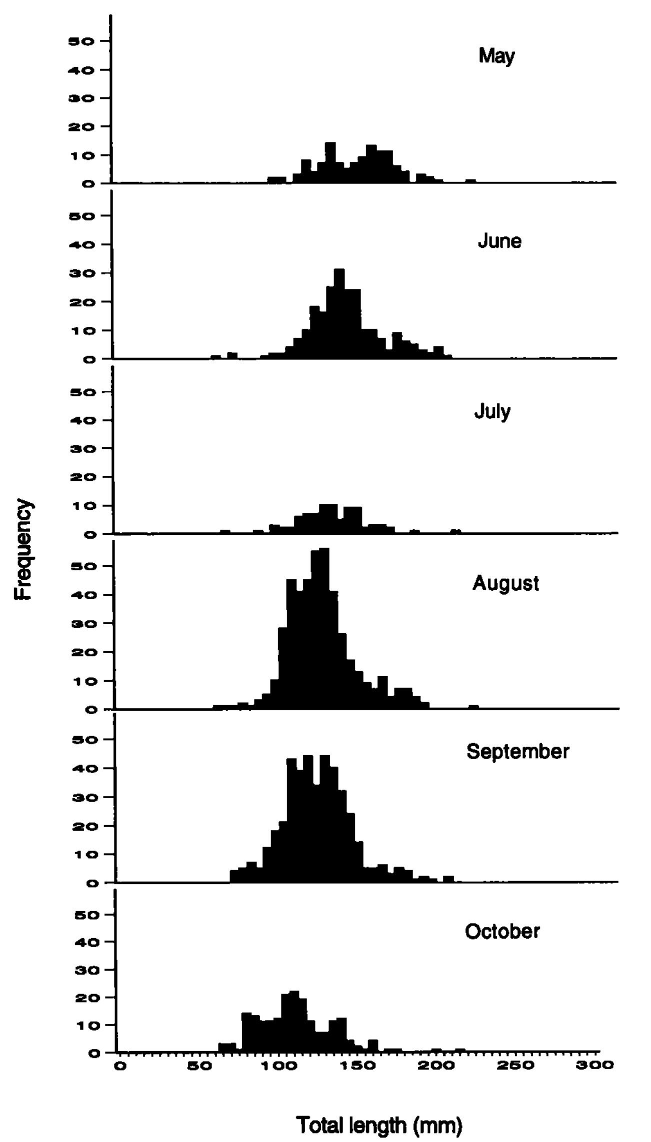

Figure 5

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, at site 1, pooled over 1989–91.

choose habitats that are of least cost bioenergetically. Several estuarine fish species have been found to be most abundant along a salinity gradient where their metabolic costs of osmoregulation were minimal, including *Ambassis* spp. (Martin, 1990), *Leiostomus xanthurus* and *Micropogonias undulatus* (Moser and Gerry, 1989), and *Paralichthys* spp. (Peters, 1971). Conversely, Peters and Boyd (1972) found that hogchokers, *Trinectes maculatus*, underwent movements that appeared physiologically disadvantageous. They concluded that other factors, in addition to salinity, must be considered. Salinity may provide a broad abiotic framework (Menge and Olson, 1990) within which biotic interactions, such as competition, predation, and prey abundance, can act to modify distributions.

Depth gradient

Smooth flounder showed clear segregation by size along the depth gradient. Larger (>100 mm TL) smooth flounder occurred primarily at the deep-water station (site 3). They were abundant only during April–June, before migrating upriver as salinity increased. Small numbers remained at site 4 throughout the summer and autumn. The tidal flats (site 5) and shallow bay (site 4) were important nursery areas for smooth flounder. Young-of-the-year smooth flounder did not show a dramatic decrease in abundance during the summer, as seen in the larger individuals, and did not appear to make a pronounced seasonal up-estuary movement. Their inferior swimming ability, compared with that of larger individuals, or their inability to osmoregulate efficiently in lower salinity areas may underlie their relatively stationary habits. The tendency for smooth flounder to segregate by size, with the smaller individuals occurring in the intertidal and shallow subtidal areas, has been found in several other flatfish species including English sole, *Parophrys vetulus* (Toole, 1980), and European plaice, *Pleuronectes platessa* (Gibson, 1973; Kuipers, 1973). Segregation by size may reduce intraspecific competition. The intertidal zone may also function as a refuge from predators for small flatfish or as an abundant source of appropriate-size prey items (Toole, 1980). Ruiz et al. (1993) found that shallow water functioned as a refuge from size-selective predation on juveniles of several species of fish and crustaceans in Chesapeake Bay. Van der Veer and Bergmann (1986) found that young-of-the-year European plaice used tidal flats as a refuge from predators rather than for feeding purposes. Potential predators on smooth flounder in Great Bay Estuary include sand shrimp (*Crangon septemspinosus*), grubbies (*Myoxocephalus aeneus*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), white perch (*Morone americanus*), great blue heron (*Ardea herodias*), and double-crested cormorants (*Phalacrocorax auritus*). Predation by large piscine predators is probably reduced in shallow water, and avian predation is likely increased. Sand shrimp were abundant in trawl samples from both channel and flats areas. The value of tidal flats as refugia from predation cannot be assessed without knowledge of the relative rates of predation by these different predatory groups.

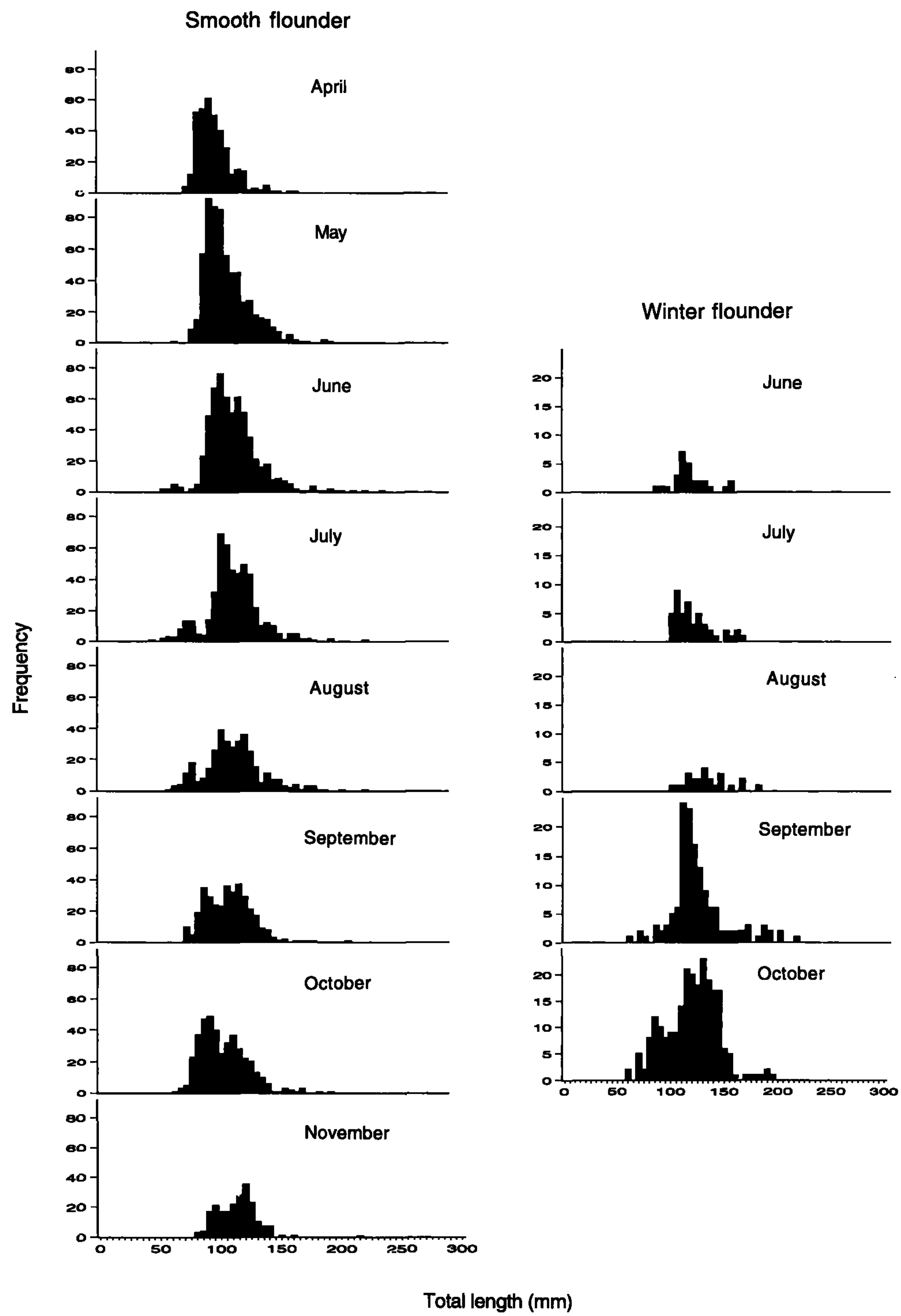

Figure 6

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, and winter flounder, *P. americanus* at site 2, pooled over 1989–91.

Winter flounder showed little segregation by size along the depth gradient. This finding is in contrast with other studies, which have shown that juvenile winter flounder segregate by size along depth gradients according to differential preferences to temperature and light intensity, with smallest individuals found

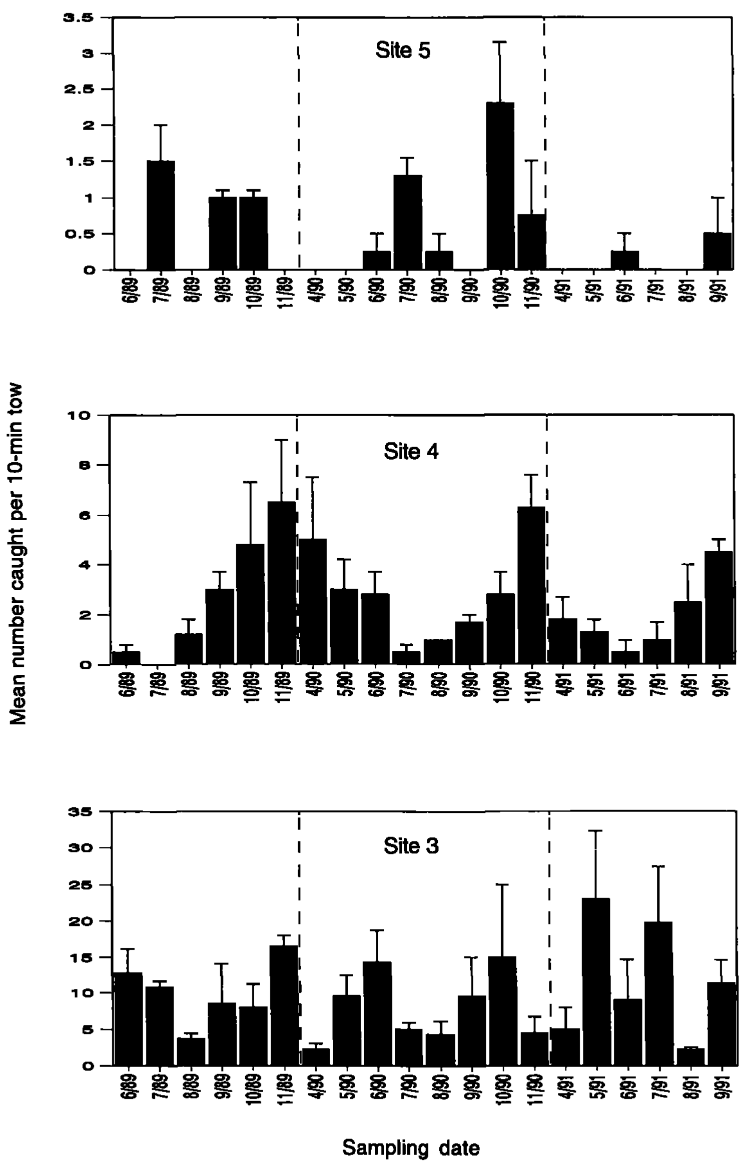

Figure 7

Mean number of winter flounder, ***Pleuronectes americanus***, caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire, May 1989–September 1991. Site 1=oligohaline; site 2=mesohaline; site 3=polyhaline. Error bars are one standard error of the mean.

at higher temperatures and light intensities (see reviews in Klein-MacPhee, 1978; Casterlin and Reynolds, 1982). It is especially interesting that winter flounder showed relatively little use of the intertidal flats. Tyler (1971), Wells et al. (1973), and Black and Miller (1991), however, found that winter flounder used intertidal flats extensively. Their studies took place in areas of higher salinity where no smooth flounder occurred. Their finding suggests that competition with smooth flounder may be a possible reason for the near absence of winter flounder from the intertidal flats habitat in Great Bay. Targett and McCleave (1974) found that the tidal mudflats in Montsweag Bay, Maine, were dominated by smooth flounder, whereas Fried (1973) found that the channel areas in the same estuary were dominated by winter flounder. Fried (1973) felt that the tidal mudflats offered smooth flounders a refugium from competition with winter flounder and that winter flounder were unable to use this habitat type for reasons other than competition with smooth flounder.

Temperature may be a factor in the winter flounder's avoidance of tidal mudflats. Hoff and Westman

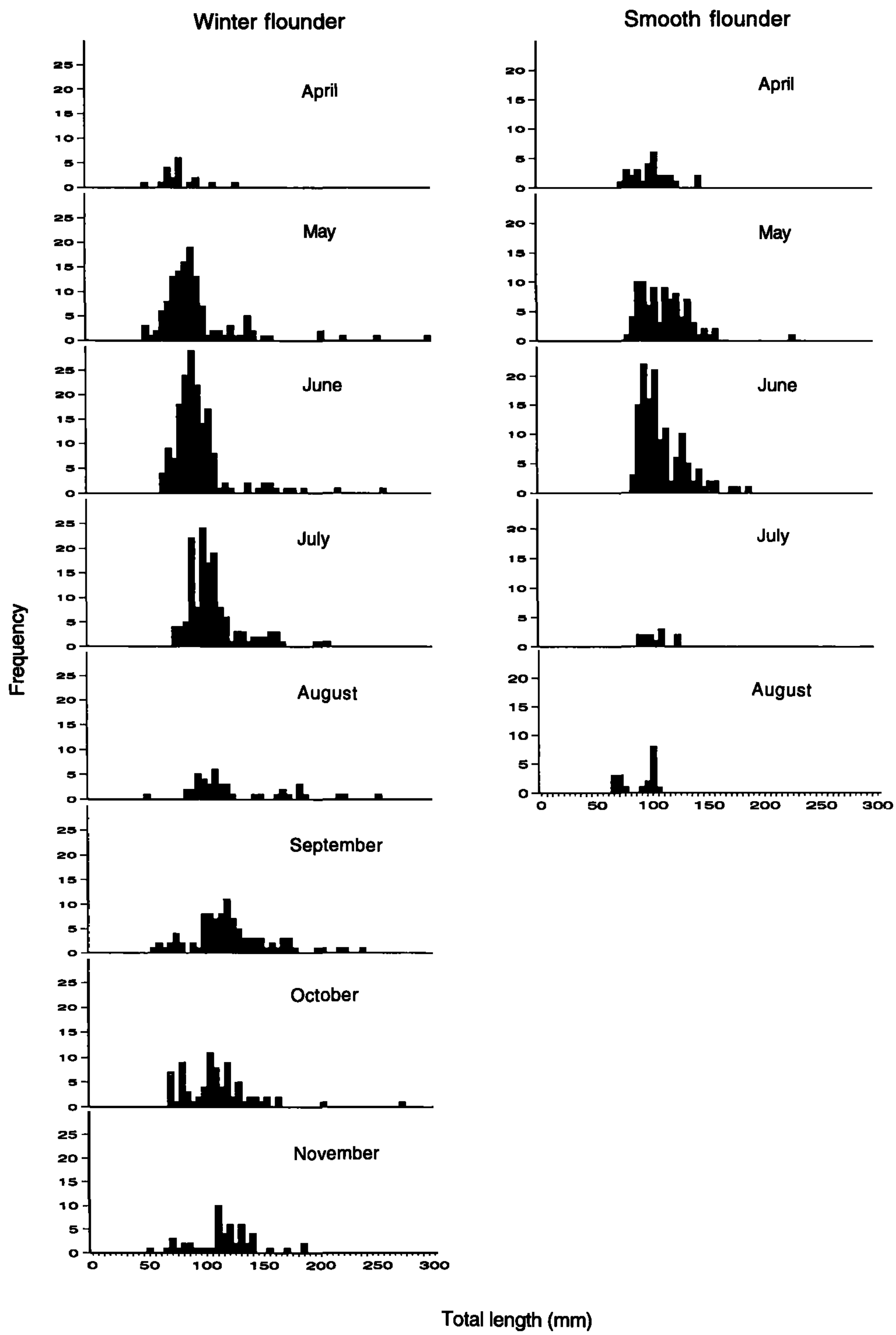

Figure 8

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, and winter flounder, *P. americanus*, at site 3, pooled over 1989–91.

(1966) found that winter flounder, acclimated to 21°C, had an upper lethal temperature of 27°C. Pearcy (1962) found an upper lethal temperature of 30°C for flounder collected during the summer in Mystic River Estuary. Olla et al. (1969) observed that winter flounder exposed to temperatures above 22.2°C. buried themselves in sediment and ceased to feed. Although comparable data do not exist for smooth flounder, Huntsman and Sparks (1924) reported that upper lethal temperatures for smooth flounder were 2–4°C higher than those for winter flounder. In Great Bay Estuary, temperature may be a factor in determining the relative distribution of the two species in late summer when water temperatures at site 5 reached 22–24.2°C but would not be a factor during most of the year. The low abundance of winter flounder at site 5 persisted during times of the year when temperature would not seem to be limiting.

Subtrate preference may play a role in excluding winter flounder from intertidal flats in Great Bay Estuary. Although the bottom type appeared similar (silty mud) at all three sites along the depth gradient (Table 1), this similarity was based on gross examination of core samples. No detailed sediment size analysis was conducted for this study (nor in Fried [1973] or Targett and McCleave [1974]), and therefore differences in sediment structure may have been present between sites but not noted on a gross scale. Sogard (1992) found that growth of winter flounder was negatively correlated with percent silt; faster growth occurred in sandier sediments. Bigelow and Schroeder (1953) found that winter flounder were more abundant on coarser sediments, in comparison with smooth flounder which were more abundant in muddier sediments. Thus, if the channel areas of Great Bay Estuary have coarser sediments than the intertidal flats, perhaps the coarser sediment may explain the difference in distribution along the depth gradient.

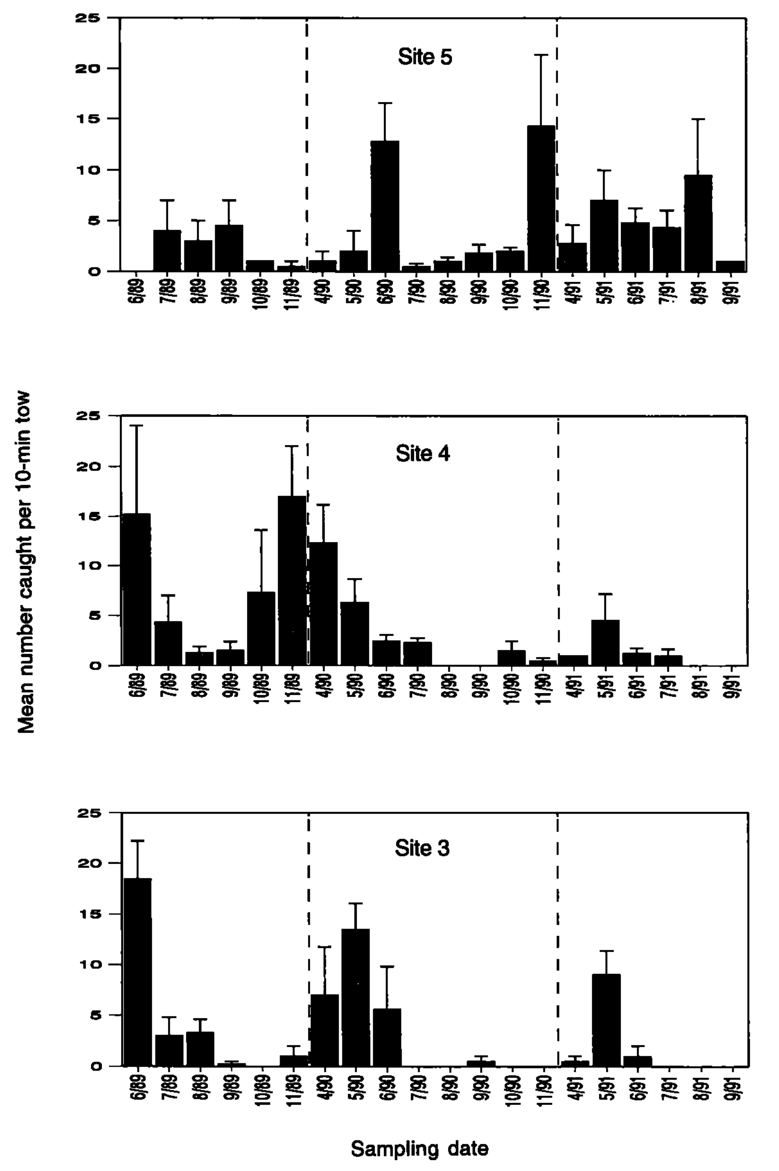

Figure 9

Mean number of smooth flounder, *Pleuronectes putnami*, caught per ten minute tow at three sites along a depth gradient in Great Bay Estuary, New Hampshire. Mean depth was greatest at site 3 (mean=6.2 m) followed by site 4 (2.1 m) and then site 5 (1.5 m). Error bars are one standard error of the mean.

Summary

Smooth and winter flounder are partially segregated as species along salinity and depth gradients in upper Great Bay Estuary. It appears that this is due to differential responses to the physical and chemical regime, but the effects of seasonal changes in biotic interactions cannot be excluded. Smooth and winter flounder feed on similar prey items in Great Bay Estuary (Laszlo, 1972; Armstrong, 1995). Competition or movements related to prey abundance may influence their respective distributions. There are many instances where com-

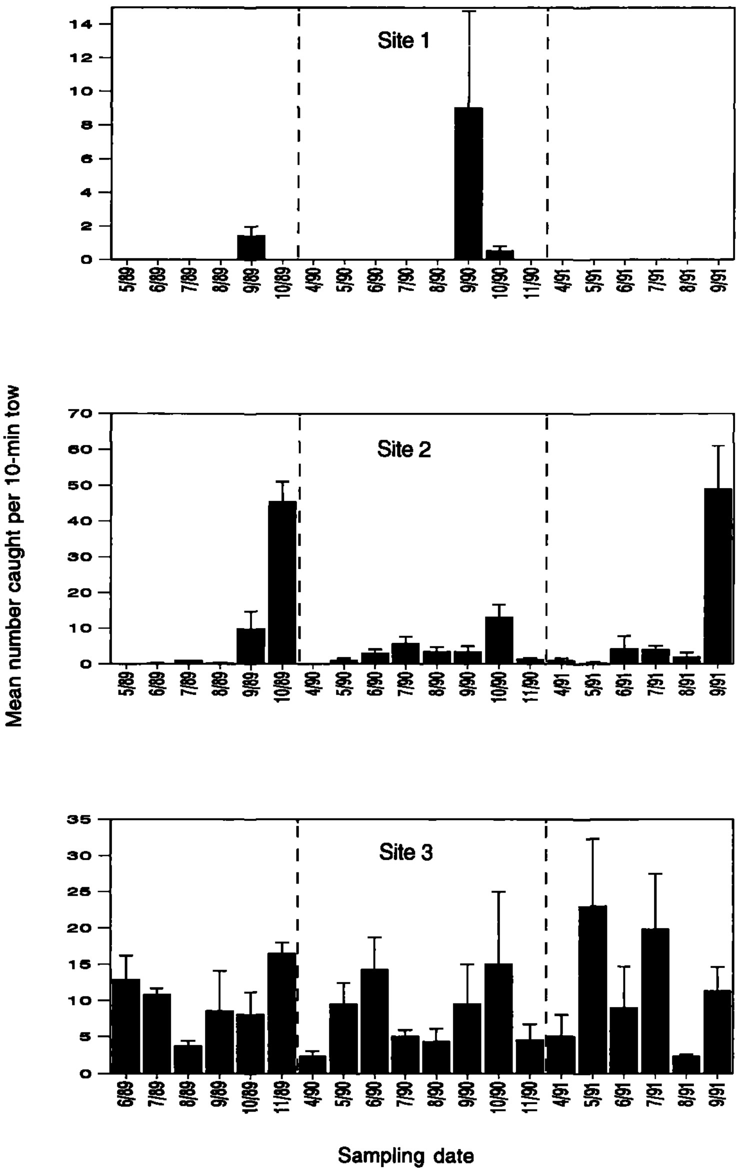

Figure 10

Mean number of winter flounder, *Pleuronectes americanus*, caught per ten minute tow at three sites along a depth gradient in Great Bay Estuary, New Hampshire. Mean depth was greatest at site 3 (mean=6.2 m) followed by site 4 (2.1 m) and then site 5 (1.5 m). Error bars are one standard error of the mean.

petition appears to play a role in the distribution of ecologically similar species along environmental gradients (Connor and Bowers, 1987). In Great Bay Estuary, low salinity and intertidal flats appear to provide at least a partial refugium for smooth flounder from competition with winter flounder.

The relation between smooth and winter flounder changes on a seasonal basis. At times their segregation on a spatial scale is nearly complete, whereas at other times, particularly April–June at site 3 and September–October at site 2, they overlap considerably. Competition theory predicts that niches should vary temporally as a function of resource abundance and of the population densities of potential competitors (Llewellyn and Jenkins, 1987). The predominant temporal pattern of niche overlap seen in studies is increased overlap during resource abundance (Schoener, 1982; Ross, 1986). The periods of great-

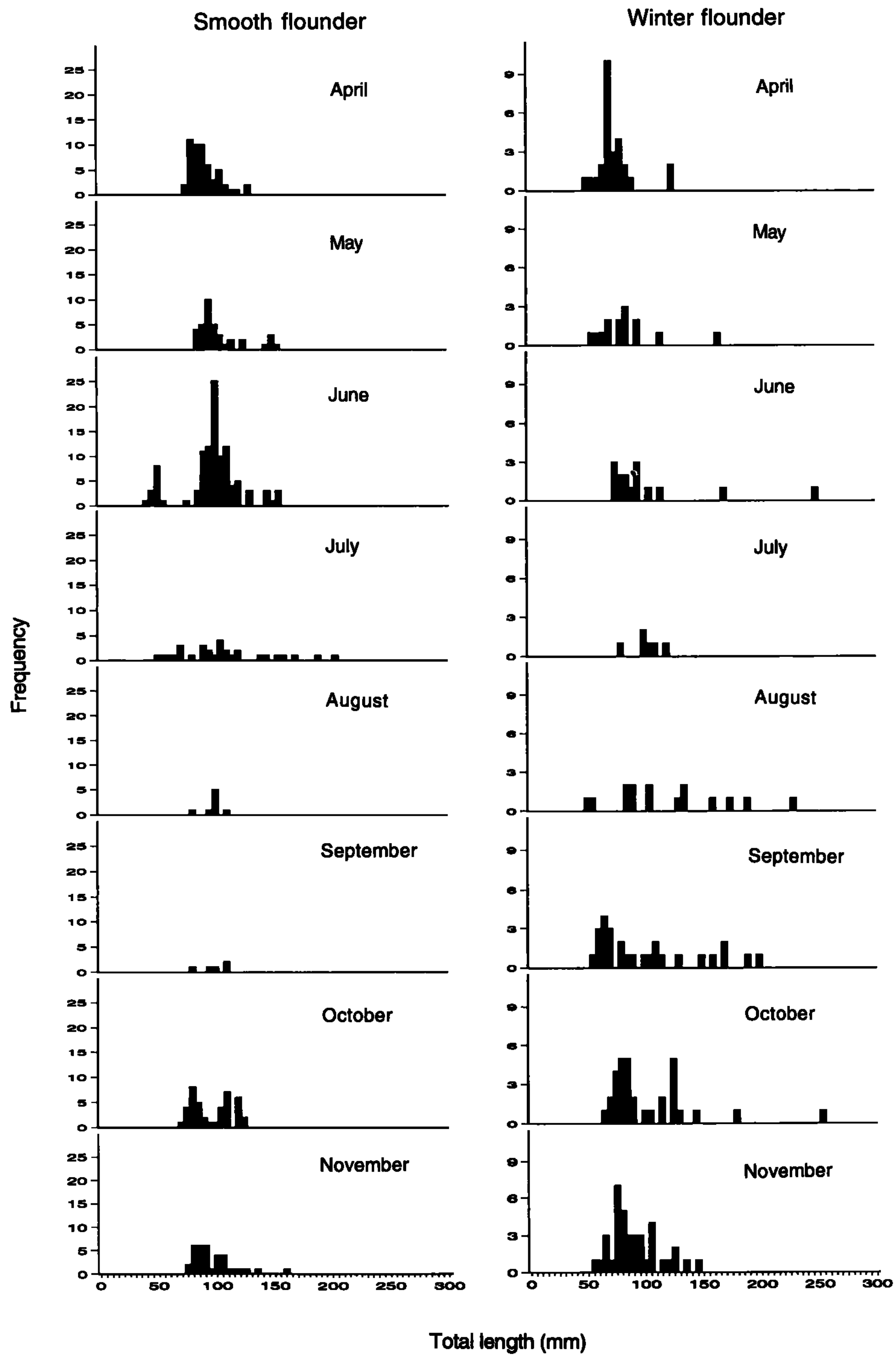

Figure 11

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, and winter flounder, *P. americanus*, at site 4, pooled over 1989–91.

est overlap in habitat use seen for smooth and winter flounder may be associated with an abundance of some resource, for example, a shared prey item(s).

The upper Great Bay Estuary is an important area for both species. This study has shown the dynamic nature of habitat use by smooth and winter flounder. Further studies are needed to assess experimentally the relative importance of abiotic versus biotic factors in determining the patterns of smooth and winter flounder spatial distributions.

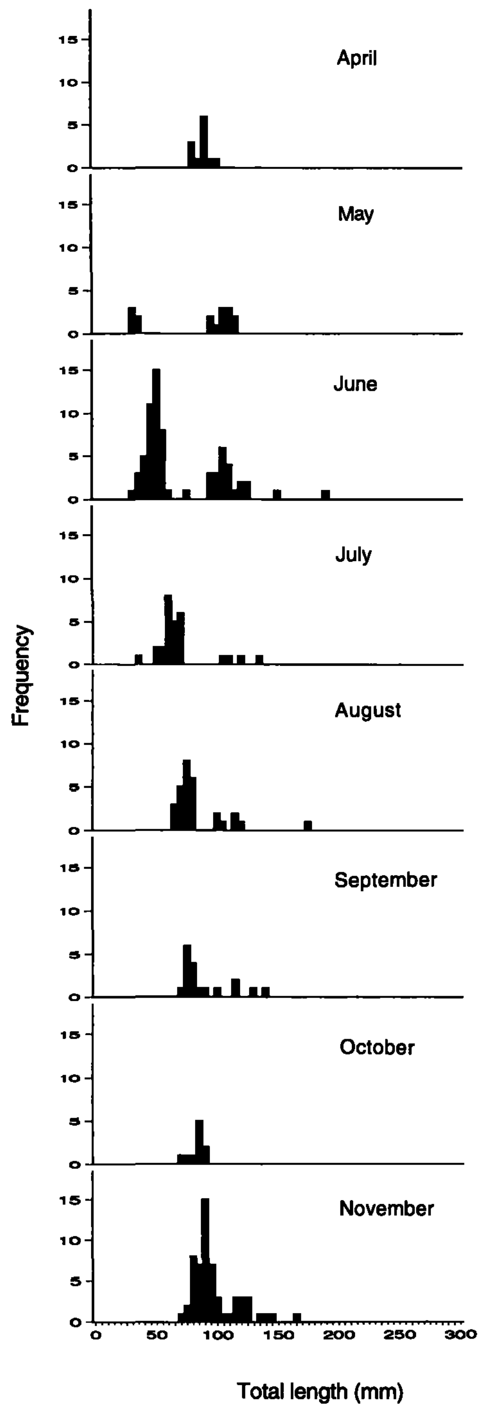

Figure 12
Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, at site 5, pooled over 1989–91.

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Literature cited

Armstrong, M. P.
1995. A comparative study of the ecology of smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, from Great Bay Estuary, New Hampshire. Ph.D. diss., Univ. New Hampshire, Durham, NH, 147 p.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull. 53, 577 p.

Black, R., and R. J. Miller.
1991. Use of the intertidal zone by fish in Nova Scotia. Environ. Biol. Fishes 31:109–121.

Casterlin, M. E., and W. W. Reynolds.
1982. Thermoregulatory behavior and diel activity of yearling winter flounder, *Pseudopleuronectes americanus* (Walbaum). Environ. Biol. Fishes 7(2):177–180.

Coggan, R. A., and P. R. Dando.
1988. Movements of juvenile Dover sole, *Solea solea* (L.), in the Tamar Estuary, south-western England. J. Fish Biol. 33:177–184.

Connor, E. F., and M. A. Bowers.
1987. The spatial consequences of interspecific competition. Ann. Zool. Fenn. 24:213–226.

Dorel, D., C. Koutsikopoulos, Y. Desaunay, and J. Marchand.
1991. Seasonal distribution of young sole (*Solea solea* L.) in the nursery ground of the Bay of Vilaine (northern Bay of Biscay). Neth. J. Sea Res. 27:4297–4306.

Dovel, W. L., J. A. Mihursky, and A. J. McErlean.
1969. Life history aspects of the hogchoker, *Trinectes maculatus*, in the Patuxent River estuary, Maryland. Chesapeake Sci. 10(2):104–119.

Fried, S. M.
1973. Distribution of demersal fishes in Montsweag Bay-Back River and lower Sheepscot River estuaries, Wiscaccet, Maine. M.S. thesis, Univ. Maine, Orono, ME, 47 p.

Gibson, R. N.
1973. The intertidal movements of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa*). J. Exp. Mar. Biol. Ecol. 12:79–102.

Gordon, D. C., and M. J. Dadswell.
1984. Update on the marine environmental consequences

of tidal power development in the upper reaches of the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1256, 292 p.

Hanson, J. M., and S. C. Courtenay.
1996. Seasonal use of estuaries by winter flounder in the southern Gulf of St. Lawrence. Trans. Am. Fish. Soc. 125:705–718.

Hoff, J. G., and J. R. Westman.
1966. The temperature tolerance of three species of marine fishes. J. Mar. Res. 24(2):131–140.

Huntsman, A. G., and M. I. Sparks.
1924. Limiting factors for marine animals. 3: Relative resistance to high temperatures. Contrib. Can. Biol., N. S. 2(6):97–114.

Jackson, C. F.
1922. Ecological features of Great Bay, New Hampshire, and a preliminary checklist of fishes. Ecology 3(1):48–54.

Kerstan, M.
1991. The importance of rivers as nursery grounds for 0- and 1- group flounder (*Platichthys flesus* L.) in comparison to the Wadden Sea. Neth. J. Sea Res. 27:353–366.

Klein-MacPhee, G.
1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 414, 43 p.

Kuipers, B.
1973. On the tidal migrations of young plaice (*Pleuronectes platessa*) in the Wadden Sea. Neth. J. Sea Res. 6:376–378.

Laszlo, P. T.
1972. Age-growth, food, and reproduction of the smooth flounder, *Liopsetta putnami* (Gill), in Great Bay, New Hampshire. Ph.D. diss., Univ. New Hampshire, Durham, NH, 75 p.

Llewellyn, J. B., and S. H. Jenkins.
1987. Patterns of niche shift in mice: seasonal changes in microhabitat breadth and overlap. Am. Nat. 129(3):365–381.

Martin, T. J.
1990. Osmoregulation in three species of Ambassidae (Osteichthyes: Perciformes) from estuaries in Natal. S. Afr. J. Zool. 25(2):229–234.

McCracken, F. D.
1963. Seasonal movements of the winter flounder, *Pseudopleuronectes americanus*, on the Atlantic coast. J. Fish. Res. Board Can. 20(2):551–585.

Menge, B. A., and A. M. Olson.
1990. Role of scale and environmental factors in regulation of community structure. Trends Ecol. & Evol. 5:52–57.

Moser, M. L., and L. R. Gerry.
1989. Differential effects of salinity changes on two estuarine fishes, *Leiostomus xanthurus* and *Micropogonias undulatus*. Estuaries 12(1):35–41.

Olla, B. L., R. Wicklund, and S. Wilk.
1969. Behavior of winter flounder in a natural habitat. Trans. Am. Fish. Soc. 4:717–720.

Oviatt, C. A., and S. W. Nixon.
1973. The demersal fish of Narragansett Bay: an analysis of community structure, distribution and abundance. Estuarine Coastal Mar. Sci. 1:361–378.

Pearcy, W. G.
1962. Ecology of an estuarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum). Bull. Bingham Oceanogr. Collect. Yale Univ. 18(1), 78 p.

Peters, D. S.
1971. Growth and energy utilization of juvenile flounder, *Paralichthys dentatus* and *Paralichthys lethostigma*, as affected by temperature, salinity, and food availability. Ph.D. diss., North Carolina State Univ., Raleigh, NC, 69 p.

Peters, D. S., and M. T. Boyd.
1972. The effect of temperature, salinity, and availability of food on the feeding and growth of the hogchoker, *Trinectes maculatus* (Block and Schneider). J. Exp. Mar. Biol. Ecol. 7:201–207.

Peterson, M. S., and S. T. Ross.
1991. Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. Estuarine Coastal Shelf Sci. 33:467–483.

Powles, H., F. Auger, and G. J. Fitzgerald.
1984. Nearshore ichthyoplankton of a north temperate estuary. Can. J. Fish. Aquat. Sci. 41:1653–1663.

Poxton, M. G., and N. A. Nasir.
1985. The distribution and population dynamics of 0-group plaice (*Pleuronectes platessa* L.) on nursery grounds in the Firth of Forth. Estuarine Coastal Shelf Sci. 21:845–857.

Riley, J. D., D. J. Symonds, and L. Woolner.
1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:223–228.

Ross, S. T.
1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2:352–388

Ruiz, G. M., A. H. Hines, and M. H. Posey.
1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99:1–16.

Saucerman, S. E., and L. A. Deegan.
1991. Lateral and cross-channel movement of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) in Waquoit Bay, Massachusetts. Estuaries 14(4):440–446.

Schoener, T. W.
1982. The controversy over interspecific competition. Am. Sci. 70:586–595.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Short, F. T. (ed.).
1992. The ecology of the Great Bay Estuary, New Hampshire and Maine: an estuarine profile and bibliography. U.S. Dep. Commer., NOAA-Coastal Ocean Program Publ., 222 p. Available from the Great Bay National Estuarine Research Reserve, Durham, NH.

Smith, S. M.
1986. Reproductive ecology, population dynamics and seasonal movements of the hogchoker (*Trinectes maculatus*) in the Elizabeth River, Virginia. M.S. thesis, College of William and Mary, Williamsburg, VA, 83 p.

Sogard, S. M.
1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser. 85:35–53.

Targett, T. E., and J. D. McCleave.
1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Am. Fish. Soc.103(2):325–330.

Terborgh, J.
1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:2–40.

Toole, C. L.
1980. Intertidal recruitment and feeding in relation to op-

timal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Environ. Biol. Fishes 5(4):38–390.

Turgeon, D. D.
1976. Distribution of the planktonic larvae of some benthic invertebrates within the Piscataqua-Great Bay Estuary, New Hampshire. Ph.D. diss., Univ. New Hampshire, Durham, NH, 165 p.

Tyler, A. V.
1971. Surges of winter flounder *Pseudopleuronectes americanus* into the intertidal zone. J. Fish. Res. Board Can. 28(11):1717–1732.

van der Veer, H. W., and M. J. N. Bergmann.
1986. Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 31(2):121–129.

Wells, B., D. H. Steele, and A. V. Tyler.
1973. Intertidal feeding of winter flounders (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30:1374–1378.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ, 718 p.