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A comparative study of the ecology of smooth flounder, Pleuronectes putnami, and winter flounder, Pleuronectes americanus, from Great Bay Estuary, New Hampshire

Michael Patrick Armstrong
University of New Hampshire, Durham

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A COMPARATIVE STUDY OF THE ECOLOGY OF SMOOTH FLOUNDER, *PLEURONECTES PUTNAMI*, AND WINTER FLOUNDER, *PLEURONECTES AMERICANUS*, FROM GREAT BAY ESTUARY, NEW HAMPSHIRE

BY

MICHAEL PATRICK ARMSTRONG
B.S., Southeastern Massachusetts University, 1980
M.A., College of William and Mary, 1987

DISSERTATION

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in Partial Fulfillment of
the Requirements for the Degree of

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This dissertation has been examined and approved.

W. Huntting Howell

Dissertation Director, Dr. W. Huntting Howell,
Associate Professor of Zoology

Larry G. Harris

Dr. Larry G. Harris, Professor of Zoology

Dr. James T. Taylor, Associate Professor
of Zoology

Dr. Peter F. Sale, Professor of Biology
University of Windsor

Dr. John A. Musick, Professor of Marine Science
College of William and Mary

April 26, 1995
Date

DEDICATION

This dissertation is dedicated to my mother, Pauline R. Armstrong, and the memory of my father, Paul P. Armstrong. You were always there when I needed you.

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ABSTRACT

A COMPARATIVE STUDY OF THE ECOLOGY OF SMOOTH FLOUNDER, *PLEURONECTES PUTNAMI*, AND WINTER FLOUNDER, *PLEURONECTES AMERICANUS*, FROM GREAT BAY ESTUARY, NEW HAMPSHIRE

by

Michael P. Armstrong
University of New Hampshire, May, 1995

Smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, co-occur in estuaries along the east coast of North America from Labrador to Massachusetts. Results of a three year sampling program indicated that the two species were partially segregated along salinity and depth gradients in upper Great Bay Estuary, New Hampshire. Along the salinity gradient, smooth flounder were most abundant at the oligo-mesohaline riverine habitat while winter flounder were most abundant at the meso-polyhaline open bay habitat. Both species exhibited a generalized up-river movement with seasonally increasing salinity. Smooth flounder showed ontogenetic changes in distribution along the depth gradient, with the smallest individuals occupying the shallowest depths. Intertidal mudflats were an important nursery area for young-of-year smooth flounder but not for young-of-year winter flounder.

Laboratory and field experiments demonstrated that the distribution of smooth and winter flounder in Great Bay Estuary was based primarily, although not completely, on physiological constraints related to salinity. For smooth flounder, growth and survival were best in 12‰ and 22‰, while for winter flounder, growth and survival were best at 22‰ and 32‰. Both flounder species occupied sites along the salinity gradient that were metabolically least costly.

Seasonal changes in resource use were examined at several estuarine sites. Smooth and winter flounder had similar diets and showed greater overlap in diet than in habitat use. Important prey types included the polychaetes *Streblospio benedicti* and *Scolecolepides viridis*, siphons of the bivalve *Macoma balthica*, and gammarid amphipods. Prey abundance changed seasonally and appeared to play a role in affecting the distribution of smooth and winter flounder. Differences in diet among estuarine sites reflected differences in the benthic fauna at these sites. Even though their diets were similar, there were no consistent patterns in niche metrics to suggest that food was limiting to smooth and winter flounder in upper Great Bay Estuary.

INTRODUCTION

The study of relationships between closely related, co-occurring species can provide meaningful insight into what forces structure ecological communities. The first step in studying relationships is to look for patterns and to characterize the dynamics of the relationship. This is done by studying both the basic ecology of the subjects including abundance, distribution and relation to abiotic factors, and the changes in the resources and habitats they depend on. Subsequently, an understanding of the processes that underlie these patterns and dynamics must be developed.

Great Bay Estuary, New Hampshire provides an opportunity to explore the relationship between two closely related species; smooth flounder, Pleuronectes putnami (Gill), and winter flounder, Pleuronectes americanus (Walbaum). On a gross scale, these two flatfish species (Family:Pleuronectidae) are morphologically and ecologically very similar. They are sympatric from Newfoundland to Massachusetts Bay. Preliminary sampling has shown both occur in significant numbers in the upper Great Bay Estuary, often accounting for a majority of the fish biomass present.

Smooth flounder have been relatively unstudied because they are small and commercially unimportant, and because they reside in boreal estuaries where little sampling has occurred. Most of the information available is general in nature and contained in faunal summaries such as Bigelow and Schroeder (1953) and Scott and Scott (1988). Smooth flounder occur along the east coast of North America from about Ungava Bay, Labrador southward to Massachusetts Bay (Scott and Scott, 1988). It is strictly an inshore fish, inhabiting shallow estuaries, river mouths and sheltered bays (Bigelow and Schroeder, 1953; Scott and Scott, 1988). Smooth flounder were first reported from Great Bay Estuary by Jackson (1922) who noted they were commonly found at the head of tidewater. It is the smallest common flatfish in the Gulf of Maine area, reaching sexual maturity between 85-100 mm TL (total length) and a maximum size of about 300 mm TL (Armstrong and Starr, 1994). Spawning in Great Bay extends from early December through February (Laszlo, 1972; Laroche, 1981) with fecundity ranging from 4,000-50,000 ova (Armstrong and Starr, 1994). Scott and Scott (1988) state that the food habits of smooth flounder are similar to those of winter flounder. Laszlo (1972) compared the diets of smooth and winter flounder from Great Bay Estuary and found them to concentrate on different prey. He concluded that there was no competition for food between these two species, however, his sample sizes were extremely small and sampling design incomplete. Little is known of the movements and migrations of smooth flounder, or their distribution and abundance within estuaries. Burn (1980) suggested that they spend their entire life in the upper estuary, based on parasitological evidence.

Winter flounder have been studied extensively because of their great commercial and recreational value. Summaries of life history information are available in Klein-MacPhee (1978) and Buckley (1989). Winter flounder occur from southern Labrador to about Chesapeake Bay and can be found from the tideline down to 143 m (McCracken, 1963). They reach sexual maturity at about 250 mm TL and a maximum size of 500 mm TL. Spawning takes place in estuaries and coastal areas from February to May depending on latitude (Bigelow and Schroeder, 1953). Winter flounder appear to feed opportunistically, eating whatever prey item is locally abundant, particularly polychaete worms, bivalves, small crustaceans and plant material (Klein-MacPhee, 1978). Movements and migrations have been studied extensively in winter flounder (e.g. Saila, 1961; Pearcy, 1962; McCracken, 1963; Kennedy and Steele, 1971; Tyler, 1971; Howe and Coates, 1975; Saucerman, 1990; Phelan, 1992). The general trend for adults in the Gulf of Maine is an offshore movement in summer when the water temperature reaches about 15°C. and an onshore movement in autumn. The movements of juveniles in the Gulf of Maine have not been characterized.

The purpose of this study was to compare the ecology of these two similar flatfish species in Great Bay Estuary, New Hampshire. The study examined the distribution, abundance and feeding habits of smooth and winter flounder, and the changes in these attributes along spatial and temporal scales. Physiological responses of these species to various salinities was also examined in an attempt to explain the patterns observed in the field. The study was divided into three sections: SECTION I- "Seasonal and ontogenetic changes in habitat use by smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, along estuarine depth and salinity gradients"; SECTION II- "The role of salinity in determining the estuarine distribution of smooth and winter flounder"; and SECTION III- "Diet and niche dynamics in two sympatric estuarine flounders".

The study was conducted in Great Bay Estuary, New Hampshire (Figure 1.1). Great Bay Estuary is a complex embayment composed of the Piscataqua River, Little Bay and Great Bay. The estuary is a tidally dominated system and the drainage confluence of seven major rivers, several small creeks and water from the Gulf of Maine (Short, 1992). Great Bay Estuary is a drowned river valley, with high tidal energy and characteristic deep channels with fringing mud flats. The estuary was formed during the most recent deglaciation of the area, approximately 14,500 years ago (Short, 1992). The total drainage is 2,409 km^2. 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, herein referred to as Great Bay, although preliminary sampling took place in lower sections of the estuary also. Great Bay extends southward from Furber Strait (Figure 1.1). It is a large, shallow estuarine 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 2.0 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 areal surface of Great Bay is exposed mud or eelgrass flat at low tide. The Squamscott and Lamprey Rivers are the major source of freshwater input to Great Bay. River flow varies considerably on a seasonal basis, generally highest during spring run-off. However, freshwater input typically represents only 2% or less of the tidal prism (Brown and Arellano, 1979). Vertical stratification of Great Bay is rare because of strong tidal and wind induced currents, although partial stratification may occur during periods of high freshwater run-off, particularly at the upper tidal reaches of rivers (Short, 1992).

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I. SEASONAL AND ONTOGENETIC CHANGES IN DISTRIBUTION AND ABUNDANCE OF SMOOTH FLOUNDER, *PLEURONECTES PUTNAMI*, AND WINTER FLOUNDER, *PLEURONECTES AMERICANUS*, ALONG ESTUARINE DEPTH AND SALINITY GRADIENTS.

Introduction

Smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, are dominant members of the fish communities in boreal estuaries along the east coast of North America, co-occurring from about Newfoundland to Massachusetts Bay. Although these two morphologically similar species are known to be sympatric over much of their geographic ranges, little is known of their overlap in distribution on an estuarine spatial scale. Smooth flounder complete their entire life cycle within estuaries. Winter flounder primarily utilize estuaries as nursery grounds, with the adults spending most of their lives in coastal waters (Bigelow and Schroeder, 1953; Pearcy, 1962; Scott and Scott, 1988). Smooth flounder are reported to prefer softer bottom substratum than winter flounder (Bigelow and Schroeder, 1953) and Jackson (1922) noted they were most abundant at the head of tidewater in Great Bay Estuary, but little else is known of their intra-estuarine 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,1990). However, because more northern estuaries differ considerably from those south of Cape Cod, most obviously in their temperature regimes, it is possible juvenile winter flounder utilize the northern estuaries differently than the southern ones.

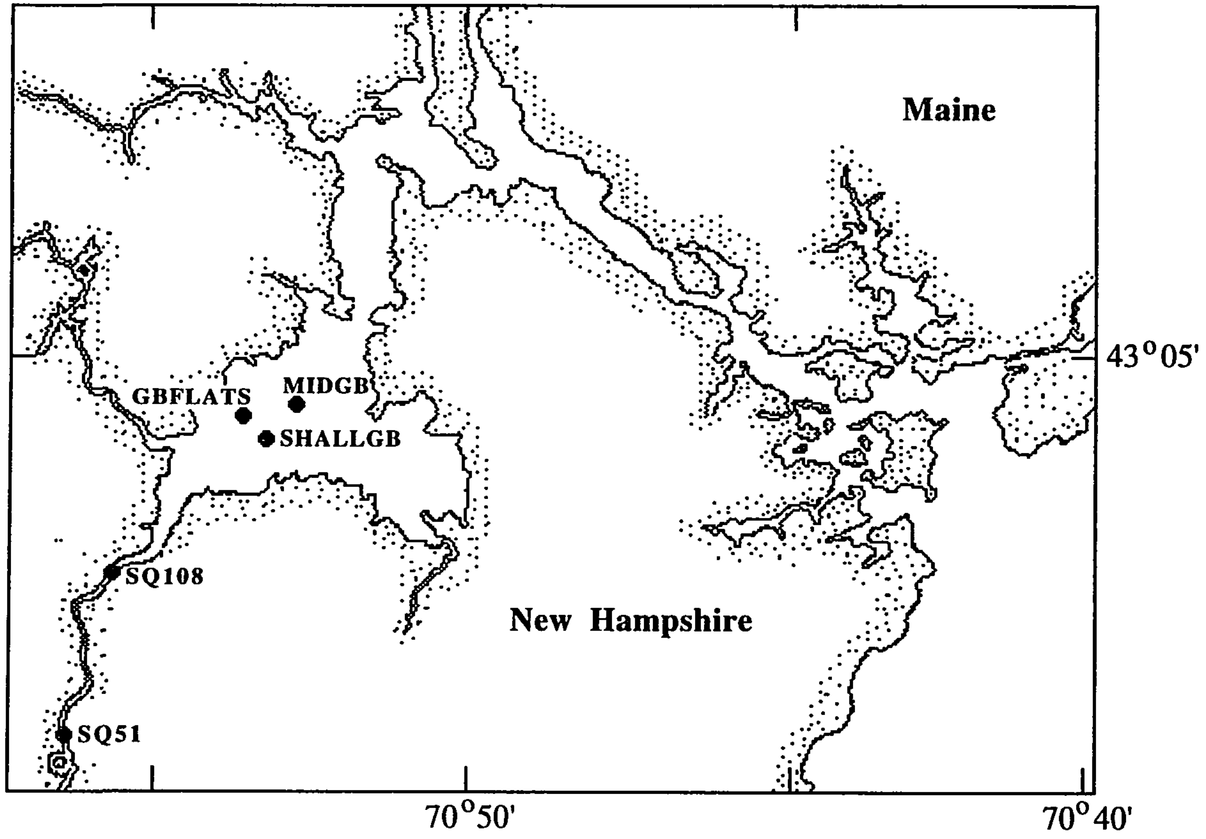
The purpose of this study was to provide a quantitative comparison of the use of various habitats in upper Great Bay Estuary by smooth and winter flounder. The habitats examined represent two gradients defined by depth or salinity. The distribution of species along such gradients has long been of interest to ecologists. Comparative studies of habitat use can help define what habitats are important to a species, especially when considering different life history stages. Gradient analysis 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 over 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 and Materials

Smooth and winter flounder were sampled monthly from May, 1989 through September, 1991 at five sites in upper Great Bay Estuary. Ice cover prevented sampling from December through March in all study years. A 4.8 m otter trawl was used for all sampling. The body of the net contained 38 mm stretch mesh and the codend contained 25 mm stretch mesh with a 6 mm liner. Preliminary studies indicated the net retained juvenile flounder as small as 25 mm TL. One sample consisted of all the flounder retained when the net was towed for ten minutes at 2.5 knots. 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, for a total of four samples/site/month. All flounder collected were measured to the nearest mm total length. Bottom temperature and salinity were measured after each tow using a Beckman Model 510 temperature, conductivity, salinity meter.

Sites SQ51 (Squamscott River at Route 51), SQ108 (Squamscott River at Route 108) and MIDGB (Middle Great Bay) were located along a salinity gradient formed by Great Bay Estuary and one of its major tributaries (Figure 1.1). 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 of the physical characteristics of these locations. SQ51 was located in the Squamscott River about four kilometers above the mouth. While the river is still tidal in this area, the water is often fresh or extremely low in salinity. SQ108 is also located in the Squamscott River but only 0.5 km above the

Figure 1.1. Chart of Great Bay Estuary, New Hampshire with sampling sites indicated.


Maine
43°05'
GBFLATS
MIDGB
SHALLGB
SQ108
New Hampshire
SQ51
70°50'
70°40'

mouth. Salinity at this site is highly variable and intermediate to the other two sites. MIDGB, the highest salinity site, was located in the middle of Great Bay proper. The depth and bottom substratum were similar at all three of these stations (Table 1.1).

Sites MIDGB, SHALLGB (Shallow Great Bay) and GBFLATS (Great Bay intertidal flats) were located along a depth gradient in a contiguous area in the middle of Great Bay. MIDGB was also used as a site in the salinity gradient and was the deepest site sampled along the depth gradient. SHALLGB represented the intermediate depth and GBFLATS was located on intertidal mudflats and therefore only sampled on a high tide. All three sites had similar bottom substratum and, due to their proximity, experienced nearly identical salinities (Table 1.1).

Monthly length frequencies at each site were pooled over all study years. 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. Samples collected during April, May and June were considered spring, July and August were considered summer, and September, October and November were included in autumn. Catches were standardized to number of fish/ten

Table 1.1. Physical characteristics of the sampling sites. SQ51, SQ108 and MIDGB make up the salinity gradient, while GBFLATS, SHALLGB and MIDGB form the depth gradient.

Station	salinity (ppt)		temperature (°C)		depth (ft)		bottom type
	mean	range	mean	range	mean	range	
SQ51	4.2	0.0-22.4	19.4	4.7-25.7	9.0	6.3-13.0	silty mud
SQ108	10.9	0.4-24.0	17.1	0.0-27.8	12.0	6.0-14.0	silty mud
MIDGB	20.3	6.5-29.9	15.4	1.8-23.9	20.2	16.0-26.0	silty mud
SHALLGB	20.9	6.5-29.5	16.4	2.3-24.9	7.0	4.9-14.5	silty mud
GBFLATS	19.8	11.0-28.5	15.2	0.2-24.2	5.0	3.5-7.2	silty mud

minute tow. Because many months contained zero catches and, in some cases, the variances were proportionate to the means, the data were transformed using a square root transformation (square root(X+1)). The Kolmogorov-Smirnov test with the Lilliefors modification and probability plots of residuals indicted 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 using Tukey's HSD test (Zar 1984).

Results

A total of 8333 smooth flounder and 2105 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 only abundant as juveniles. However, the length frequencies of the two flounders were similar (Figures 1.2a and 1.2b) because adult smooth flounder are about the same size as juvenile winter flounder. Smooth flounder were captured from many different year classes while winter flounder were primarily age 0+, 1+ and 2+, based on length frequencies.

Salinity followed a typical temperate estuarine seasonal pattern (Figures 1.3a and 1.3b). The general trend at all stations was for salinity to be lowest in April, increase over the late spring and summer months reaching the highest levels during August and September, and declining

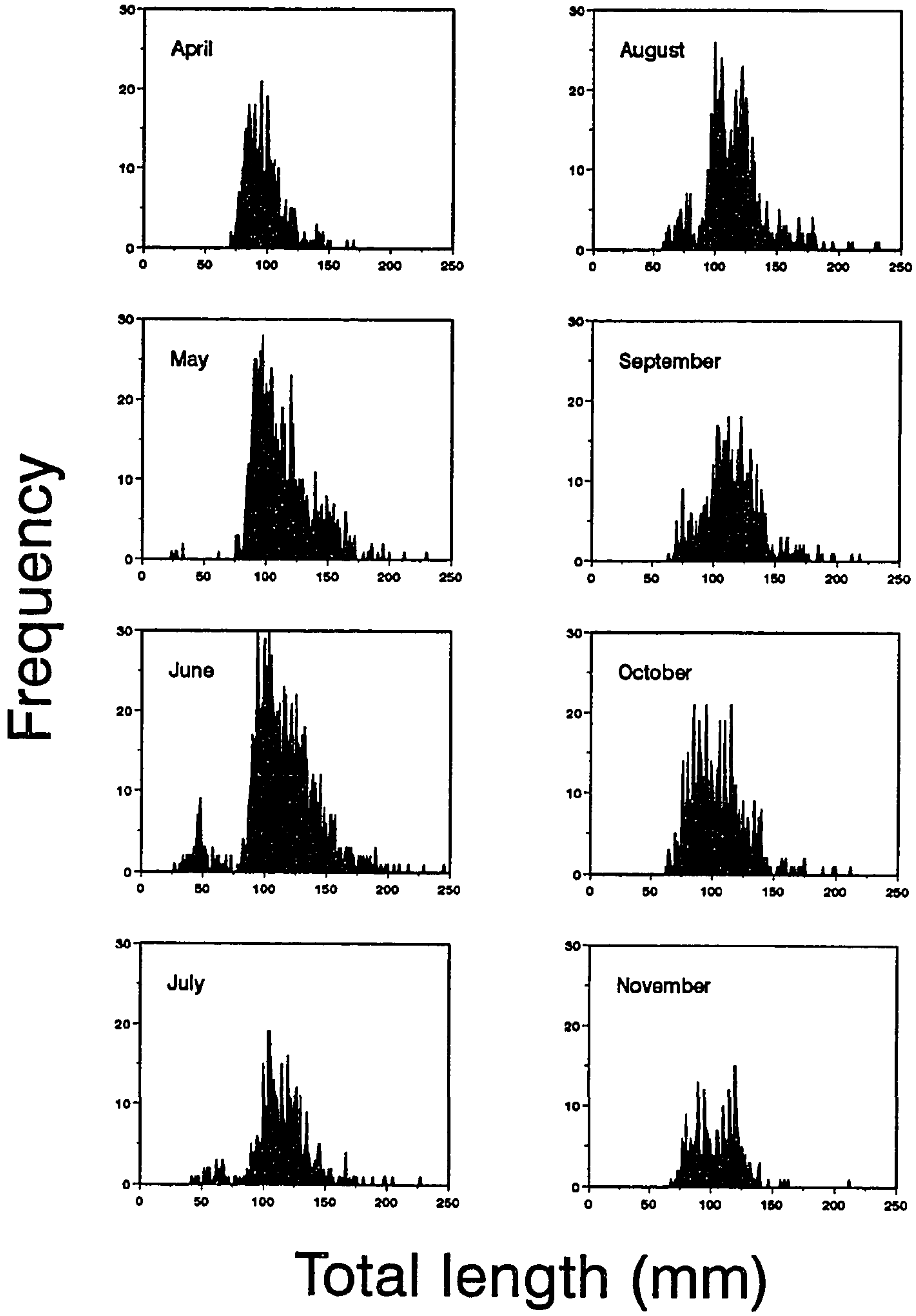


Figure 1.2a. Monthly length frequencies of smooth flounder from all sites pooled, 1989-1991.

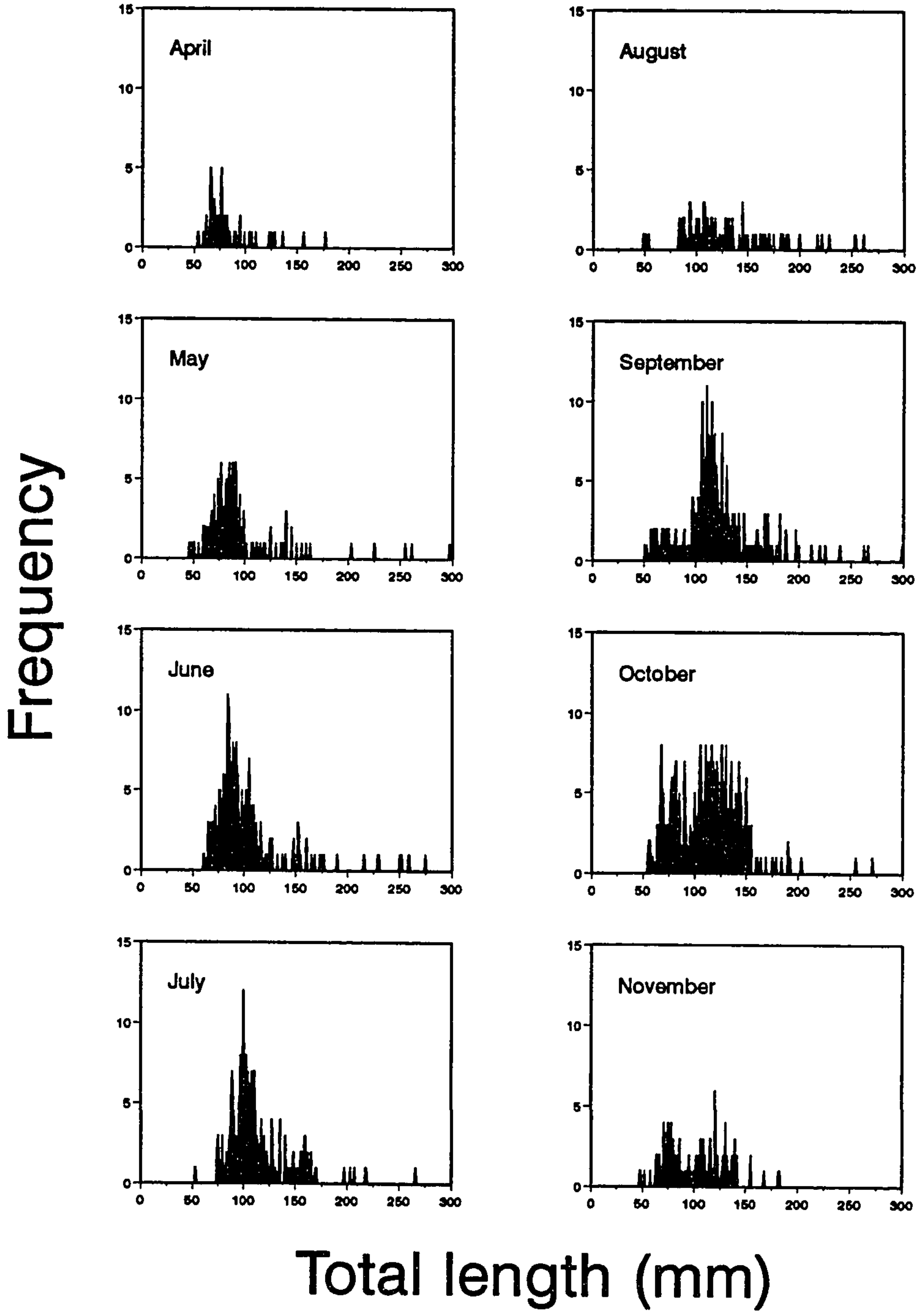


Figure 1.2b. Monthly length frequencies of winter flounder from all sites pooled, 1989-1991.

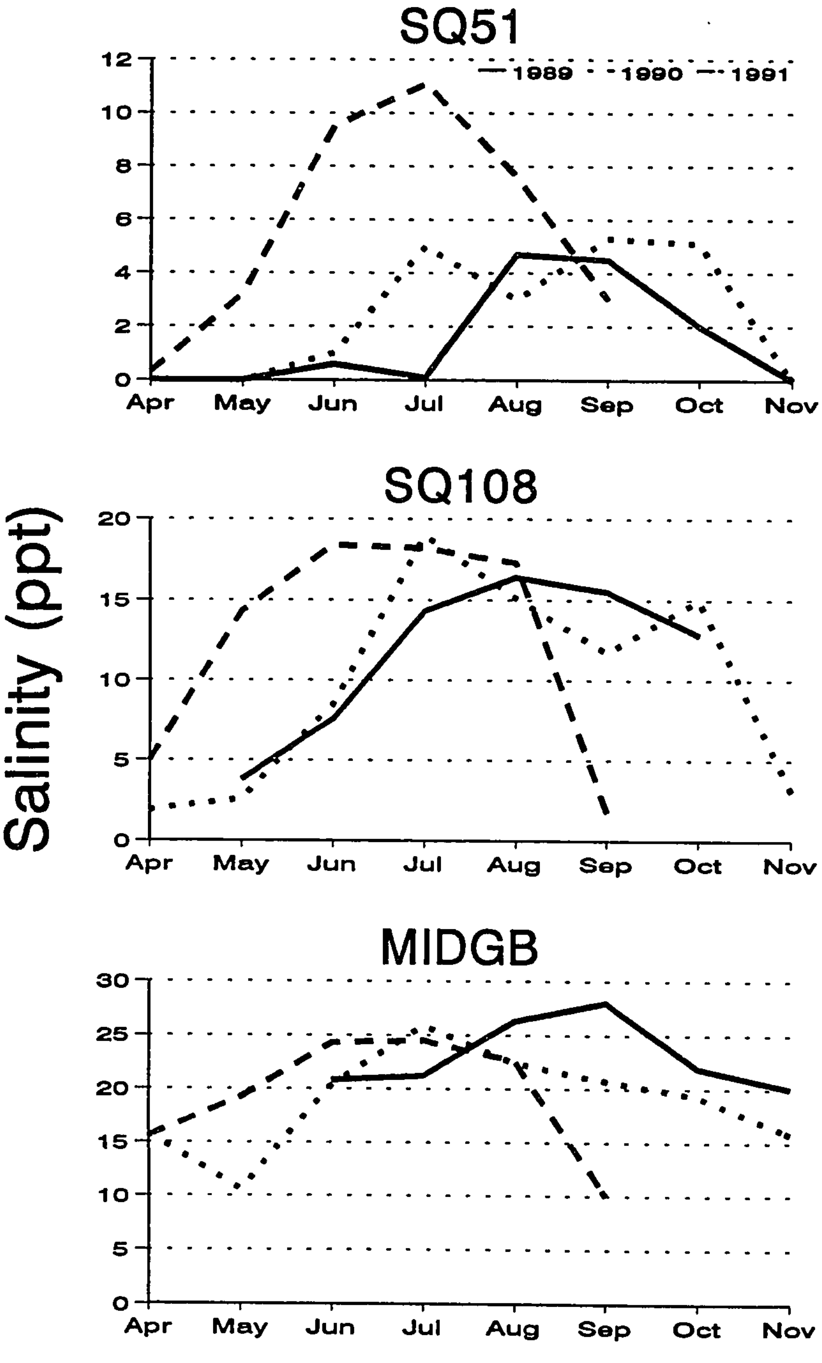


Figure 1.3a. Monthly mean salinity at three sites along a salinity gradient in Great Bay Estuary, New Hampshire, 1989-1991.

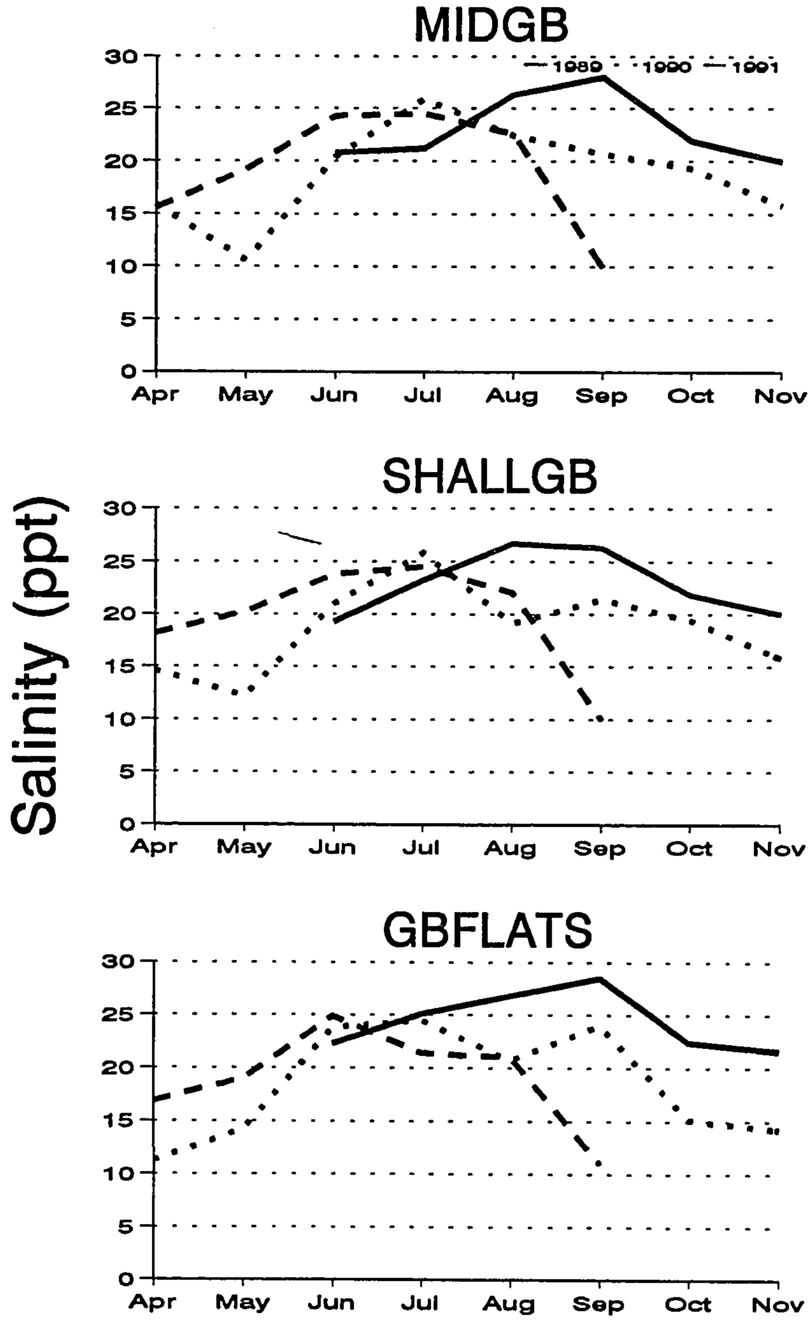


Figure 1.3b. Monthly mean salinity at three sites along a depth gradient in Great Bay Estuary, New Hampshire, 1989-1991.

into autumn. These seasonal patterns were especially pronounced at SQ51 and SQ108. Salinity in the spring of 1991 was higher than the other two years at all sites, the result of a small spring run-off and an uncharacteristically dry spring. Another salinity anomaly that occurred in 1991 was a sudden decrease in salinity in September caused by massive rainfall from Hurricane Bob which passed through the area in late August of that year. The sites comprising the depth gradient had similar patterns of salinity in all years of the study.

Salinity Gradient

Both species were found to be unevenly distributed along the salinity gradient and their distributions changed seasonally (Table 1.2). At SQ51, smooth flounder were very abundant at particular times of the year. In 1989 and 1990 smooth flounder were abundant in mid to late summer (Figure 1.4). The influx of smooth flounder was associated with seasonal changes in the salinity regime from fresh to oligohaline (Figure 1.3a). In 1991 smooth flounder were present at SQ51 in all months sampled. In this year salinity was higher than the two previous years (Figure 1.3a). Length frequencies of smooth flounder at SQ51 were different from those at SQ108 (Figures 1.5a, 1.5b). Larger fish made up a larger percentage of the catch at SQ51, indicating differential migration among size classes. Winter flounder were rarely collected at SQ51 (Figure 1.6).

Table 1.2. Results of ANOVAs testing for differences in catches of smooth and winter flounder among three sites along the salinity gradient (SQ51, SQ108, MIDGB) and three sites along the depth gradient (GBFLATS, SHALLGB, MIDGB). 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.

	Smooth	Winter
Salinity Gradient		
1989		
Spring	SQ51<MIDGB<SQ108	SQ51=SQ108<MIDGB
Summer	MIDGB<SQ51=SQ108	SQ51=SQ108<MIDGB
Autumn	MIDGB<SQ51=SQ108	SQ51<MIDGB<SQ108
1990		
Spring	MIDGB=SQ51<SQ108	SQ51=SQ108<MIDGB
Summer	MIDGB<SQ51=SQ108	SQ51<SQ108=MIDGB
Autumn	MIDGB<SQ108=SQ51	$p>0.05$
1991		
Spring	MIDGB<SQ108=SQ51	SQ51=SQ108<MIDGB
Summer	MIDGB<SQ108=SQ51	SQ51=SQ108<MIDGB
Autumn	MIDGB<SQ51<SQ108	SQ51<MIDGB<SQ108
Depth Gradient		
1989		
Spring	$p>0.05$	GBFLATS<SHALLGB<MIDGB
Summer	$p>0.05$	SHALLGB=GBFLATS<MIDGB
Autumn	MIDGB=GBFLATS<SHALLGB	GBFLATS<SHALLGB<MIDGB
1990		
Spring	$p>0.05$	GBFLATS<SHALLGB=MIDGB
Summer	$p>0.05$	GBFLATS=SHALLGB<MIDGB
Autumn	MIDGB=SHALLGB<GBFLATS	GBFLATS=SHALLGB<MIDGB
1991		
Spring	$p>0.05$	GBFLATS=SHALLGB<MIDGB
Summer	MIDGB=SHALLGB<GBFLATS	GBFLATS=SHALLGB<MIDGB
Autumn	MIDGB=SHALLGB<GBFLATS	$p>0.05$

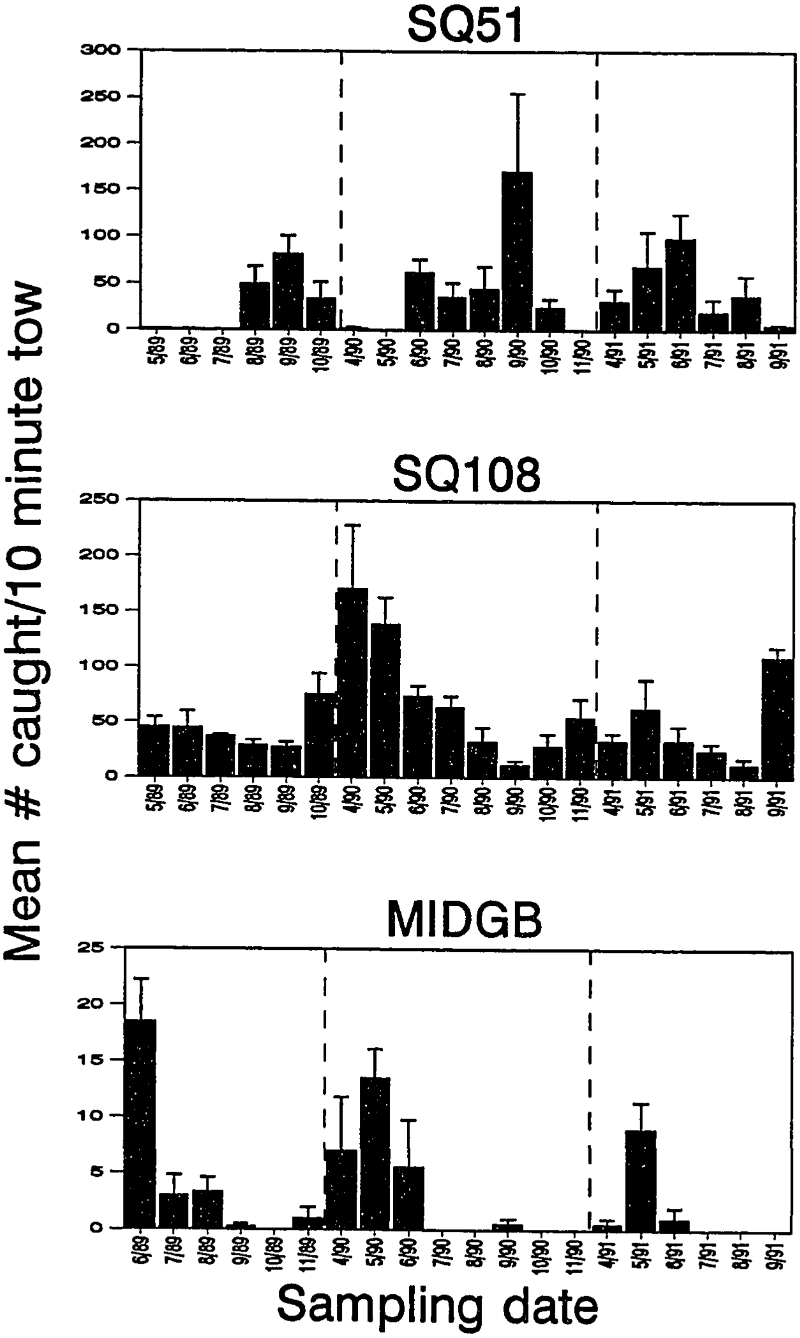


Figure 1.4. Mean number of smooth flounder caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire. Error bars indicate one standard error of the mean.

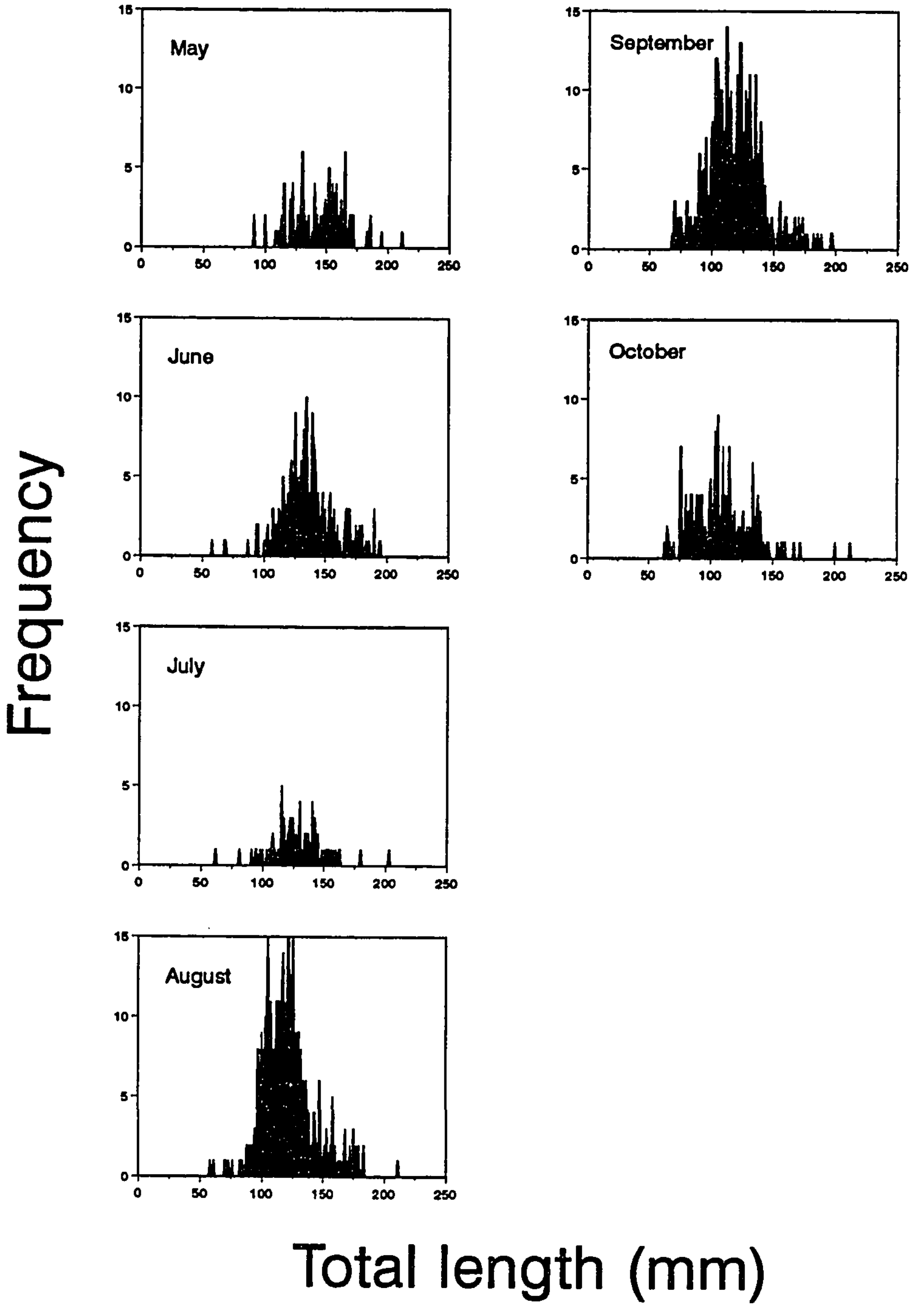


Figure 1.5a. Monthly length frequencies of smooth flounder at site SQ51, 1989-1991.

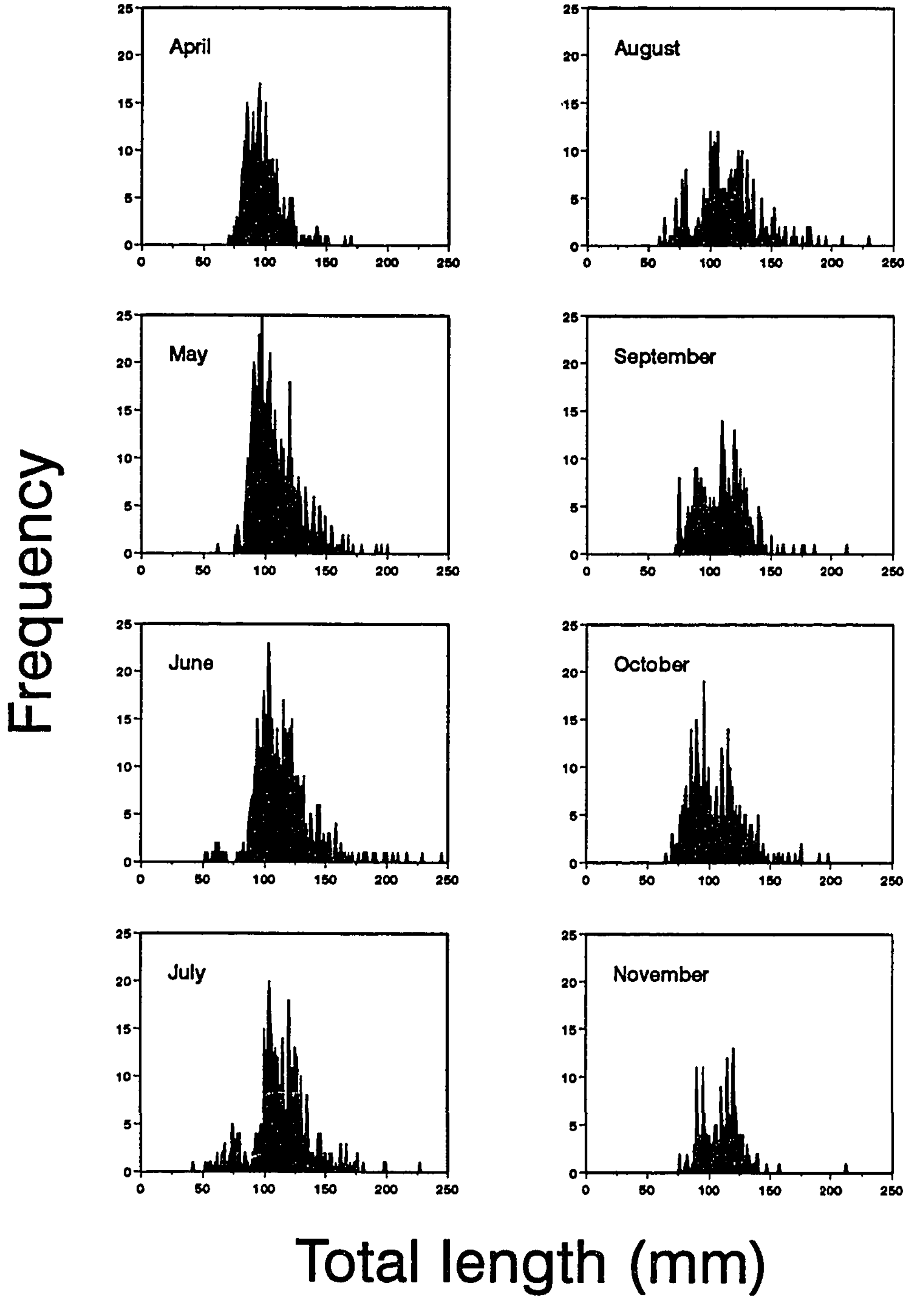


Figure 1.5b. Monthly length frequencies of smooth flounder at site SQ108, 1989-1991.

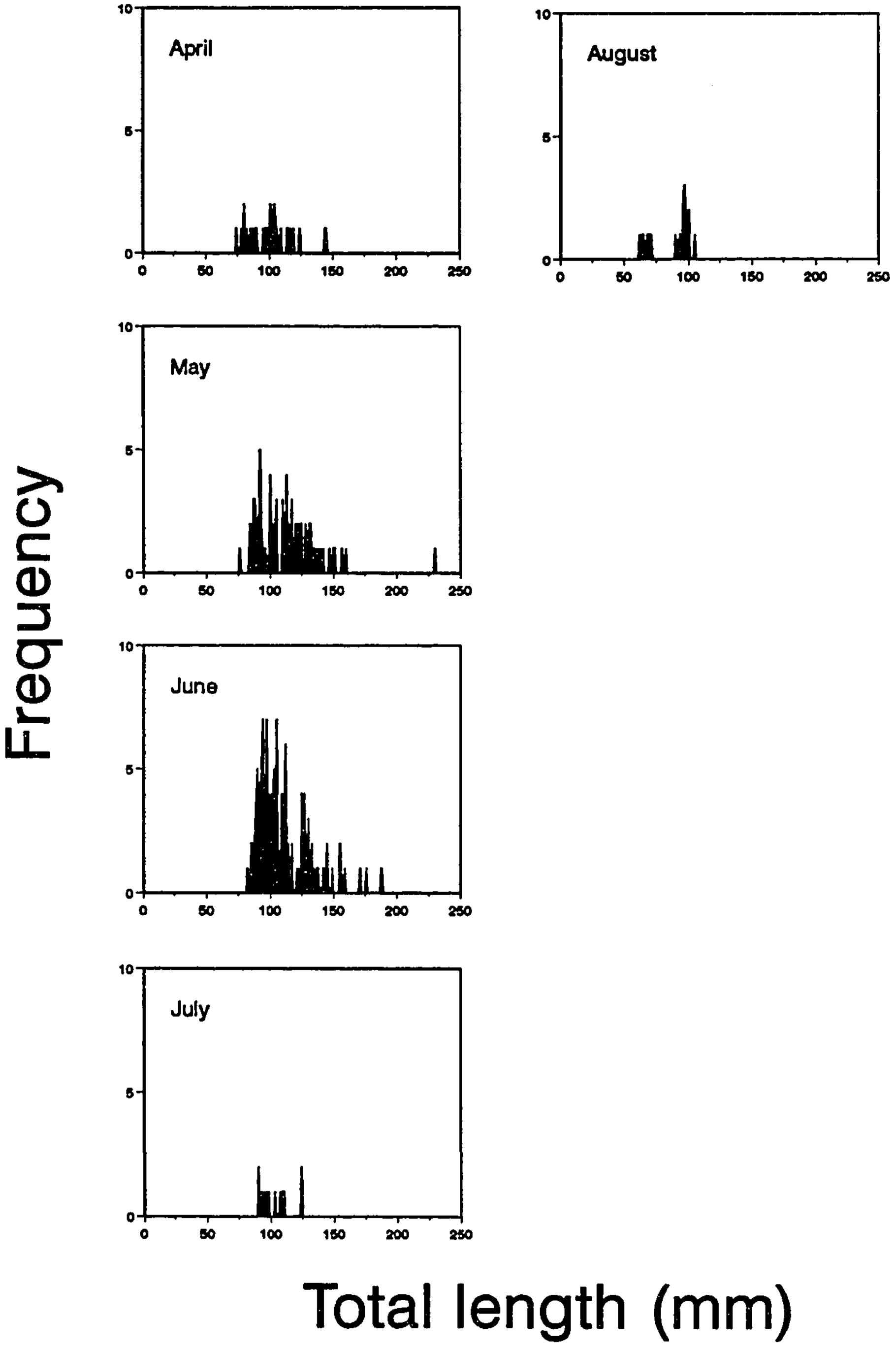


Figure 1.5c. Monthly length frequencies of smooth flounder at site MIDGB, 1989-1991.

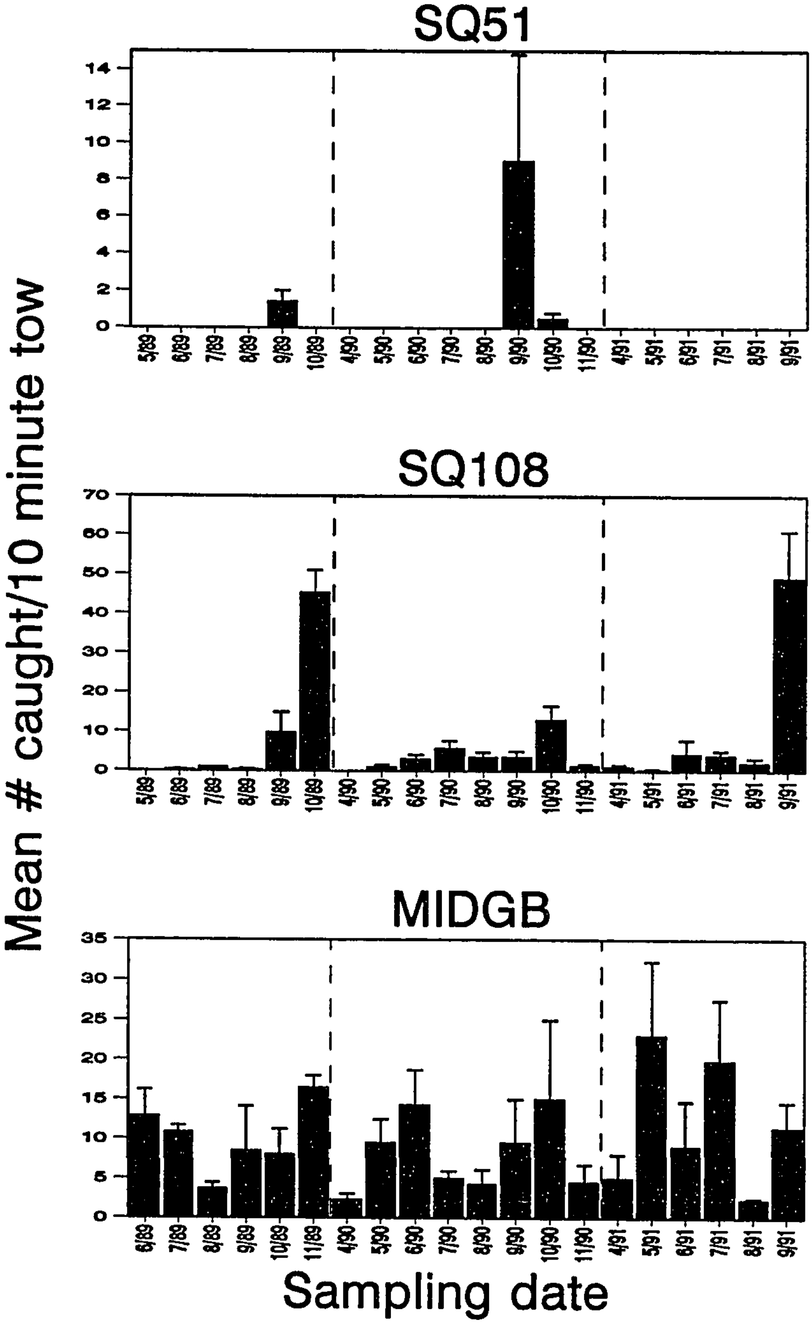


Figure 1.6. Mean number of winter flounder caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire. Error bars are one standard error of the mean.

They were only found there on a few occasions in September and October when salinity was at a seasonal high.

Smooth flounder were abundant at SQ108 during all months. Their average abundance was highest at this site compared to all other sites sampled. Their abundance was generally high in the spring, lower in late summer to early autumn, and high again in mid to late autumn (Figure 1.4). This trend was opposite that observed for SQ51. Correlation analysis of catches of smooth flounder at SQ51 and SQ108 indicated a significant, but loose negative relationship (p=.032, r=-0.48) (Figure 1.8). When catches were high at SQ51, they tended to be low at SQ108. This indicates 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 travel the three kilometers between the sites than smaller flounders. Winter flounder were abundant at SQ108 only during late summer and early autumn (Figure 1.6), although even during these periods of abundance, the catches of winter flounder were always significantly lower than smooth flounder except during autumn of 1991 when there was no significant difference (p=.074) in catches between the species. The movement of winter flounder into SQ108 from Great Bay proper was associated with relatively high salinities (Figure 1.3a) and also relatively low abundances of smooth flounder (Figure 1.4). The length frequencies of winter flounder collected from SQ108 and MIDGB were similar (Figures 1.7a,1.7b).

Smooth flounder occurred at MIDGB in relative abundance only in April, May and June. Catches of smooth flounder decreased significantly after June in all years. Winter flounder were most abundant at this site compared to the other two sites comprising the salinity gradient. 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

Similar to the salinity gradient results, the two species of flounder showed differential use of the three habitats that made up the depth gradient. There were also differences in the sizes of flounder that utilized the three depths. Seasonal changes in distribution were less pronounced than those exhibited along the salinity gradient. A broad size range of smooth flounder utilized MIDGB (Figure 1.5c). However, their abundance dropped off sharply after June of each year as previously discussed (Figure 1.9). Winter flounder showed little seasonal trends in abundance at this station (Figure 1.11). A broad size range of juvenile winter flounder was found here. A distinct influx of young-of-year winter flounder could be seen at MIDGB in August through November of each year (Figure 1.7b).

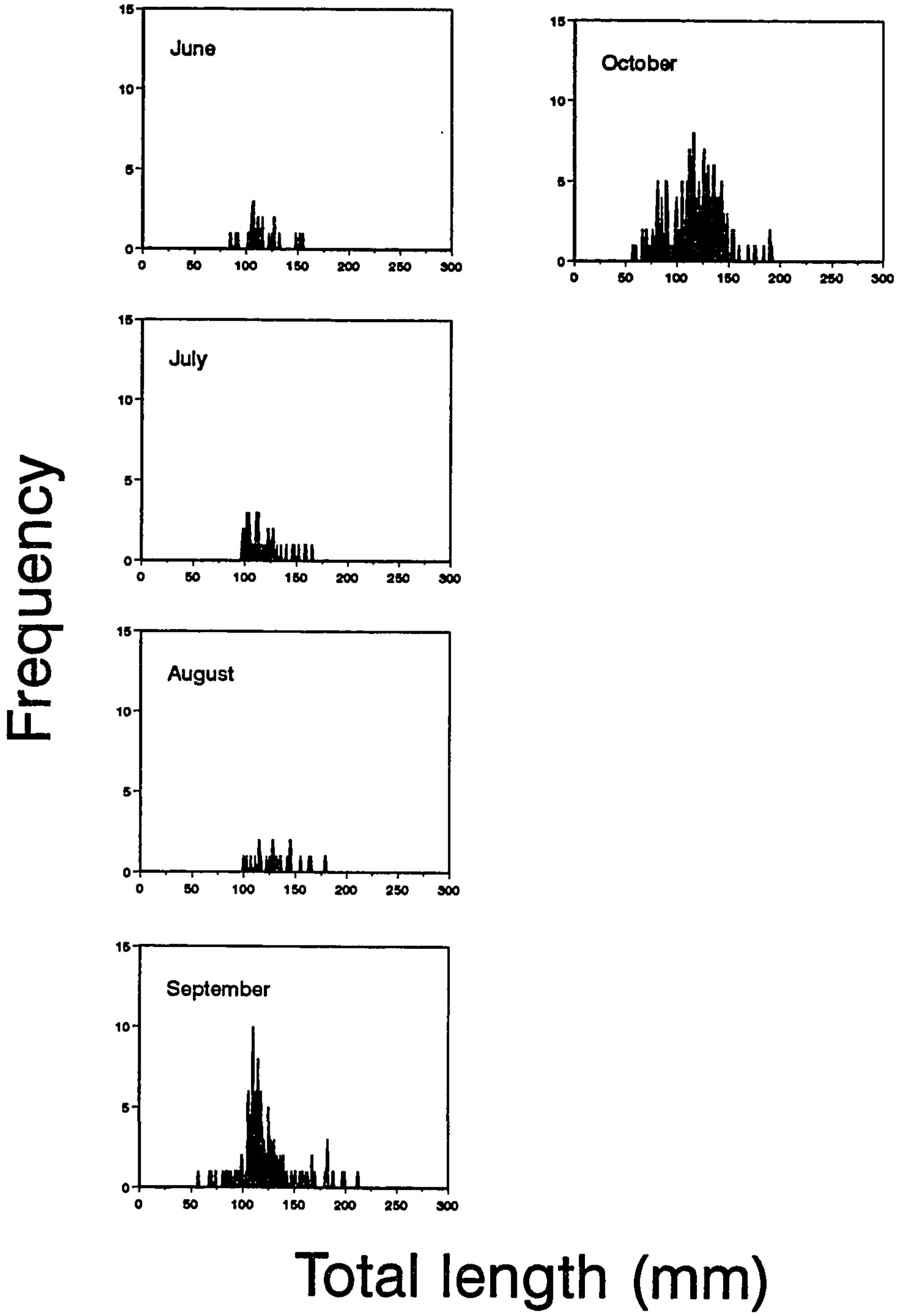


Figure 1.7a. Monthly length frequencies of winter flounder at site SQ108, 1989-1991.

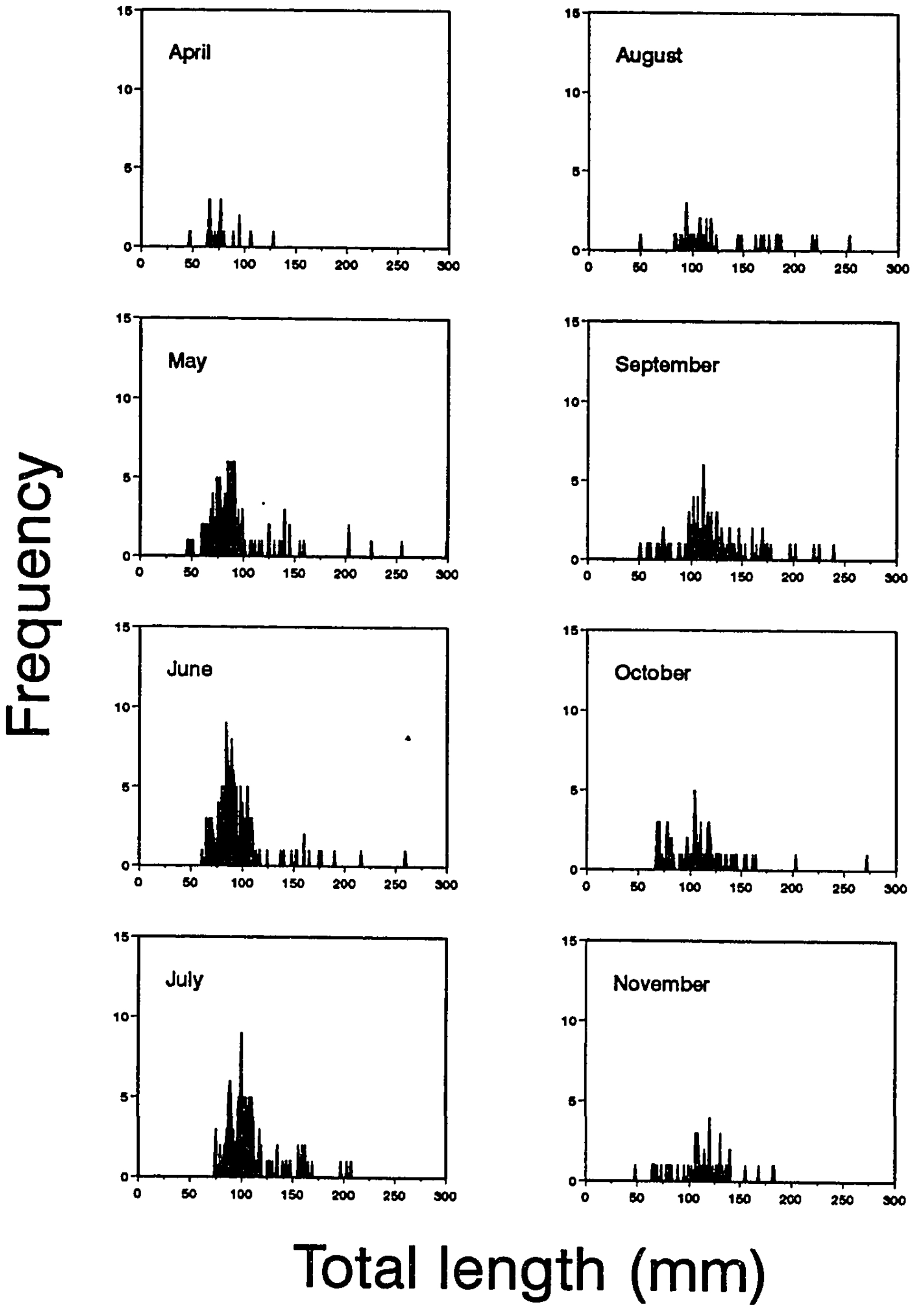


Figure 1.7b. Monthly length frequencies of winter flounder at site MIDGB, 1989-1991.

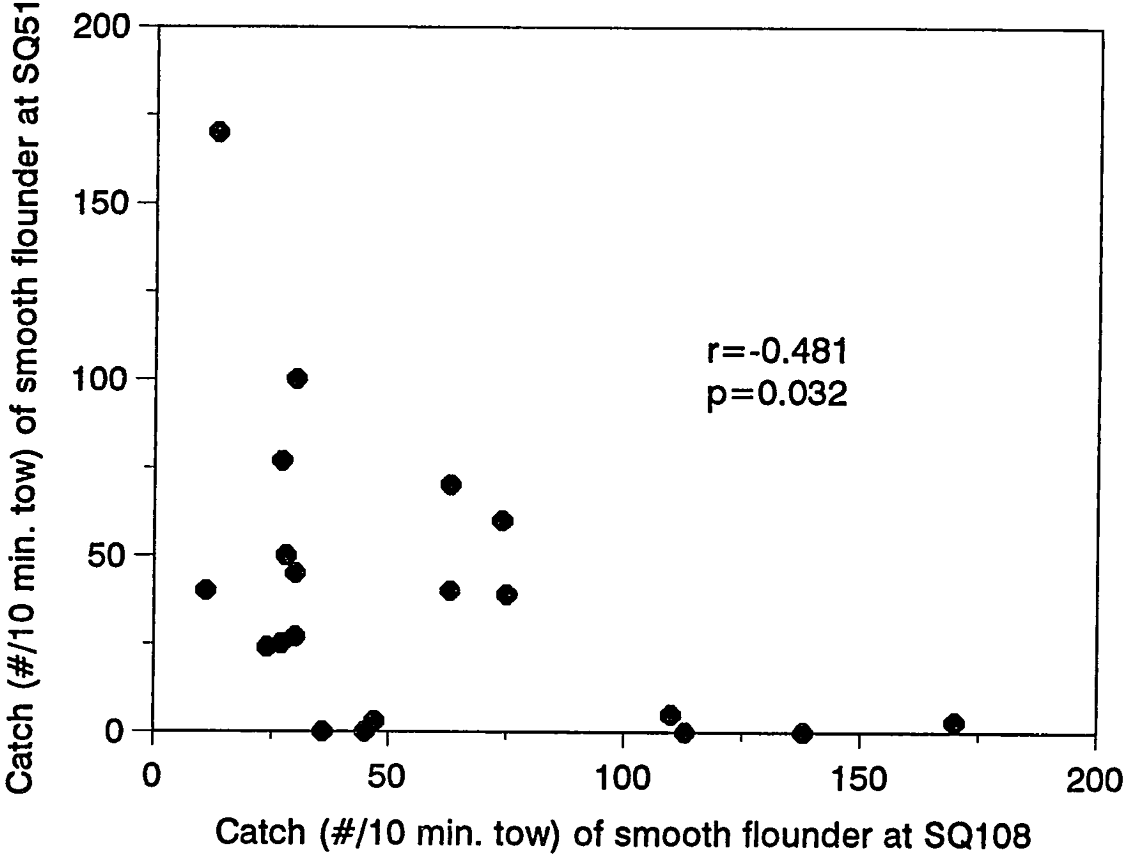


Figure 1.8. Relationship between catch of smooth flounder at site SQ108 and the concurrent catch of smooth flounder at site SQ51.

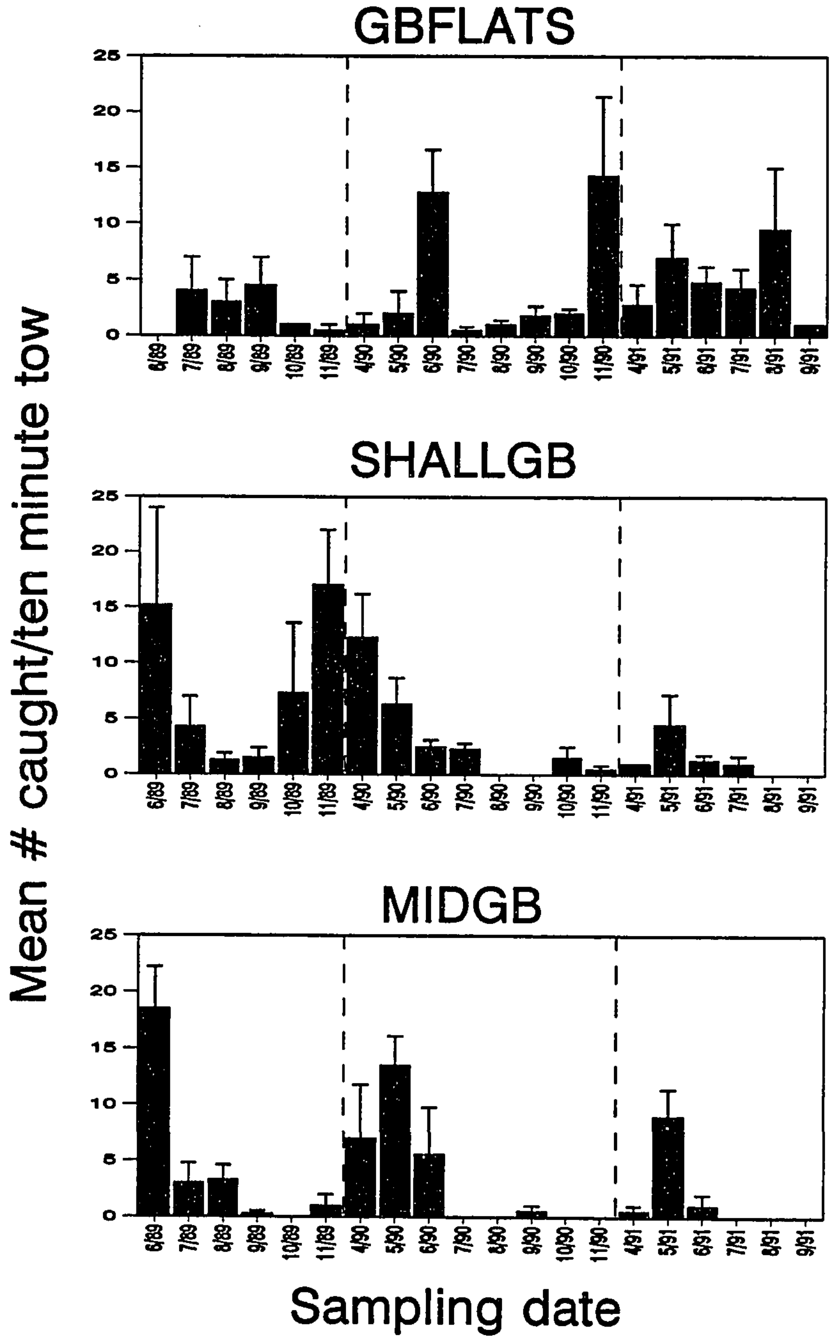


Figure 1.9. Mean number of smooth flounder caught per ten minute tow at three sites along a depth gradient in Great Bay Estuary, New Hampshire. Error bars are one standard error of the mean.

At SHALLGB, smooth flounder showed little significant seasonal changes in abundance (Figure 1.9), although there was a trend for catches to be lowest in late summer and early autumn. Length frequencies differed between MIDGB and SHALLGB. At SHALLGB, few larger smooth flounder were present during any season (Figure 1.10a), while young-of-year, which were absent from MIDGB, were collected at most times. Abundance of winter flounder at SHALLGB was lowest in all years in early summer (Figure 1.11) and catches were always smaller than at MIDGB. Length frequencies indicate that smaller winter flounder made up a greater proportion of the catch at SHALLGB compared to MIDGB (Figure 1.12).

Catches at GBFLATS were very variable for both species and showed no clear seasonal trends. Smooth flounder catches at GBFLATS were dominated by young-of-year. Few larger (>100 mm TL) individuals were ever caught at this site (Figure 1.10b), in marked contrast to MIDGB (Figure 1.5b) but similar to SHALLGB (Figure 1.10a). Winter flounder occurred at GBFLATS only sporadically and in very low numbers (Figure 1.11). Catches of winter flounder were a mix of different size 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 use of these various

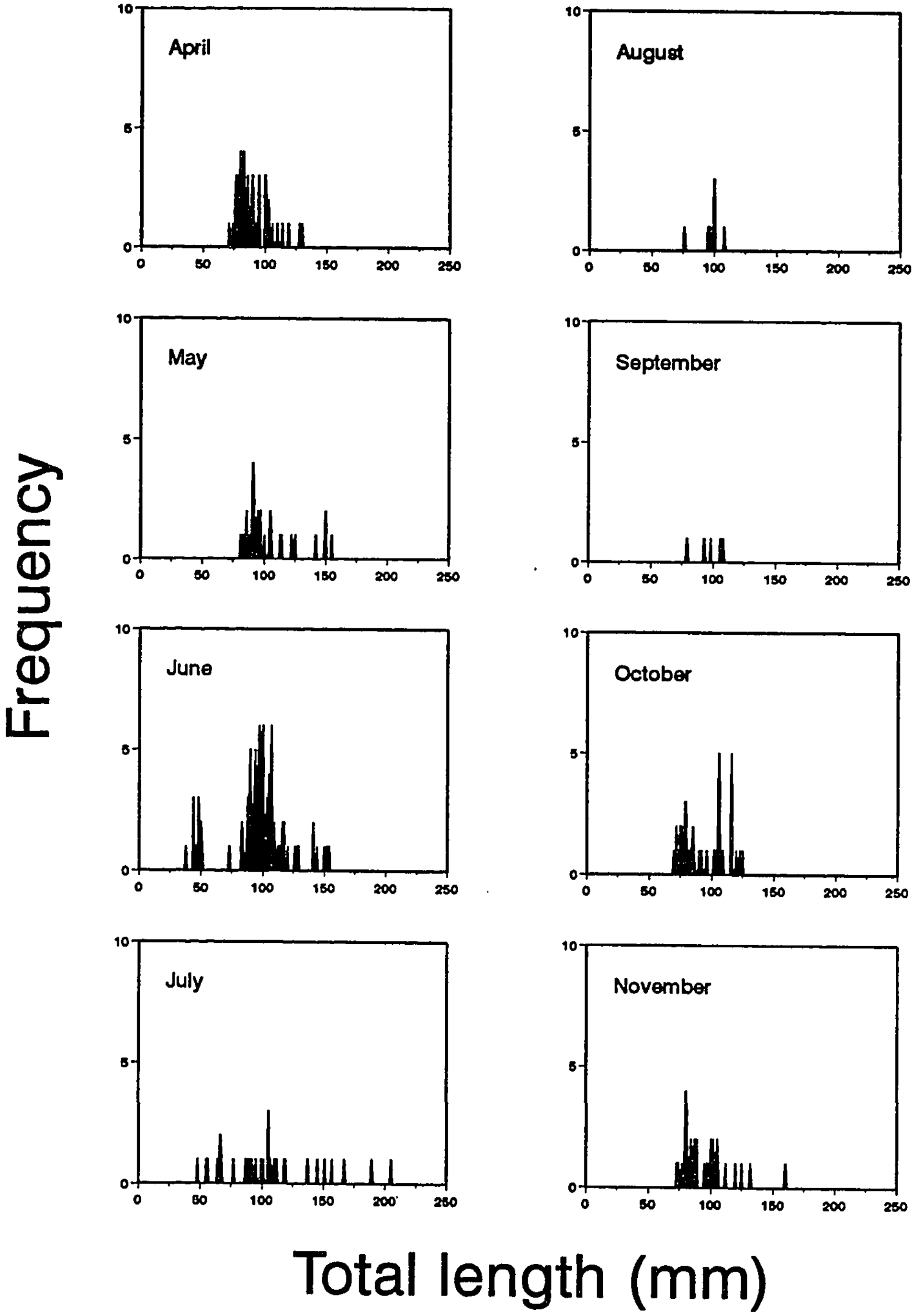


Figure 1.10a. Monthly length frequencies of smooth flounder at site SHALLGB, 1989-1991.

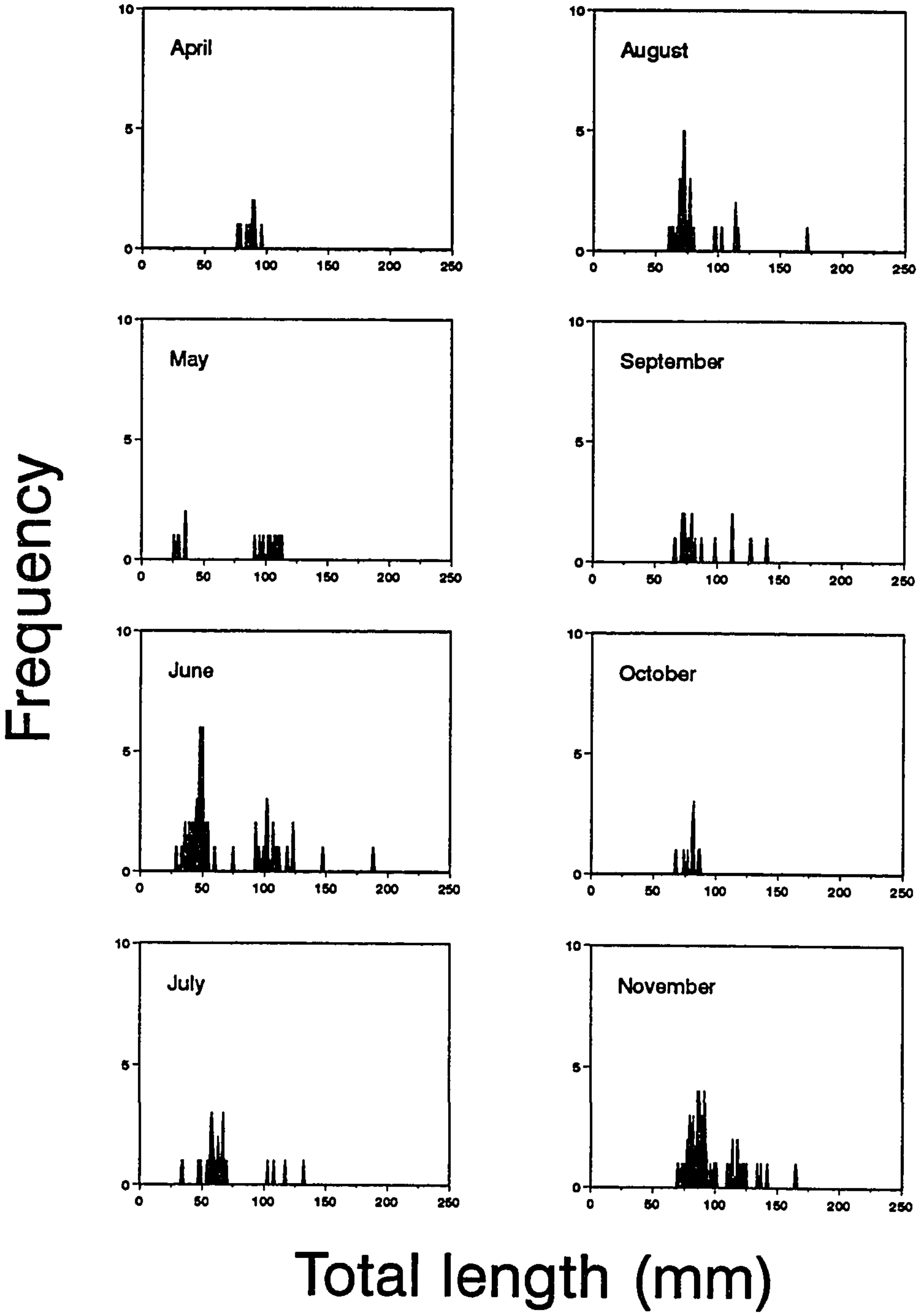


Figure 1.10b. Monthly length frequencies of smooth flounder at site GBFLATS, 1989-1991.

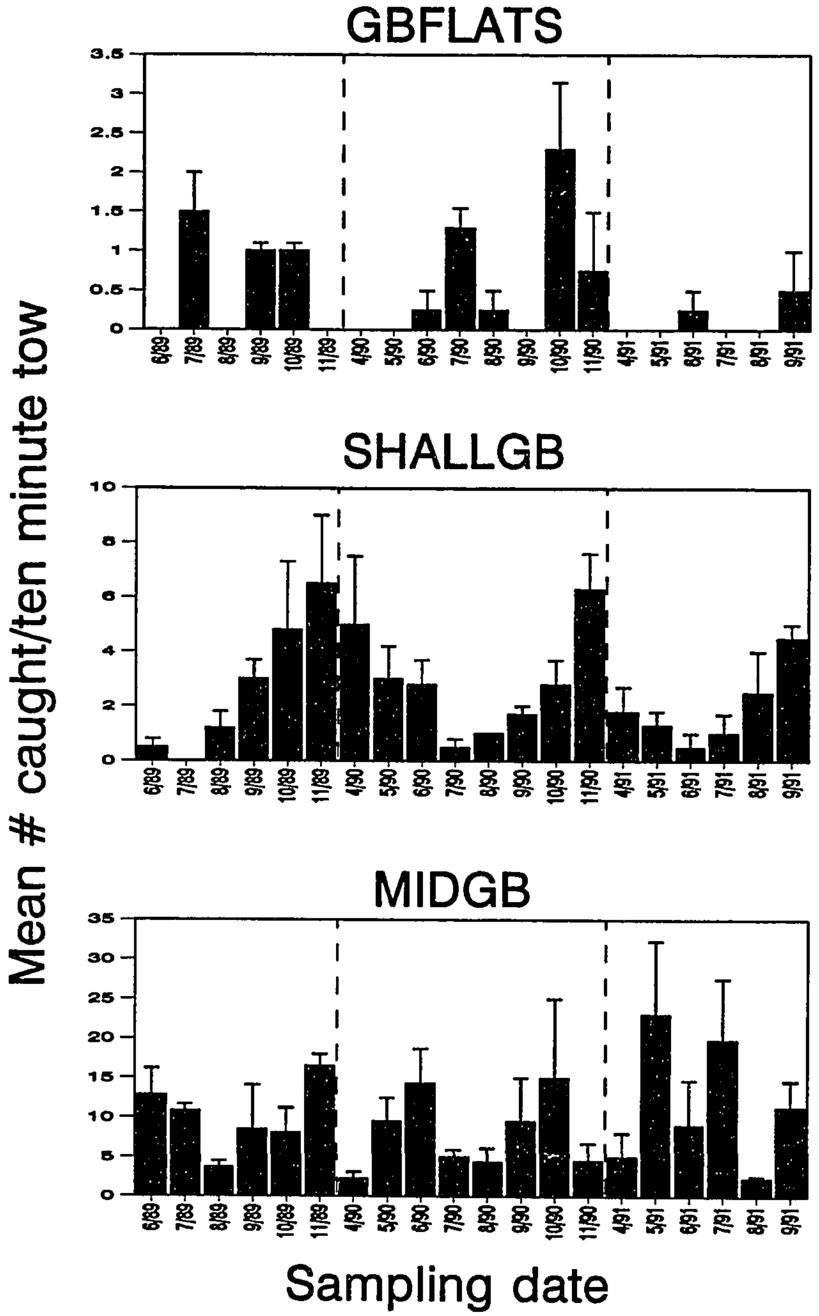


Figure 1.11. Mean number of winter flounder caught per ten minute tow at three sites along a depth gradient in Great Bay Estuary, New Hampshire. Error bars are one standard error of the mean.

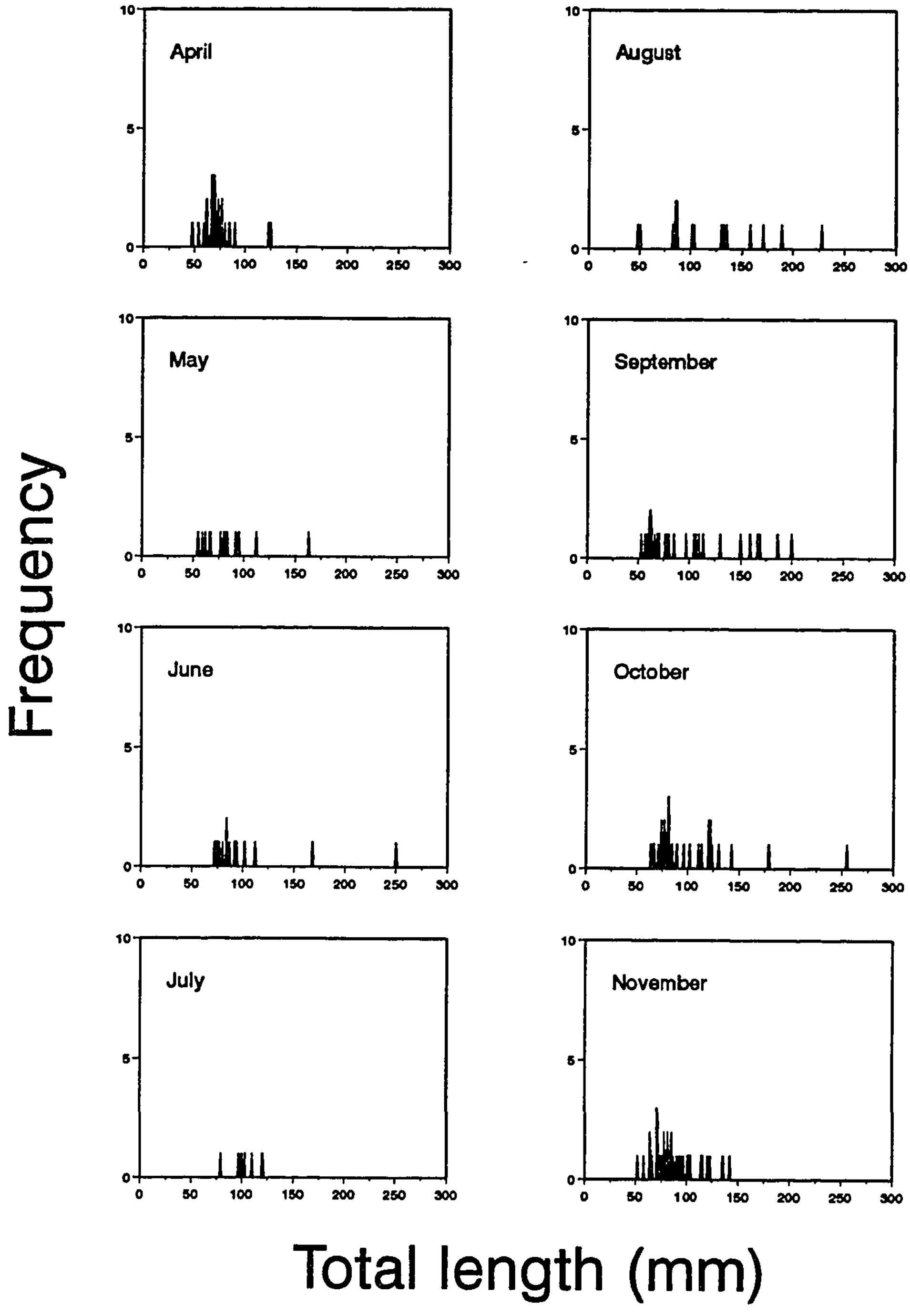


Figure 1.12. Monthly length frequencies of winter flounder at site SHALLGB, 1989-1991.

habitats by these two flounder species. Although smooth and winter flounder are sympatric over much of their ranges when examined on a geographic scale, the evidence presented here indicates they utilize habitats within the estuaries differently, and their habitat usage is subject to seasonal variations.

Salinity Gradient

In general smooth flounder had a center of greatest abundance at SQ108, which was the oligo-mesohaline river mouth habitat. Strong seasonal movements were seen into and out of the oligohaline riverine station (SQ51) and the meso-polyhaline station in Great Bay proper (MIDGB). 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 in larger smooth flounder. Greater movements by larger individuals is probably related to their superior locomotor abilities simply due 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 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, and Fried (1973), studying the same estuary, found that smooth flounder were not present above 28.5 ppt, while 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 oligo-mesohaline part of the estuary, is in agreement with these previous studies.

MIDGB was the site of greatest abundance for winter flounder. Seasonal movements into SQ108 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 only looked at temperature or light as important abiotic factors that influence seasonal or short term movements (McCracken, 1963; Oviatt and Nixon, 1973; Casterlin and Reynolds, 1981). 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 stations were higher in salinity than both SQ51 and SQ108 so he did not sample a habitat that might be only seasonably available. Pearcy (1962) also documented a movement of young-of-year winter flounder from the lower estuary to the upper estuary during the summer months. Indirect evidence for a similar movement by young-of-year winter flounder in Great Bay Estuary is presented here. No young-of-year winter flounder were caught in upper Great Bay until late summer and early autumn (see Figure 1.2), indicating an influx from the lower estuary. This was not an artifact of gear selectivity because young-of-year smooth flounder were caught down to a size of about 25 mm TL, indicating that small young-of-year winter flounder would have been caught also if they were present. Winter flounder spawn in the lower portion of the estuary where the salinity is about 31-32.5 ppt (Buckley, 1989). Juveniles show little movement for a few months after metamorphosis (Saucerman, 1990), so it is not until they reach a larger size (30-50 mm TL) that they begin to move into the upper estuary.

Salinity must be 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 may serve as part of a continuum of physiological stress, ordering habitats from benign to harsh relative to species tolerances (Peterson and Ross, 1991). Species seeking to maximize growth must choose habitats that are bioenergetically least costly. Several estuarine fish species have been found to be most abundant along a salinity gradient where their metabolic cost of osmoregulation is 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*, undergo movements that appear physiologically disadvantageous. They concluded 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 (MIDGB). They were abundant only during April-June, before migrating upriver as salinity increased. Small numbers remained at SHALLGB throughout the summer and autumn. The tidal flats (GBFLATS) and shallow bay area (SHALLGB) were important nursery areas for smooth flounder. These smaller flounder did not show a dramatic decrease in abundance during the summer as seen in the larger individuals. Young-of-year smooth flounder did not appear to make the pronounced seasonal up-estuary movement. Their inferior swimming ability as compared to larger individuals or an inability to efficiently osmoregulate in the lower salinity areas may be the causes of 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 plaice, Pleuronectes platessa (Kuipers, 1973; Gibson, 1973). Segregation by size may reduce intraspecific competition. The intertidal zone may also function as a refuge from predators for small flatfish, or an abundant source of appropriate sized 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 plaice, Pleuronectes platessa, utilized tidal flats as a refuge from predators rather than for feeding purposes.

Winter flounder showed little segregation by size along the depth gradient. This is in contrast to other studies which have shown that juvenile winter flounder segregate by size along depth gradients based on differential preferences to temperature and light intensity, with the smallest individuals withstanding higher temperatures and light intensities (see review in Klein-MacPhee, 1978; Casterlin and Reynolds, 1982). It is especially interesting that winter flounder showed relatively little use of the intertidal flats habitat. Tyler (1971), Wells et al. (1973) and Black and Miller (1991) found that winter flounder used intertidal flats extensively. These studies took place in higher salinity areas where no smooth flounder occurred. Competition with smooth flounder cannot be dismissed as 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 while Fried (1973) found that the channel areas were dominated by winter flounder. Fried (1973) felt the tidal mudflats offered smooth flounders a refugium from competition with winter flounder. Temperature may also be a factor in the winter flounder's avoidance of this habitat. Hoff and Westman (1966) found that winter flounder acclimated to 21.0°C had an upper lethal temperature of 27.0°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. Though comparable data do not exist for smooth flounder, Huntsman and Sparks (1924) reported that the upper lethal temperatures for smooth flounder were 2-4°C higher than 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 GBFLATS reached 22-24.2°C but would not be a factor during most of the year. The low abundance of winter flounder at GBFLATS persisted during times of the year when temperature would not seem to be limiting.

Summary

Smooth and winter flounder partially segregated by species along salinity and depth gradients in upper Great Bay Estuary. It appears much of the segregation is due to differential responses to the physico-chemical regime, but the effect of seasonal changes in biotic interactions is unknown but possibly important. Little is known of the food habits of these two species in sympatry or of the dynamics of prey abundance in Great Bay. Competition or movements related to prey abundance may be influencing their respective distributions. There are many instances where competition appears to play a role in the distribution of ecologically similar species along environmental gradients (Connor and Bowers, 1987).

The relationship between smooth and winter flounder changes on a seasonal basis. At times their segregation on a spatial scale is nearly complete, while at other times, particularly April-June at MIDGB and September-October at SQ108, they overlap considerably in habitat use.

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 need to experimentally assess the relative importance of abiotic versus biotic factors in determining the patterns seen in their spatial distributions.

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II. THE ROLE OF SALINITY IN DETERMINING THE ESTUARINE DISTRIBUTION OF SMOOTH AND WINTER FLOUNDER

Introduction

Smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, are important components of the fauna in estuaries of the northwest Atlantic Ocean. They occur sympatrically from Labrador to Massachusetts although a recent study (Armstrong, Section I) demonstrated that these two species were spatially segregated within Great Bay Estuary, New Hampshire. The segregation was primarily along a salinity gradient and the degree of separation changed seasonally. Armstrong (Section I) noted that the movements of smooth and winter flounder were closely associated with salinity changes. He suggested that spatial segregation of the two flounder species was primarily the result of their differing salinity tolerances, although he could not exclude the role of biotic factors such as prey abundance, predation or competition. Smooth flounder were most abundant in a salinity range of about 5-25 parts per thousand (ppt) and winter flounder were most abundant in salinities above about 15 ppt.

Physiological adaptations along a gradient are well studied in plants but less well documented in animals

(Dunson and Travis, 1994). There is little appreciation of abiotic influences and physiological tolerances on patterns of habitat segregation, especially among closely related species (Dunson and Travis, 1991). A natural salinity gradient along the estuarine axis may serve as part of a continuum of physiological stress, ordering habitats from benign to harsh relative to species tolerances (Peterson and Ross, 1991). Evidence suggests that segregation of closely related species along estuarine salinity gradients appears to be common in fishes. Martin (1989, 1990) found that niche separation of three species of Ambassidae in a South African estuary was based principally on their relative abilities to osmoregulate in hypo-osmotic conditions. Similar results have been found for two species of Mugilidae (Lasserre and Gallis, 1975), three species of Cyprinodontidae (Nordlie and Walsh, 1989) and three species of Pleuronectes (Spaargaren, 1976).

This study presents the results of three experiments designed to compare the abilities of smooth and winter flounder to grow or respire under a variety of salinity conditions. In experiment I, growth and survival were examined in a closed laboratory system at 2, 12, 22, and 32 ppt salinity. These salinities simulate the salinities available in a typical boreal estuary. In experiment II, growth and survival were examined in flounder grown in situ at two locations along a salinity gradient in Great Bay

Estuary. Experiment III indirectly compared the metabolic responses of smooth and winter flounder to a sudden salinity decrease by measuring changes in oxygen consumption.

The goal of these three experiments was to provide evidence that the contrasting distribution of smooth and winter flounder along an estuarine salinity gradient (Armstrong, Section I) was based primarily on their respective abilities to efficiently osmoregulate at different salinities, and that the centers of abundance within the estuary for each species corresponded to a point along the salinity gradient that was energetically least costly and therefore maximized for growth.

Methods and Materials

All flounders used in the three experiments were collected by otter trawl from Great Bay Estuary, New Hampshire. They were maintained in flow-through seawater tanks at the Jackson Estuarine Laboratory for a minimum of two weeks prior to the experiments to ensure that all individuals used in the experiments were healthy and feeding. In order to reduce variation in the experiments, only flounder between 95 and 120 mm total length were used.

Experiment I- Growth at Four Salinities

Eight 75 liter glass aquaria were partitioned into ten separate chambers using plexiglass panels. Each chamber was 15 cm width X 15 cm length X 30 cm height and contained about 7.5 liters of water. Four aquaria were placed in each of two 750 liter constant temperature water baths. One flounder was placed in each chamber, with smooth and winter flounder placed alternately for a total of five individuals of each species in each aquarium (Figure 2.1). The salinity in all aquaria was initially 20 ppt, as this was approximately the mean salinity of the holding tanks at the Jackson Estuarine Laboratory. Salinities were adjusted to experimental salinities over seven days. Over the same time period, the temperature of the water baths was raised from 12°C. to 19°C. The flounder were acclimated at these conditions for an additional seven days before the experiment was begun. Four salinities were used in the experiment: 2, 12, 22, and 32 ppt. The three lower salinities were made by diluting full strength seawater obtained from the flow-through system at the U.N.H. Coastal Laboratory with aged tap water. The highest salinity was made by adding either aged tap water or artificial sea salt, depending on the salinity of the seawater entering the laboratory. One salinity was randomly assigned to each aquarium in a water bath, and the procedure was repeated for the other water bath, yielding the configuration seen in Figure 2.1.

The flounder were grown for 14 days. Prior to the experiment, food was withheld for 24 hours, and each fish was lightly blotted and weighed to the nearest milligram. Each fish was fed an excess of partially-thawed bloodworms

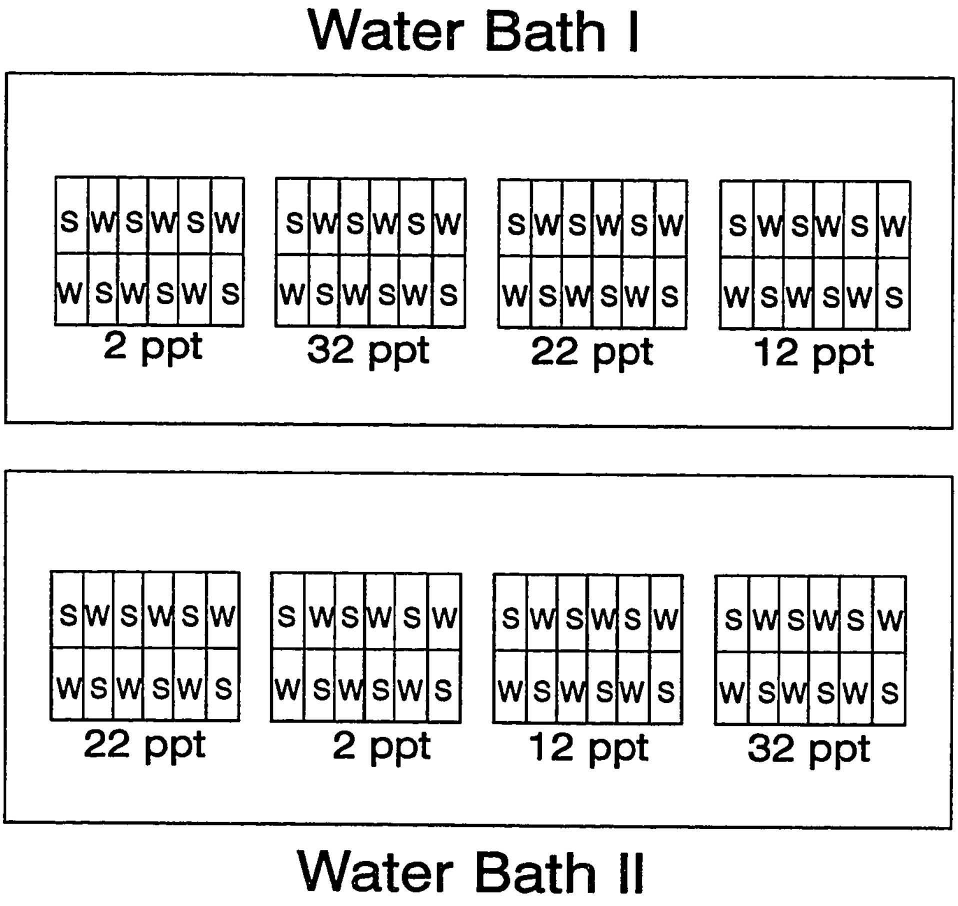


Figure 2.1. Schematic drawing of the experimental design for Experiment I- growth of smooth and winter flounder at four salinities. S=smooth flounder; W=winter flounder.

(Tubifex sp.) daily. The following day all uneaten food was removed and a 75% water change was done on alternate days.

Growth was measured as the total weight change over 14 days. Total weight change was divided by the starting weight of the flounder, yielding percent weight change (PWC).

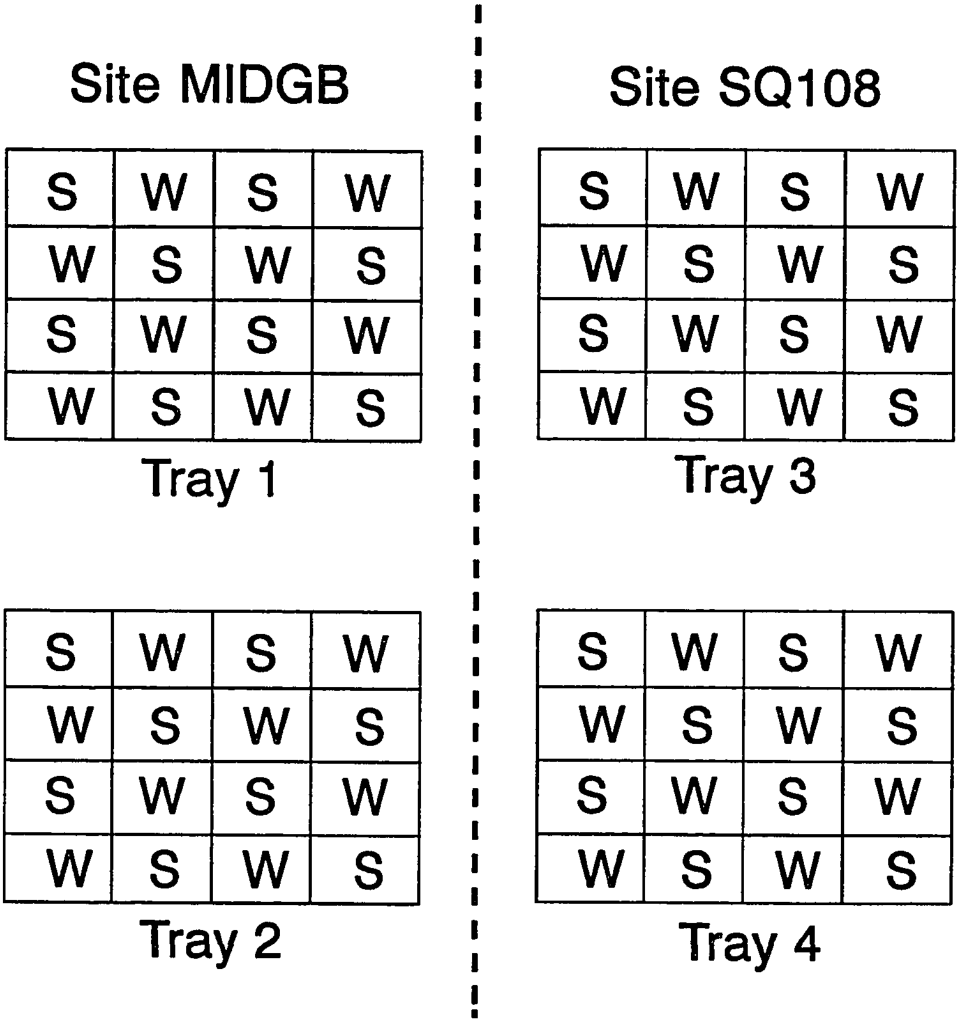
A two-way ANOVA was used two test for significant effects of SALINITY (2, 12, 22, 32 ppt) and WATER BATH (I, II) on PWC. A Model I ANOVA was used because both factors were considered fixed. This is obvious for SALINITY but less so for WATER BATH. I was only concerned with the specific water baths used in the experiment and was not interested in considering the effect of using different tanks in general. In this case, WATER BATH is considered a fixed effect (Zar, 1984). PWC was transformed by the square root-arcsine transformation prior to analysis. The Kolmogorov-Smirnov test with the Lilliefors modification and probability plots of residuals indicated no significant departures from the assumption of normality and Levene's test indicated homogeneity of variances. A two-way contingency table was used to detect differences in mortality at each salinity (Sokal and Rohlf, 1969).

Experiment II- Growth Under Field Conditions

Smooth and winter flounder were grown for fourteen days in plastic cubicles (15 cm width X 12 cm length X 12 cm height) attached to weighted platforms. The cubicles had a

3 cm X 6 cm screened (0.2 mm mesh) opening on all sides to allow open water circulation while excluding potential prey items so that differences in prey abundance between experimental sites could be excluded as a factor affecting growth. Sixteen cubicles were attached to each platform, and two platforms were deployed at each of two sites in Great Bay Estuary. Each platform held eight smooth flounder and eight winter flounder placed alternately in the cubicles for a total of sixteen individuals of each species at each site (Figure 2.2). One site was located at the mouth of the Squamscott River (SQ108) and the other site was in the middle of Great Bay proper (MIDGB) (see Figure 1.1). When deployed, the platforms rested on the bottom in about 6 meters of water. The platforms were raised to the surface daily and each flounder was fed to excess with partially thawed bloodworms (Tubifex sp). Bottom water temperature and salinity were recorded at this time.

The flounder were grown under these conditions for 14 days during May, 1991. At that time of year, salinity is relatively low in the estuary, and Armstrong (Section I) found that only smooth flounder occurred at the lower salinity station, SQ108, while both smooth and winter flounder occurred at the higher salinity station, MIDGB. Trawl samples taken at these two sites while this experiment was in progress agreed with Armstrong's (Section I) findings.



Site MIDGB

S	W	S	W
W	S	W	S
S	W	S	W
W	S	W	S

Tray 1

S	W	S	W
W	S	W	S
S	W	S	W
W	S	W	S

Tray 2

Site SQ108

S	W	S	W
W	S	W	S
S	W	S	W
W	S	W	S

Tray 3

S	W	S	W
W	S	W	S
S	W	S	W
W	S	W	S

Tray 4

Figure 2.2. Schematic drawing of experimental design for Experiment II- growth of smooth and winter flounder at two estuarine sites. S=smooth flounder; W=winter flounder.

Growth was measured the same as in Experiment I. Transformation of PWC and tests for normality and homogeneity of variances were also the same as Experiment I. A nested ANOVA was used to test for significant effects of SITE and PLATFORM, with platform nested beneath site. A two-way contigency table was used to detect differences in mortality between sites.

Experiment III- Changes in Oxygen Consumption in Response to a Salinity Challenge.

Smooth and winter flounder were transferred from flow-through holding tanks at the Jackson Estuarine Laboratory to a constant temperature cold room. They were then held in a recirculating seawater system at 15°C. and 20 ppt for two weeks prior to the experiment. Flounder were starved for 48 hours prior to the experiment to prevent increases in metabolism associated with feeding (Jobling and Spencer-Davies, 1980).

Oxygen consumption rates for the two species were measured using a flow-through respirometer equipped with a constant temperature water jacket maintained at 15°C (see Figure 1 in Jury et al. (1994) for a schematic of the apparatus). The oxygen tension of water entering and leaving the animal chamber was measured with Strathkelvein polarographic oxygen electrodes (electrode model no,. 1302; meter no. 781). The analog outputs of the oxygen meters were digitized, stored, and displayed on a computer using an

8-channel analog-digital converter and the oscilloscope simulation program MacScope. The oxygen concentration was measured initially in the "in" electrode chamber receiving completely oxygenated water. The water then ran from this chamber to the animal chamber and then to the "out" electrode chamber where oxygen tension was measured again. The flow rate was held constant at 27.5 ml/minute using a Masterflex peristaltic pump. At this flow rate, oxygen tension never dropped more than 25%, eliminating possible changes in metabolism associated with hypoxia (Beamish, 1964; Voyer and Morrison, 1971; Steffensen et al., 1982). Oxygen consumption was measured for five individuals of each species before and after a salinity drop from 20 ppt to 10 ppt according to the following experimental protocol.

One individual was placed in the respirometer and allowed to acclimate for one hour at 20 ppt. The oxygen levels of intake and exhaust water were then recorded for one hour, after which the salinity was lowered to 10 ppt over a ten minute period. The fish was then allowed to acclimate to the new salinity for one hour, prior to recording oxygen levels again for one hour. Oxygen consumed was measured as the difference between the oxygen levels in the intake and exhaust water and was standardized to ml O_2/hour/g. The mean oxygen consumption over the two one-hour time periods, one at 20 ppt and one at 10 ppt, were used in all calculations. Percent change in oxygen consumption (PCO) was calculated by the formula:

$$PCO = (C10-C20)/C20$$

where C10 = oxygen consumption rate at 10 ppt

C20 = oxygen consumption rate at 20 ppt

PCO was transformed using the square root-arcsine transformation and deviations from normality and homogeneity of variances were tested for using the previously mentioned tests. A t-test was used to detect a difference in PCO between the species. T-tests were also used to detect differences in rates of oxygen consumption between species and between treatments.

Results

Experiment I

Smooth flounder. Salinity had a significant effect on PWC and mortality. The two-way ANOVA showed a significant effect from SALINITY but no significant effect from WATER BATH or the interaction of SALINITY X WATER BATH (Table 2.1). The data from both water baths were then pooled and the Tukey multiple range test (Zar, 1984) was used to make pairwise comparisons between salinity treatments. Mean percent weight change was highest at 12 ppt (0.50%) and 22 ppt (0.40%) and lowest at 2 ppt (-9.97%). Two groups were indicated by the Tukey test with weight change at 32 ppt (-4.95%) included in both groups (Figure 2.3). Many individuals, especially those grown in 2 ppt and 32 ppt,

Table 2.1. Results of two-way ANOVA for smooth flounder, *Pleuronectes putnami*, Experiment I.

Source	Sum-of Squares	DF	Mean-Square	F-Ratio	P
Salinity	0.098	3	0.033	10.714	0.0001
Water Bath	0.002	1	0.002	0.720	0.406
Salinity x Water Bath	0.026	3	0.009	2.811	0.066
Error	0.061	20	0.003		

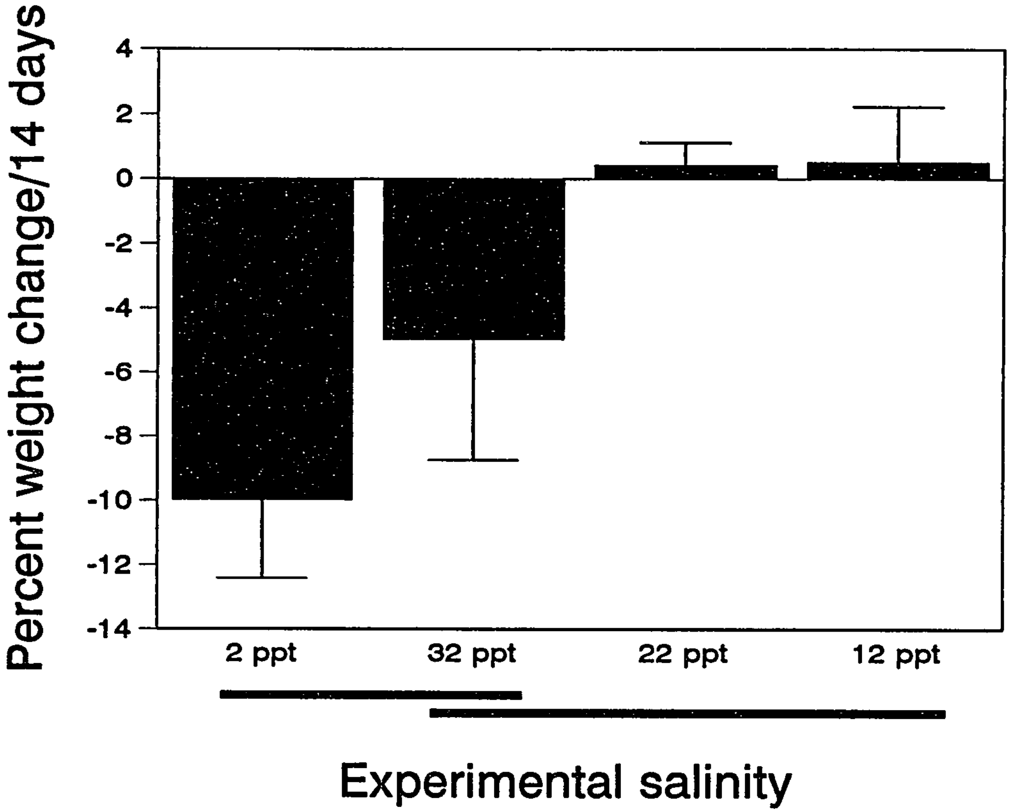


Figure 2.3. Weight change in smooth flounder grown for 14 days at four different salinities, Experiment I. Horizontal bars beneath the x-axis labels indicate treatments that are not significantly different.

exhibited weight loss even though all individuals appeared to be feeding during the experiment.

A significant difference in mortality was detected among the four salinities (Pearson chi^2=10.476, p=0.015). The number of individuals surviving the experiment was lowest at 32 ppt (Figure 2.4).

Winter flounder. Winter flounder also showed significant differences in PWC and mortality among salinities. Similar to the results for smooth flounder, the two-way ANOVA showed significant effects for SALINITY but no effect from WATER BATH or the interaction of WATER BATH X SALINITY (Table 2.2), so the data were pooled for use in the Tukey multiple range test. Positive growth occurred at 22 ppt (2.91%), while slight weight loss occurred at 32 ppt (-0.60%), moderate weight loss at 12 ppt (-4.79%) and massive weight loss at 2 ppt (-19.00%). The Tukey test indicated two groupings, one including 12 ppt, 22 ppt, and 32 ppt, and the other containing only 2 ppt (Figure 2.5). As with the smooth flounder, weight loss occurred in many individuals even though all experimental animals appeared to be feeding.

Mortality was significantly different among salinities (Pearson chi^2=12.500, p=0.006). Mortality was much greater at the lower salinities (Figure 2.4).

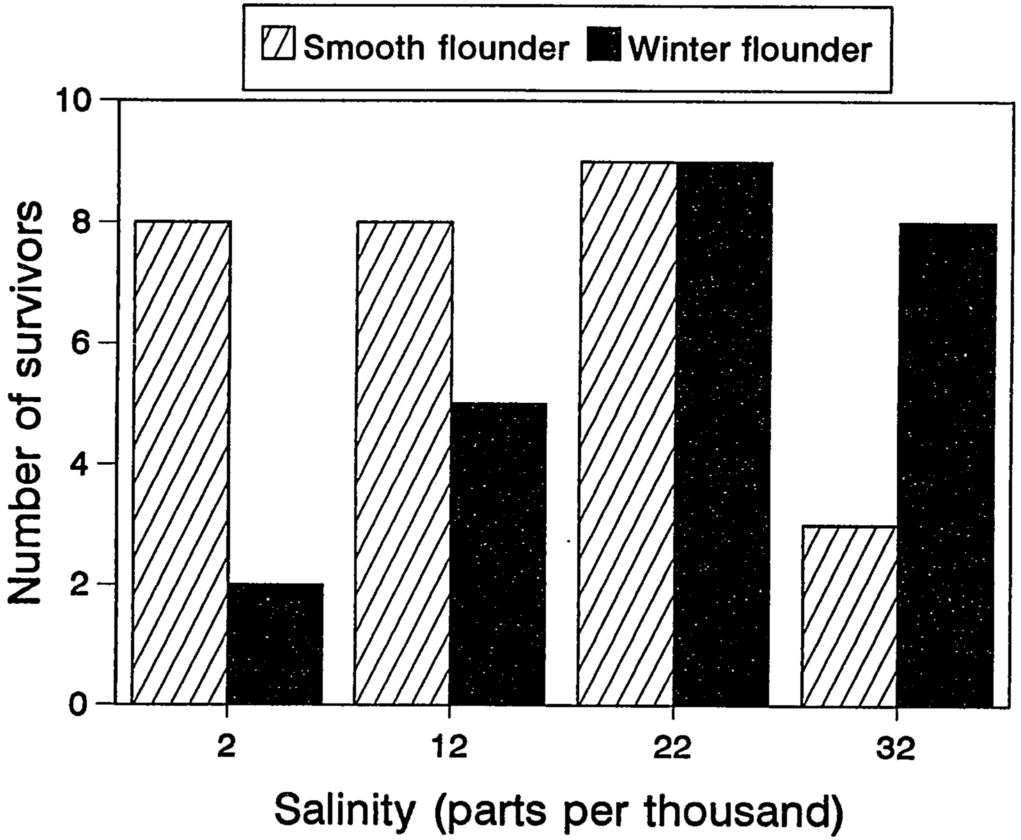


Figure 2.4. Survival of smooth and winter flounder grown at four salinities for 14 days, Experiment I.

Table 2.2. Results of two-way ANOVA for winter flounder, *Pleuronectes americanus*, Experiment I. Results for 2 ppt are not included because there were no survivors in Water Bath 1.

Source	Sum-of Squares	DF	Mean-Square	F-Ratio	P
Salinity	0.024	2	0.012	2.036	0.163
Water Bath	0.004	1	0.004	0.597	0.451
Salinity x Water Bath	0.007	2	0.004	0.615	0.553
Error	0.096	16	0.006		

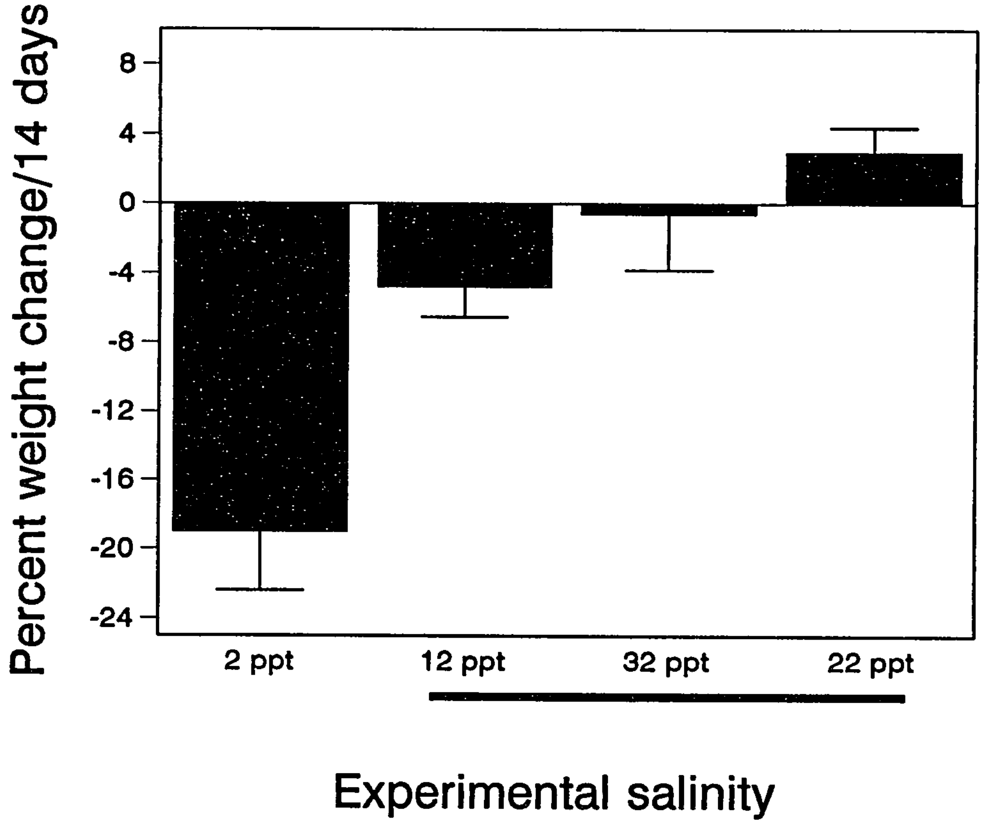


Figure 2.5. Weight change in winter flounder grown at four salinites for 14 days, Experiment I. Horizontal bar beneath the x-axis labels indicates treatments that are not significantly different.

Experiment II

During the course of the experiment, salinity at SQ108 ranged from 1.2 to 14.3 ppt with a mean of 6.7 ppt, while at MIDGB salinity ranged from 6.5 to 21.9 ppt with a mean of 15.8 ppt. Mean temperature at the sites was 17.6°C. and 14.7°C. at SQ108 and MIDGB, respectively.

Smooth flounder. Percent weight change was not significantly different between sites or between trays within each site (Table 2.3). Mean weight change was negative at both sites (Figure 2.6) but mortality was low (MIDGB=0%; SQ108=25%) and not significantly different (Pearson chi^2=2.872, p=0.090) (Figure 2.7) between sites.

Winter flounder. All winter flounder died in one of the trays at SQ108, so an incomplete nested ANOVA design was used. Weight loss was significantly greater at SQ108 than MIDGB, and there was no significant difference between trays at MIDGB (Table 2.4, Figure 2.6). Mortality was significantly higher at SQ108 (Pearson chi^2=16.762, p=0.0001) (Figure 2.7).

Experiment III

Both species showed increases in oxygen consumption when salinity was lowered from 20 ppt to 10 ppt. Smooth flounder had a mean percent increase in oxygen consumption of 29.2% (S.E.=8.5,) and winter flounder had a mean increase of 51.5% (S.E.=17.4) (Table 2.5) but these values were not

Table 2.3. Results of Nested Anova on growth of smooth flounder, *Pleuronectes putnami* in Experiment II.

Source	Sum-of Squares	DF	Mean-Square	F-Ratio	P
SQ108 Trays	0.001	1	0.001	0.156	0.696
MIDGB Trays	0.001	1	0.001	0.204	0.656
MIDGB vs. SQ108	0.001	1	0.001	0.313	0.582
Error	0.075	21	0.004		

Table 2.4. Results of incomplete Nested Anova on growth of winter flounder, *Pleuronectes americanus* in Experiment II.

Source	Sum-of Squares	DF	Mean-Square	F-Ratio	P
MIDGB Trays	0.002	1	0.002	0.478	0.499
MIDGB vs. SQ108	0.026	1	0.026	6.978	0.017
Error	0.063	17	0.004		

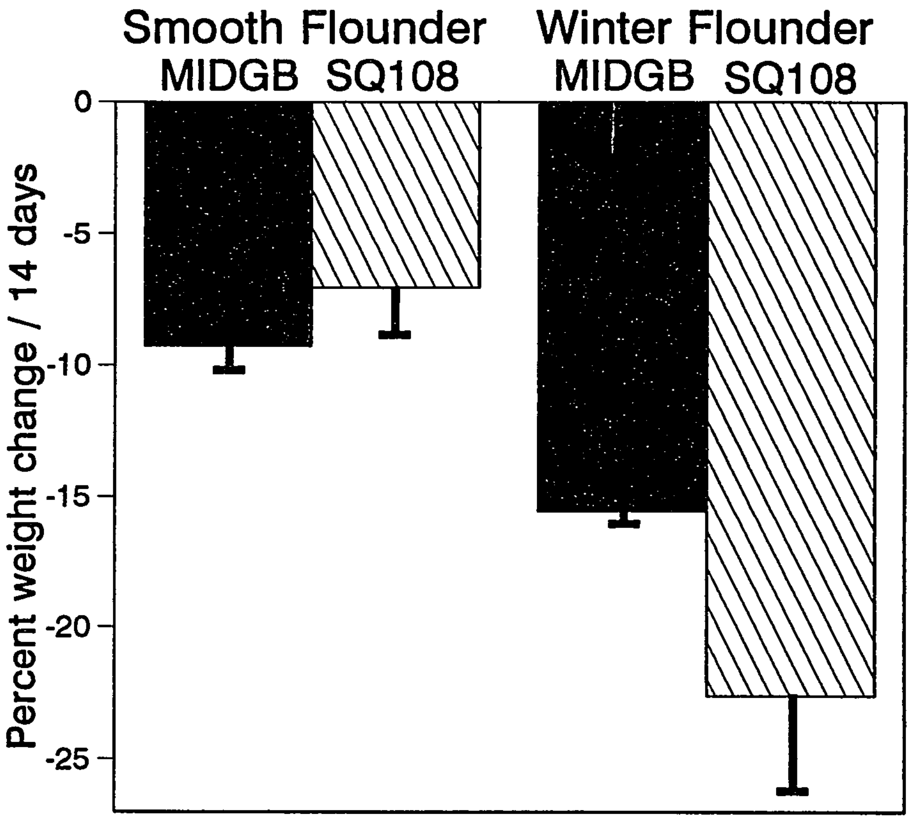


Figure 2.6. Weight change in smooth and winter flounder grown for 14 days at two estuarine sites, Experiment II. Error bars are one standard error.

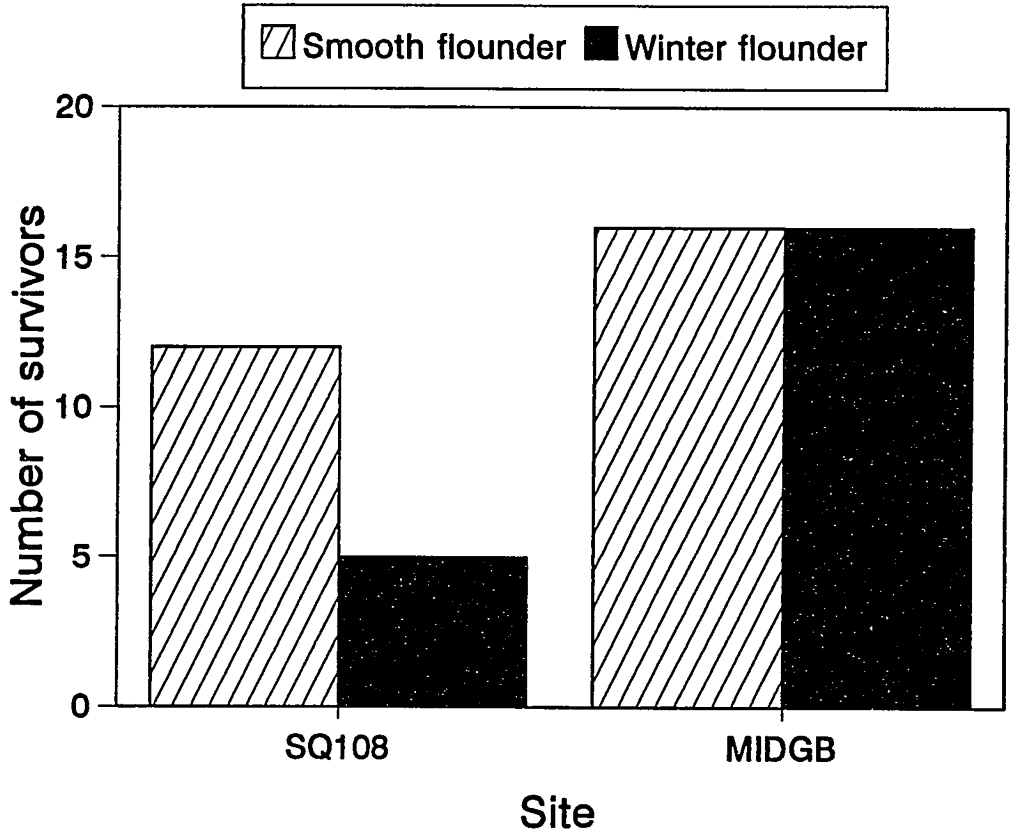


Figure 2.7. Survival of smooth and winter flounder at two estuarine sites, Experiment II.

Table 2.5. Oxygen consumption rates (ml O_2/hour/gram) for individual test animals at 20 ppt and 10 ppt salinity from Experiment III.

Species	20 ppt	10 ppt	Percent increase
smooth	0.0849	0.1205	41.9
smooth	0.1122	0.1307	16.4
smooth	0.0876	0.1354	55.0
smooth	0.0632	0.0754	8.5
smooth	0.1332	0.1654	24.2
winter	0.0698	0.0884	26.8
winter	0.0933	0.1165	24.9
winter	0.0743	0.1140	53.4
winter	0.0750	0.1012	35.0
winter	0.0376	0.0822	118.5

Table 2.6. Mean oxygen consumption in ml O_2/hour/gram (1 standard error of the mean) by smooth and winter flounder at 20 ppt and 10 ppt salinity and mean percent increase in O_2 consumption when flounder were moved from 20 ppt to 10 ppt. Results of t test comparisons within (to the right of the comparison) and between (beneath the comparison) species.

	20 ppt	10 ppt		% change
Smooth flounder	0.096(0.012)	0.125(0.015)	t=2.692, p=0.027*	29.2(8.5)
Winter flounder	0.070(0.009)	0.100(0.007)	t=2.346, p=0.047*	51.6(17.5)
	t=1.636, p=0.140	t=1.360, p=0.211		t=1.153, p=0.282

significantly different (Table 2.6). Both species showed significant increases in oxygen consumption going from 20 ppt to 10 ppt but there was no significant difference in oxygen consumption between species at either salinity (Table 2.6).

Discussion

Experiment I

Laboratory experiments indicated significant differences in mean weight change among salinities for both species and a trend in survivorship paralleling those for growth. Smooth flounder had the least weight loss and lowest mortality at 12 and 22 ppt, while winter flounder had the least weight loss and lowest mortality at 22 and 32 ppt.

Many individuals showed weight loss during the course of the experiment rather than weight gain as expected. Weight gain in similarly sized winter flounder has been shown to be about 1-2% per day in flow through culture systems (Hoornbeek et al., 1982; Bejda et al., 1992). However, under the conditions of this experiment, mean weight change was negative in all but three treatments (winter flounder @ 22 ppt, smooth flounder @ 12 and 22 ppt) even though all experimental animals appeared to be feeding, and where growth was positive it was much less than the expected growth rate. One would expect weight loss or a decreased growth rate at salinities that are beyond the physiological capabilities of the test species. Differing weight change among salinities is the summation of the differing metabolic costs of osmoregulation and maintenance of ionic balance at each salinity and the effects of salinity on feeding rate and food conversion efficiency (Kinne, 1960). There are several possible reasons for the poor growth across salinities found in this experiment. The test animals were stressed on alternate days by a water change. Stress was possibly induced by both the physical disturbance and slight changes in water quality associated with the water change. This had at least a temporary effect of raising their metabolic rate. Fletcher (1992) found that handling stress markedly disturbed the water balance in plaice, *Pleuronectes platessa,* causing a weight loss that had a recovery period of greater than one day. Because a static system was used, declining water quality over the 48 hours between water changes may also have had an effect. Oxygen concentration was kept at or near saturation by gentle aeration and the ammonia level was checked daily and was always undetectable. The nutritional quality of the food used in the experiment, *Tubifex* sp., was not known. It is possible that the nutritional quality was so low that even though normal amounts of food were consumed, the flounder were unable to meet the needs of routine metabolism. However, *Tubifex* sp. has been used successfully to grow the flounder, *Platichthys flesus* (Gutt, 1985). The reason for the lack of normal growth is unknown but may have been the result of a combination of these factors.

Despite the lack of expected growth, weight change was used as a measure of the relative costs of existing at each salinity in comparison to the other salinities, with the assumption that whatever factors caused poor growth, with the exception of salinity, acted equally across all salinity treatments. The salinities can be ordered from low to high in respect to the metabolic costs. For smooth flounder, the greatest costs were at the extremes used in the experiment, 2 and 32 ppt. For winter flounder, it was at the two lowest salinities used, 2 and 12 ppt, although I include 12 ppt with caution because it was not statistically significantly different. It is felt that it is acceptable to discuss trends in the results even though statistical significance is lacking in some cases. If we consider the growth data in conjunction with the survival rate, it makes a stronger case for both. These data indicate that the two species differ in their abilities to inhabit different salinities and suggest that it is more energetically costly for winter flounder to penetrate into the oligo-mesohaline areas of the estuary than it is for smooth flounder. Conversely it is more costly for smooth flounder to enter polyhaline areas than it is for winter flounder. If minimizing the costs of osmoregulation is an important factor in controlling the distribution of these two estuarine species, we should expect to find smooth flounder in a salinity range of about 7-27 ppt and winter flounder in salinity greater than about 17 ppt (These numbers are the midpoints between treatments). This agrees closely with their distribution in Great Bay Estuary (Armstrong, Section I). It also agrees with a study by Fried (1973) that showed that smooth flounder were restricted to waters less than 28.5 ppt in two estuaries in Maine. Obviously, the two species' respective osmoregulatory abilities play a major role in controlling their distributions. It is important, however, to recognize that there may be other factors acting in concert with salinity to alter the species' distributions. These factors include the interaction between salinity and temperature, which can be very important (Kinne, 1960). Other factors include biotic variables such as prey availability, predation risk (Werner et al. 1983; Sogard,1992), and inter- or intra-specific competition (Werner and Gilliam, 1984; Mittelbach, 1988) which can modify the relative energetic cost of existing in a particular location along a salinity gradient and therefore modify habitat selection. There is evidence that other factors may be acting in addition to salinity. For instance, in all years examined, smooth flounder left MIDGB in early summer even though salinity appeared favorable. In addition, in 1991, winter flounder delayed their migration upstream into SQ108 even though salinity appeared to be high enough (Armstrong, Section I).

Several closely-related estuarine fish species have been found to be most abundant along a salinity gradient where their metabolic cost of osmoregulation is lower compared to other areas including three species of Ambassidae (Martin, 1990) and two sciaenids (Moser and Gerry, 1989). Salinity tolerance was found to be an important factor in determining the spatial segregation of several species of goby from Swan Estuary in Australia (Gill and Potter, 1993). Gutt (1985) found that juveniles of the euryhaline flounder (Platichthys flesus) grew significantly faster in 5 and 15 ppt as compared to 0 and 35 ppt. This is similar to results for smooth flounder in the present experiment. He found that poor food conversion and reduced food intake contributed to poor growth at 0 and 35 ppt. Under laboratory conditions, juvenile southern (Paralichthys lethostigma) and summer (P. dentatus) flounder grew best under different physical regimes (Peters, 1971; Peters and Kjelson, 1975). Southern flounder grew best in low salinities and high temperature while summer flounder grew best in higher salinities and more moderate temperatures. Field studies showed that the two species were segregated in estuaries accordingly (Powell and Schwartz, 1977). Burke et al. (1991) demonstrated that this habitat segregation is established soon after settlement. Malloy and Targett (1991) found no significant effect of salinity on growth rates of summer flounder in contrast to the above study.

They suggested other factors control distribution. Peters and Boyd (1972) demonstrated that hogchokers (Trinectes maculatus) exhibit migratory behavior which appears to place them in environments that do not maximize growth. They suggested that these movements may be in response to predation or food availability.

Experiment II

Experiment II exposed the flounder to physico-chemical conditions found in the field. The results for both growth and survival provide conclusive evidence that winter flounder are excluded from SQ108 in the springtime by physico-chemical factors, most likely salinity. During the spring they are unable to penetrate into the mouth of the Squamscott River because of low salinity. It is not simply more metabolically costly for winter flounder to reside at SQ108 at this time of year, it is lethal to most individuals. Smooth flounder are more plastic in their salinity requirements. They appear to be adapted to inhabit both SQ108 and MIDGB. The results of this field experiment agree with the findings of Experiment I and with the distribution data from Armstrong (Section I). Additional stresses were found in the field experiment that were not found in the laboratory experiment including salinity and temperature changes associated with the tidal cycle. These stresses can only increase the metabolic costs of iono- and osmoregulation, especially for species that are not well adapted to exist in such an environment.

Experiment III

This experiment subjected the two flounder species to a salinity challenge in the form of a 10 ppt drop in salinity over 15 minutes. Such a challenge can occur at station SQ108 where salinity routinely drops by 15-18 ppt over 6 hours on an ebbing tide and eddies created by mixing of waters of different salinities can create sudden drops in salinity of several ppt on a much shorter time scale (personal observation). A salinity challenge experiment is more realistic than the static salinity experiments done by many researchers because under estuarine field conditions fish seldom have time to acclimate to salinity conditions.

The rates of oxygen consumption found in this study (range 0.04-0.17 ml O_2/g/hr) are similar to values obtained for winter flounder in other studies. Frame (1973) obtained a range of 0.01-0.13 ml O_2/g/hr at 16°C while Voyer and Morrison (1971) measured oxygen consumption in a range of 0.04-0.09 ml O_2/g/hr at 9.9-10.7°C. Standard metabolism of the flounder, Platichthys flesus, was found to be 0.042 ml O_2/g/hr at 10°C. (Steffensen et al., 1982) of which about 17% was used for osmoregulation (Kirschner, 1993).

Both species showed significant increases in the amount of oxygen consumed when subjected to a relatively abrupt salinity decrease. There was no significant difference between the species in the percent increase in consumption, indicating that, metabolically speaking, both species responded equally to the challenge. In addition, there was no significant difference in the oxygen consumption rate between the species at either salinity. This suggests that it is not the short term metabolic costs of iono- and osmoregulation that accounts for the differences in growth and mortality in Experiment I and II but rather some other factor that has energetic costs such as changes in food conversion efficiency or the rate of food consumption.

The significant increase in oxygen consumption in lower salinity seen in both species is consistent with the generalization of Prosser (1973) that, for euryhaline species, metabolism increases at reduced salinities. Increases in respiration rates associated with lower salinities have been found in a number of estuarine fish species (e.g. Marais, 1978; Nordlie, 1978; Barton and Barton, 1987). Moser and Gerry (1989) found oxygen consumption rates in spot, Leiostomus xanthurus and croaker, Micropogonias undulatus in general, decreased when salinity was reduced. Field collections and behavioral experiments showed that croaker avoided areas with large salinity fluctuations but respiration experiments failed to find a significant difference in the response of the two species to salinity challenges, similar to the present experiment.

Frame (1973) measured oxygen consumption in winter flounder subjected to salinity drops from 30 ppt to 20 ppt or from 30 ppt to 10 ppt. He found that oxygen consumption was significantly higher at 30 ppt than at the two lower salinities and that there was no difference in oxygen consumption between 20 and 10 ppt. He attributed the lower metabolic rate at the reduced salinities to a reduced cost of osmoregulation as the test salinities approached an isotonic condition with the internal environment of the winter flounder. Because his flounder were acclimated at a different salinity (30 ppt) and because oxygen consumption was never directly compared at 10 and 20 ppt, it is difficult to compare the results of our two studies.

Summary

Smooth and winter flounder appear to be adapted to different optimal salinities. Smooth flounder have a lower cost of metabolism and greater survival in habitats of lower salinity, typical of estuarine riverine areas, and may in fact be maladapted for existing in full strength salinity and therefore excluded from coastal regions. Winter flounder appear to be excluded from the furthest upper reaches of estuaries by a greater cost of osmoregulation and increased mortality in low salinity areas. The physiological stress imposed by low salinity is likely the greatest factor determining the intra-estuarine distribution of smooth and winter flounder. However, a role for biotic factors remains possible.

The physiological consequences of habitat selection are ecologically very important. The habitat an animal occupies influences its physiological capacities and ultimately it ecological performance (Huey, 1991). Habitat selection by smooth and winter flounder along an estuarine salinity gradient may have a profound effect on the interactions between the species. Salinity certainly plays an important role in mediating those interactions by causing at least partial intra-estuarine segregation of the two species.

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III. DIET AND NICHE DYNAMICS IN TWO SYMPATRIC ESTUARINE FLOUNDERS.

Introduction

Smooth flounder, Pleuronectes putnami, and winter flounder, Pleuronectes americanus, are important members of the ichthyofauna in boreal estuaries along the northeast coast of North America. They have been noted as potential competitors (Scott and Scott, 1988) yet little is known of their overlap in use of resources. Much is known of the food habits of winter flounder (see reviews in Klein-MacPhee (1978) and Buckley (1989)) because of their commercial and recreational importance. Little of this work has been done in areas where they co-occur with smooth flounder. The little information that exists on food habits of smooth flounder (Laszlo, 1972; Imrie and Daborn, 1981; Scully, 1983) indicates they feed on prey types that are similar to those consumed by winter flounder. Therefore a potential for overlap in food usage exists in areas where they utilize the same habitat. Armstrong (Section I) demonstrated that the two species overlapped partially in their habitat use in Great Bay Estuary, New Hampshire, and that the overlap was seasonally dynamic with movements of the two species driven primarily by the estuarine salinity regime (Armstrong, Section II). He speculated on the role of biotic factors such as prey abundance and competition as additional factors controlling movements.

Patterns of resource utilization can provide insights into species interactions although the interpretation of these data relevant to competition theory remains a contentious issue. The study of resource exploitation provides the most straightforward means of attaining a preliminary assessment of the relative importance of interactive processes within natural communities (Winemiller, 1989). Competition theory predicts that niches of species should vary spatially, as a function of distributions of closely related, potentially competing species, and temporally, as a function of variation in resource abundance and population densities of potential competitors (Llewellyn and Jenkins, 1987). The predominant temporal pattern of niche overlap seen in empirical studies is decreased overlap during times of resource scarcity (Schoener, 1982; Ross, 1986). This has been interpreted as evidence of the importance of competition in structuring communities. Other studies (Wiens, 1977, 1984; Wiens and Rotenberry, 1979; Rotenberry, 1980) have de-emphasized the role of competition in structuring communities.

Boreal estuaries are spatially and temporally dynamic systems. They exhibit extreme changes in both biological and physical characteristics on several temporal scales, ranging from minutes to years, but dominated by somewhat predictable seasonal changes. Of particular interest to the study of interactions between species in estuaries is the potential for changes in resource abundance and the mediation of biological interactions by physiological constraints.

This study examines diet and habitat use in smooth and winter flounder in upper Great Bay Estuary. Comparisons of diet are made between species and among several sites, and ontogenetic changes in diet are examined. Niche overlap for diet and habitat use and dietary niche breadth are examined on a seasonal basis in relation to changes in resource abundance. The pattern of changes in these measurements are interpreted relative to the role of smooth and winter flounder as potential competitors.

Methods and Materials

Food Habits

Smooth and winter flounder were collected by trawl each month from April - November, 1990 at stations SQ108, MIDGB, and GBFLATS (see Figure 1.1). Flounder were fixed whole in formalin immediately after capture. Flounder greater than about 200 mm TL had formalin injected into the abdominal cavity prior to immersion in formalin. After fixation in formalin for a minimum of three days, stomachs were removed and stored in 50% isopropanol. Stomachs were rinsed in fresh water prior to any further analysis. Before removing the contents of the stomach, fullness was estimated by eye and assigned a subjective stomach fullness index (SFI) value of 0 to 5 with 0 appearing completely empty and 5 fully distended. Prey items were sorted to the lowest practical taxa, counted, and a blotted wet weight was taken to the nearest 0.0001 g.

Smooth and winter flounder were separated into five size classes based on their total length (1-50 mm; 51-100 mm; 101-150 mm; 151-200 mm; and >200 mm). The relative contribution of different types of food to the total diet was determined using: (1) percent frequency of occurrence (the number of stomachs in which a food type occurred expressed as a percentage of the total number of stomachs containing food); (2) percent volume (the volume of each food type expressed as a percentage of the total volume of food from all stomachs); (3) percent numerical abundance (the number of individuals of each type of food expressed as a percentage of the total number of food items found in all stomachs). An index of relative importance, IRI (Pinkas et al., 1971), which incorporates all three of these measurements, was calculated for each prey type from the formula:

$$IRI = (N+V)F$$

where N = percent numerical abundance

V = percent volume

F = percent frequency of occurrence

Prey types with the highest IRI value were considered the major food items in the diets of these two flounder. Using this index, some of the bias inherent in using numerical, volume, or frequency of occurrence measures alone is eliminated. For example, more representative prey are not dominated by numerically rare but high biomass prey, or by numerically abundant prey which may contribute little to the total prey biomass.

Cluster analysis was used to detect natural groupings based on stomach data. Clustering was based on IRI values for prey types using the single linkage method with a Euclidean distance measure (Wilkinson, 1988). Prior to clustering, data were grouped by flounder species, site of capture, and size class.

Selectivity by smooth and winter flounder on potential benthic prey was determined using Ivlev's (1961) index of electivity (E), calculated as follows:

$$E = r_i - p_i / r_i + p_i$$

where r_i = percent of prey species i in the diet

p_i = percent of prey species i in the benthos

Percent numerical abundance was used in this calculation and in the following calculations of niche overlap and niche breadth.

Niche Overlap, Niche Breadth and Prey Abundance

The relative abundance of macrobenthic organisms was obtained from a concurrent study on the benthic community at the sites where trawl samples were taken (R. Grizzle, unpublished data). Five replicate 0.0085 m^2 cores were taken in all months that trawl samples were taken. The benthic samples were processed by standard benthological techniques and individuals were sorted to the lowest possible taxon and counted.

Resource overlap coefficients (D) for habitat and food use were calculated using the formula of Schoener (1968):

$$D_{jk} = 1 - 0.5\Sigma|p_{ij} - p_{ik}|$$

where p_{ij} and p_{ik} are the frequencies of utilization of the i^{th} resource by the j^{th} and k^{th} species, respectively. This index ranges from 0, when there is no overlap in resource usage between the species, to 1, when there is complete overlap in resource use, with values greater than 0.6

considered to be biologically significant (Wallace, 1981). It has been found to be independent of sample size (Kohn and Riggs, 1982) and among the least biased of the overlap measures (Linton et al., 1981; Wallace, 1981). Habitat use data was based on trawl collections at five sites in upper Great Bay Estuary as reported in Armstrong (Section I). Both habitat use and diet data were pooled into spring, summer, and autumn.

Niche breadth (B) was calculated for habitat and diet data using Levins' formula (Levins, 1968):

$$B = 1/\Sigma p_i^2$$

where p_i is the proportional use of prey type i. The value of B varies from 1 to n, where n is the number of prey categories. To compare values of B with different n values, normalization is required. Niche breadth was standardized by the formula (Evans, 1983):

$$B_s = (B-1)/(n-1)$$

This standardized measure ranges from 0 to 1 and decreases as the diet becomes more dominated by a few prey types.

Both niche overlap and niche breadth were calculated for individuals of size class 101-150 mm. This was the most abundant size class and the only class that had sufficient sample sizes in all seasons. This eliminated possible bias resulting from variation in the abundance of other size classes which may have functionally different niches.

Results

Food Habits

The contents of 519 smooth flounder stomachs and 393 winter flounder stomachs were used in the analyses. Seventeen different prey types were identified. Important prey types (by IRI) included siphons of the small, deposit-feeding bivalve, *Macoma balthica*, the polychaetes *Streblospio benedicti* and *Scolecolepides viridis*, gammarid amphipods, isopods, and cumaceans. The stomach content data pooled over all sites are presented by size class in Table 3.1 for smooth flounder and Table 3.2 for winter flounder.

The following discussions of prey abundance in the diets are based on numerical abundance so that abundance in the stomachs can be compared with abundance from benthic core samples. The most important prey species for smooth flounder at SQ108 were *M. balthica*, *S*. *benedicti* and *S*.*viridis* (Figure 3.1). These species were also important for winter flounder along with the mudcrab, *Rhithropanopeus harrisii* (Figure 3.2).

Size-related ontogenetic shifts in feeding were evident for both flounder species. Cumaceans were important in the diet of small (51-100 mm) smooth flounder but were absent in the diets of larger individuals. Preference by the smaller individuals for this small prey are probably related to gape size limitations to feeding on the larger, but more abundant

Size Class (TL mm)

	1-50				51-100				101-150				151-200				200+			
	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI
Polychaeta																				
Heteromastus filiformis	0.0	0.0	0.0	0.0	0.1	0.1	1.0	0.2	0.5	2.7	3.3	10.6	0.2	0.1	2.6	0.8	0.0	0.0	0.0	0.0
Nereis sp.	0.0	0.0	0.0	0.0	0.1	2.2	1.4	3.3	0.0	0.6	0.4	0.3	1.8	11.6	10.3	137.5	5.6	97.2	33.3	3425.7
Scoloplos sp.	0.2	1.0	4.8	6.0	0.5	0.6	2.4	2.8	0.1	0.0	1.2	0.2	0.2	0.1	2.6	0.8	0.0	0.0	0.0	0.0
Aricidea catherinae	0.0	0.0	0.0	0.0	0.2	0.1	1.9	0.7	0.2	0.1	1.2	0.4	0.4	0.1	2.6	1.2	0.0	0.0	0.0	0.0
Eteone heteropoda	0.0	0.0	0.0	0.0	0.4	0.1	7.2	3.4	0.8	0.1	11.4	10.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Streblospio benedicti	4.6	2.1	33.3	223.3	24.2	16.9	66.7	2737.5	38.4	15.8	72.4	3922.1	51.0	12.6	59.0	3751.5	38.9	0.4	66.7	2618.5
Scolecolepides viridis	0.0	0.0	0.0	0.0	3.8	25.2	21.7	630.3	8.8	40.8	29.3	1451.8	22.4	40.3	38.5	2411.1	16.7	1.1	33.3	592.3
Unidentified spionid	0.0	0.0	0.0	0.0	0.2	0.8	1.9	1.9	0.3	0.3	2.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipoda																				
Gammarid amphipod	0.0	0.0	0.0	0.0	3.4	0.5	9.7	38.0	7.2	2.5	16.3	157.1	4.4	0.2	20.5	94.6	16.7	0.1	33.3	557.7
Isopoda	0.0	0.0	0.0	0.0	0.2	3.4	3.4	11.9	1.1	4.5	15.0	84.1	2.8	3.1	25.6	150.9	16.7	0.4	33.3	568.5
Cumacea	3.1	1.0	23.8	98.1	9.0	0.5	19.3	184.5	0.2	0.0	3.3	0.8	0.2	0.1	2.6	0.6	0.0	0.0	0.0	0.0
Decapoda																				
Rhithropanopeus harrisii	0.0	0.0	0.0	0.0	1.2	0.5	1.9	3.2	0.1	0.4	1.2	0.5	0.0	0.0	0.0	0.0	5.6	0.8	33.3	213.3
Crangon septemspinosus	0.0	0.0	0.0	0.0	0.0	0.6	0.5	0.3	0.0	5.6	0.4	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pelecypoda																				
Macoma balthica	92.1	95.8	100.0	18792.1	56.5	41.9	64.3	6320.2	41.1	17.9	47.6	2807.5	11.0	1.1	30.8	372.8	0.0	0.0	0.0	0.0
Mya arenaria	0.0	0.0	0.0	0.0	0.1	0.3	1.4	0.5	0.5	2.3	3.3	9.1	4.4	17.0	5.1	109.6	0.0	0.0	0.0	0.0
Unidentified pelecypod	0.0	0.0	0.0	0.0	0.2	6.1	1.9	12.3	0.4	3.2	5.3	18.7	0.4	0.3	5.1	3.7	0.0	0.0	0.0	0.0
Plant material	0.0	0.0	0.0	0.0	0.1	0.1	1.9	0.3	0.2	3.2	4.1	13.7	0.8	13.5	10.3	146.3	0.0	0.0	0.0	0.0
Sample size=	21				207				246				39				3			

Table 3.1. Diet of five size classes of smooth flounder. N=percent by number; W=percent by weight; O=percent by occurrence; IRI=Index of relative importance.

Size Class (TL mm)

	0-50				51-100				101-150				151-200				200+			
	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI	N	W	O	IRI
Polychaeta																				
Heteromastus filiformis	0.0	0.0	0.0	0.0	0.1	0.1	1.7	0.3	0.1	0.0	0.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nereis sp.	0.0	0.0	0.0	0.0	1.1	19.6	5.1	105.1	1.7	39.8	6.1	253.1	0.6	0.0	5.9	3.5	9.1	32.7	25.0	1044.7
Scoloplos sp.	0.0	0.0	0.0	0.0	1.5	2.8	15.3	65.5	0.9	0.6	7.9	11.4	0.2	0.2	2.9	1.1	0.0	0.0	0.0	0.0
Aricidea catherinae	10.0	16.7	50.0	1333.3	0.3	0.4	3.4	2.5	0.5	0.1	3.7	2.2	0.6	0.1	2.9	1.9	1.1	0.0	6.3	6.7
Eteone heteropoda	0.0	0.0	0.0	0.0	2.4	4.0	18.6	119.2	2.0	0.6	15.9	40.9	0.6	0.1	8.8	5.9	0.0	0.0	0.0	0.0
Streblospio benedicti	50.0	50.0	50.0	5000.0	35.4	32.5	75.1	5101.4	30.0	9.4	66.5	2617.5	16.4	0.7	35.3	604.3	17.6	0.1	12.5	221.7
Scolecolepides viridis	0.0	0.0	0.0	0.0	0.9	6.9	11.3	88.1	4.7	18.0	22.0	498.4	7.0	5.3	23.5	287.9	1.1	0.1	6.3	7.5
Unidentified spionid	0.0	0.0	0.0	0.0	0.3	0.3	2.8	1.7	0.7	0.5	3.7	4.4	0.8	0.1	2.9	2.5	0.0	0.0	0.0	0.0
Amphipoda																				
Gammarid amphipod	10.0	16.7	50.0	1333.3	46.2	24.9	57.6	4093.8	38.4	6.3	56.1	2512.1	56.8	2.6	32.4	1920.2	23.5	0.1	25.0	589.6
Isopoda	0.0	0.0	0.0	0.0	0.3	3.9	5.6	23.6	1.4	3.3	13.4	63.2	0.9	1.5	14.7	36.2	0.0	0.0	0.0	0.0
Cumacea	30.0	16.7	100.0	4666.7	5.7	1.8	32.2	239.4	4.9	0.3	21.3	111.5	0.6	0.0	8.8	5.3	19.8	0.0	12.5	247.6
Decapoda																				
Rhithropanopeus harrisii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	5.1	11.6	119.9	4.3	26.8	17.6	548.7	0.5	1.0	6.3	9.8
Crangon septemspinosus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.8	0.6	6.6	1.5	54.0	17.6	979.7	1.6	3.0	18.8	85.4
Pelecypoda																				
Macoma balthica	0.0	0.0	0.0	0.0	5.8	2.6	21.5	180.4	8.7	1.9	23.8	251.4	7.9	0.4	8.8	73.8	0.0	0.0	0.0	0.0
Mya arenaria	0.0	0.0	0.0	0.0	0.0	0.1	0.6	0.1	0.5	1.8	1.8	4.2	0.9	0.9	5.9	11.1	24.1	60.3	43.8	3690.4
Unidentified pelecypod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.6	0.2	0.4	1.2	5.9	9.6	0.5	0.7	6.3	7.8
Plant material	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.2	0.1	1.2	2.4	3.2	0.6	6.1	8.8	58.5	1.1	2.0	12.5	38.5
Sample size=	2				174				166				34				16			

Table 3.2. Diet of five size classes of winter flounder. N=percent by number; W=percent by weight; O=percent by occurrence; IRI=index of relative importance.

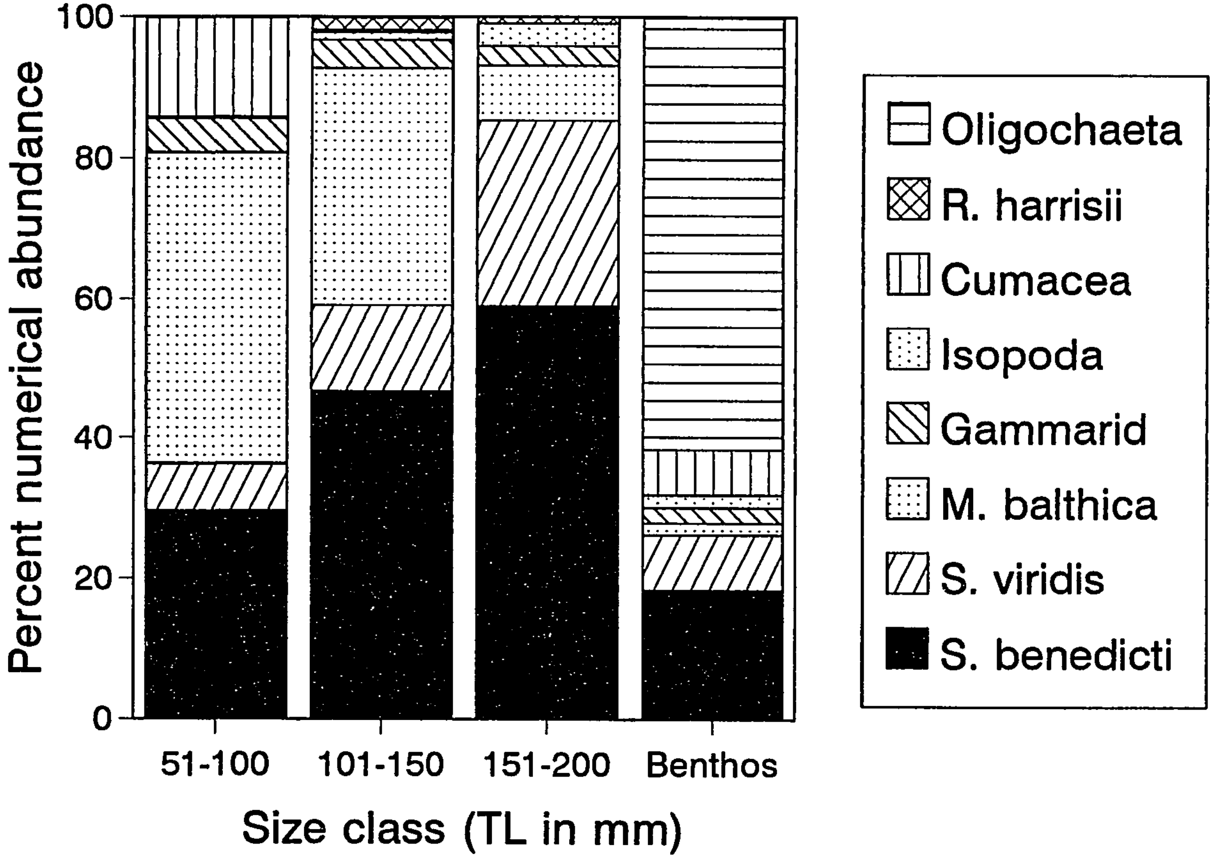

Figure 3.1. Percent numerical abundance of prey types in smooth flounder stomachs and in benthic cores from site SQ108.

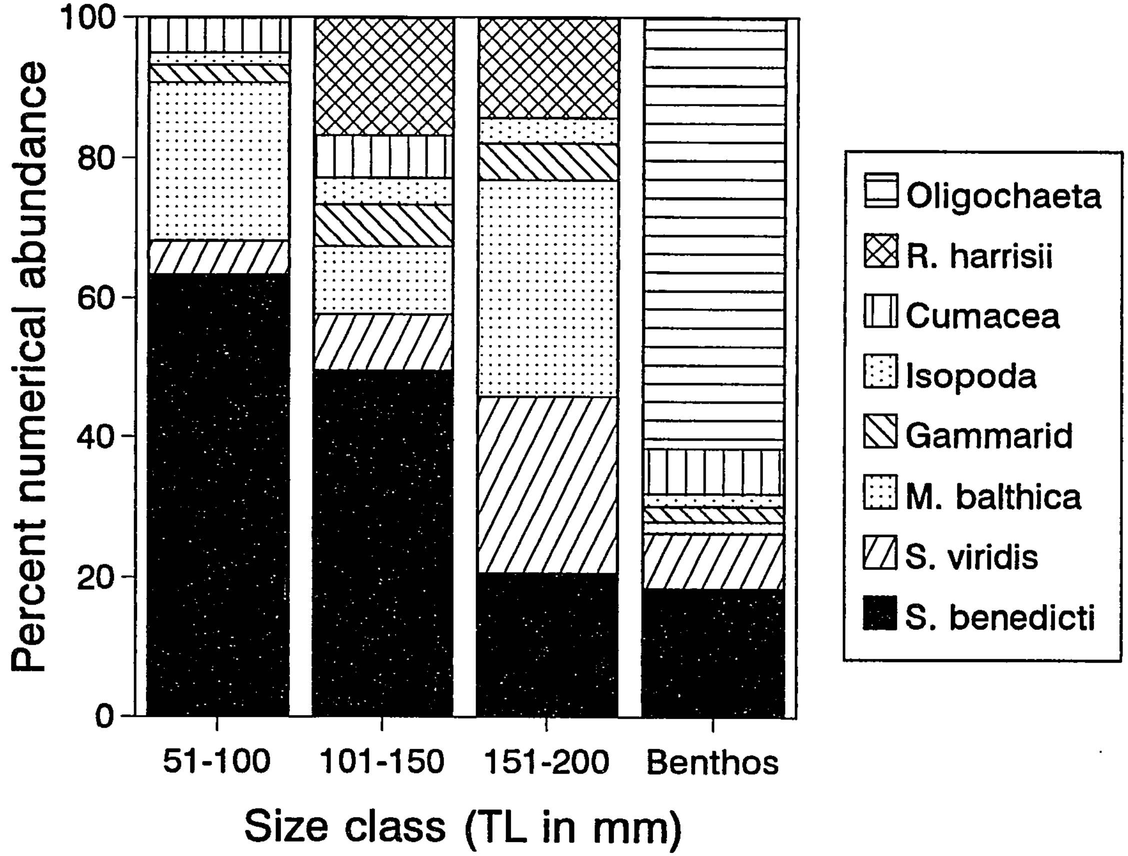

Figure 3.2. Percent numerical abundance of prey types in winter flounder stomachs and in benthic cores from site SQ108.

polychaete worms. Winter flounder also showed decreasing use of cumaceans with increasing size but they remained an important prey item into the 101-150 mm size class. Winter flounder may continue to prey on cumaceans at a larger size because the gape of their mouth is slightly smaller at a given length compared to smooth flounder (Armstrong, unpublished data) and this limits their ability to prey on larger items in comparison to smooth flounder of the same size. Decreasing utilization of M. balthica with increasing size was also seen for smooth flounder, although it remained an important prey item throughout all size ranges examined. Winter flounder did not show a decrease in importance of M. balthica with increasing body size. Both species of flounder fed only on the siphons of M. balthica. The relative importance of S. benedicti increased with size in smooth flounder but decreased with size in winter flounder. Overall, it was the major prey item for both species at SQ108. S. viridis is a larger polychaete than S. benedicti and its importance in the diet of both species increased with increasing body size. The consumption of gammarid amphipods was similar among all size classes of both flounder species. The most important difference between the diets of smooth and winter flounder at SQ108 was the differential use of R. harrisii. Although mudcrabs were poorly represented in the benthic cores, they were abundant in the trawl samples. This estuarine mudcrab was an important prey species to the two larger size classes of winter flounder, but of only minor importance to smooth flounder. It is difficult to understand this difference in terms of gape size limitations. It may represent a difference between the species in foraging behavior or a morphological difference other than gape size such as a difference in pharyngeal teeth.

Oligochaetes were the most abundant organism in the benthic core samples (Figures 3.1 and 3.2) but were not found in the stomachs of either flounder. The abundance of other prey species in the diets loosely followed their abundance in the core samples with the exception of M. balthica, which was grossly over-represented in stomachs compared to their abundance in the core samples. Selectivity for prey items was very similar between smooth and winter flounder (Figure 3.3) indicating similar prey preferences. The only prey types that appeared to be avoided were oligochaetes and the polychaete, Heteromastus filiformis.

At MIDGB, small smooth flounder (51- 100 mm) preyed on a greater number of prey items than at SQ108 (Figure 3.4). Streblospio benedicti was the most abundant prey item. The middle size class of smooth flounder and all size classes of winter flounder (Figure 3.5) were dominated by only two prey types, S. benedicti and gammarid amphipods. The use of

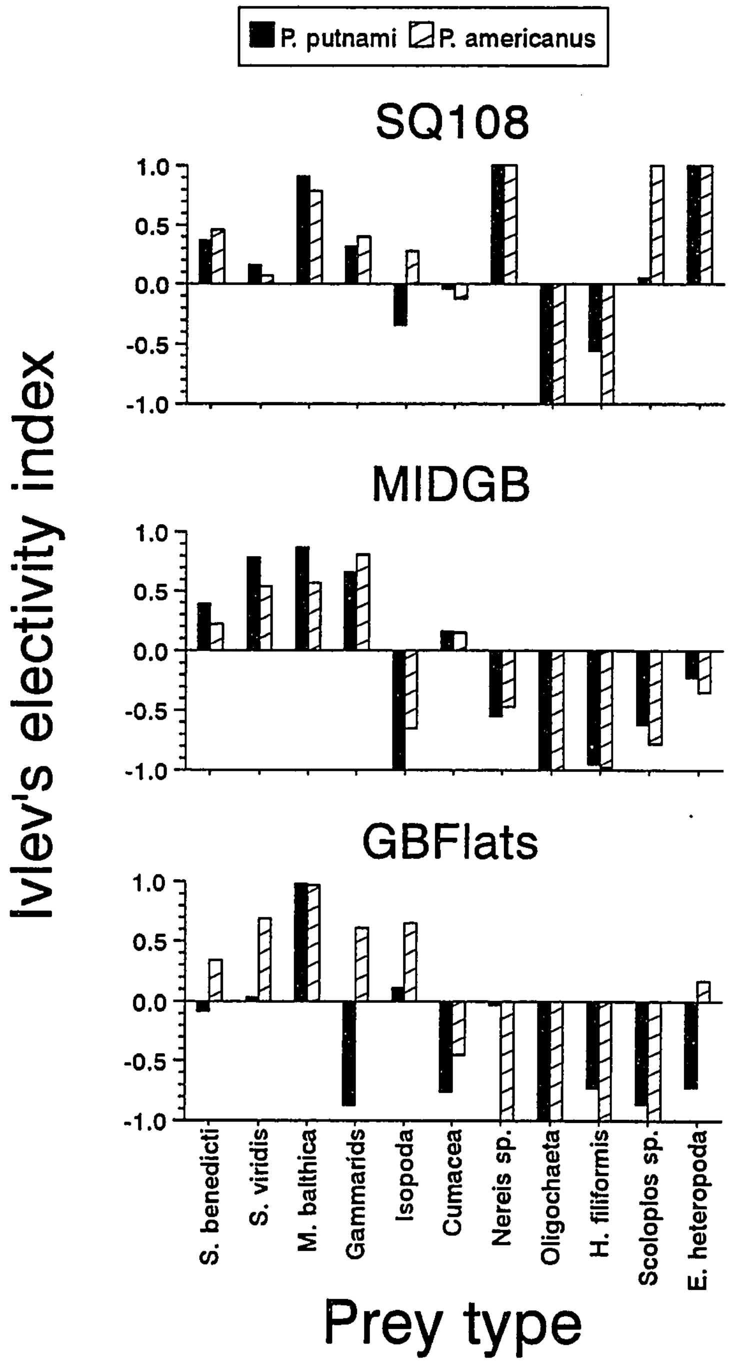

Figure 3.3. Prey electivity for smooth and winter flounder from three sites in Great Bay Estuary.

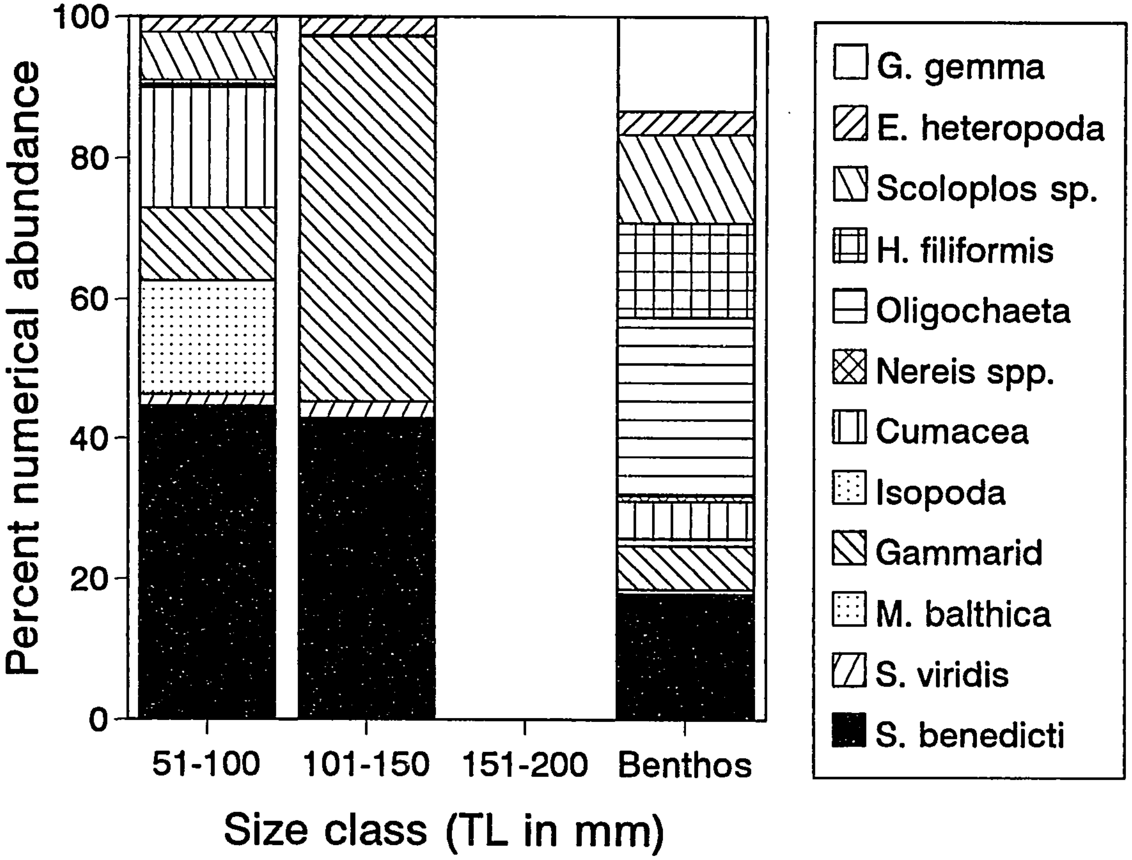

Figure 3.4. Percent numerical abundance of prey types in smooth flounder stomachs and in benthic cores from site MIDGB.

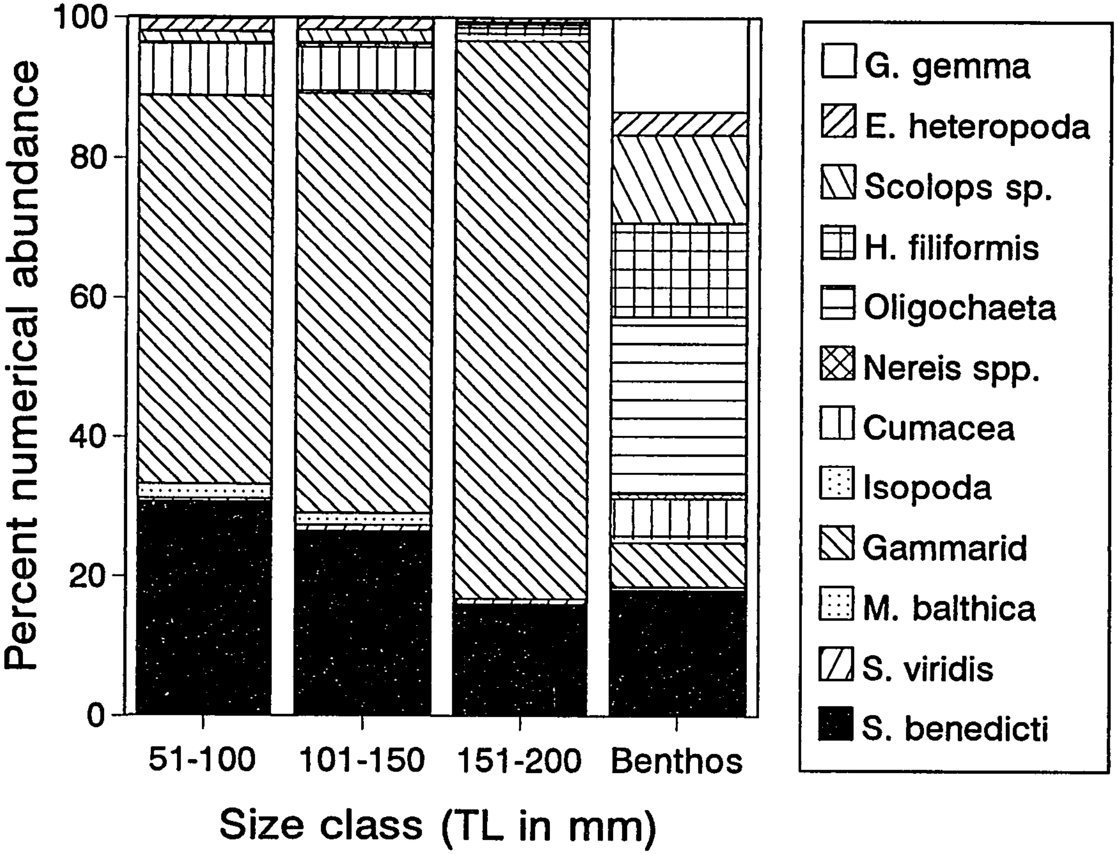

Figure 3.5. Percent numerical abundance of prey types in winter flounder stomachs and in benthic cores from site MIDGB.

cumaceans showed an ontogenetic change similar to that seen at SQ108.

The benthic core samples contained a higher diversity of organisms at MIDGB than at SQ108 (Figure 3.4). The fauna was less dominated by oligochaetes and contained several additional polychaetes and the bivalve, *Gemma*. There was little difference in selectivity of prey types between smooth and winter flounder. Types that were negatively selected for included oligochaetes, isopods, the polychaetes *Nereis* sp., *H. filiformis*, *Scoloplos* sp., and *Eteone heteropoda*, and the bivalve, *Gemma gemma*.

The diet of smooth flounder at GBFLATS was dominated by *M. balthica* in all size classes (Figure 3.6). Note that the size classes presented are different from those shown for SQ108 and MIDGB. The benthic cores were dominated by *G. gemma* (Figure 3.6). Ivlev's electivity index showed significant positive selection for *M. balthica* only (Figure 3.3). No results are presented for winter flounder because insufficient samples were collected due to the rarity of winter flounder at this site.

Cluster analysis separated groups principally based on habitat (Figure 3.7). Smooth flounder from GBFLATS clearly formed one group. The separation between SQ108 and MIDGB was less clear but there was a trend for flounder from one habitat to cluster adjacent to one another. There was no clear separation based on size class or species.

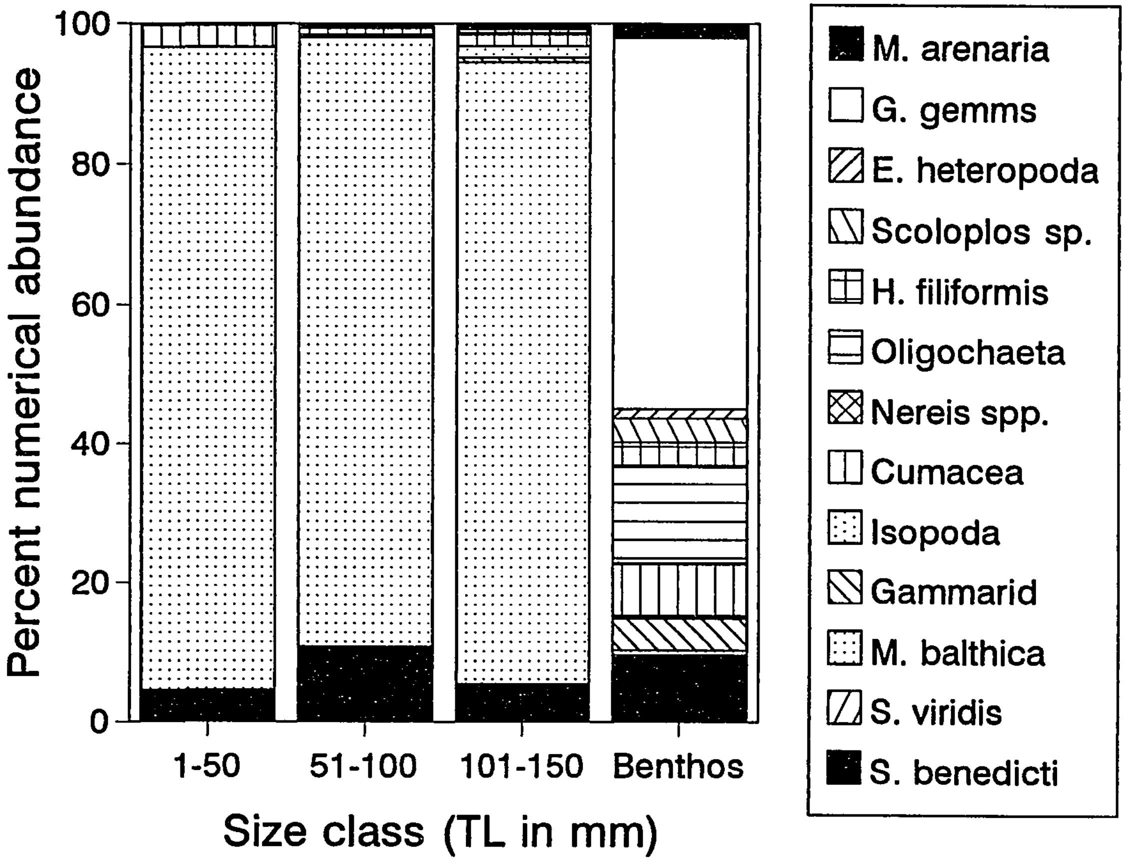

Figure 3.6. Percent numerical abundance of prey types in smooth flounder stomachs and in benthic cores from site GBFLATS.

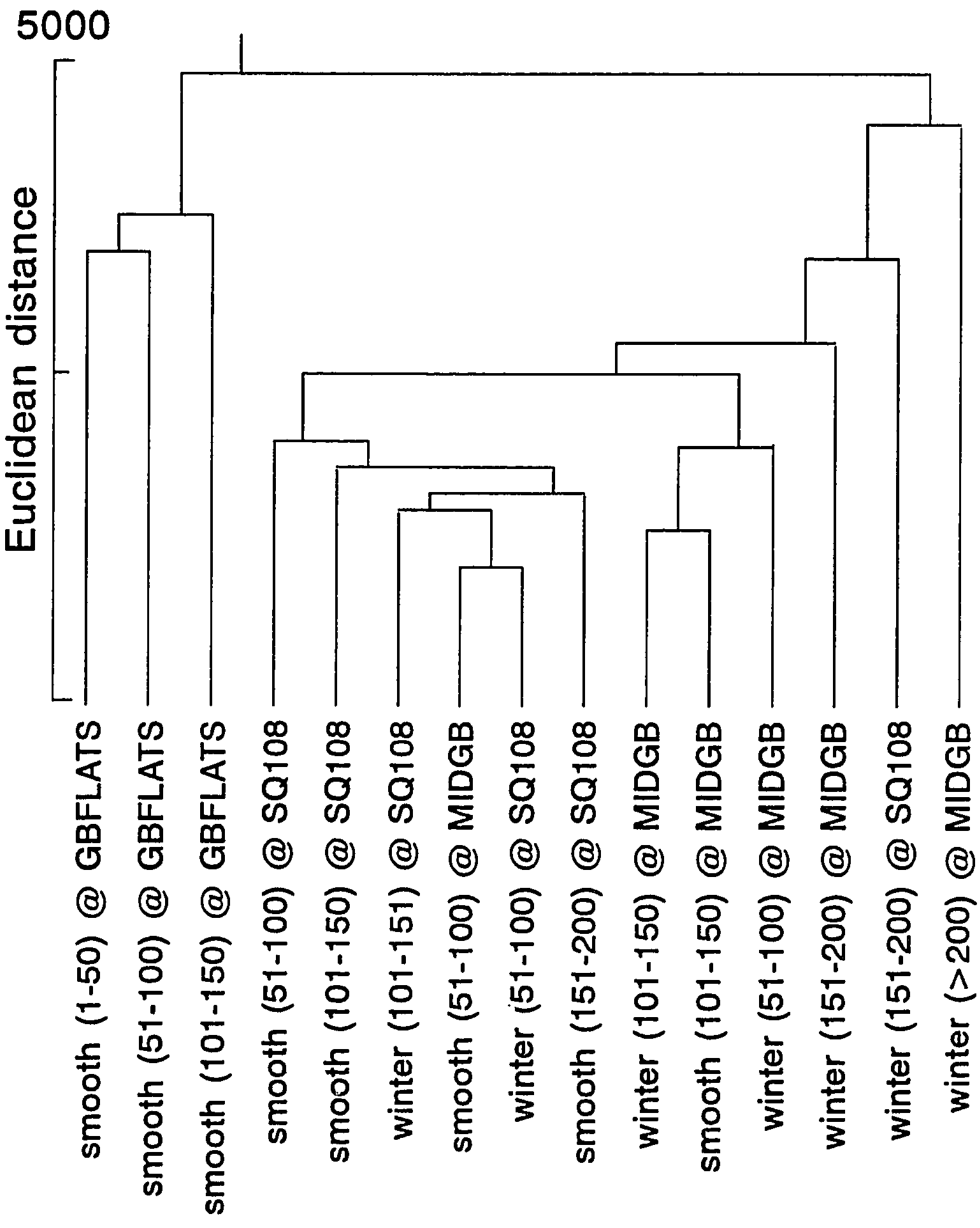

Figure 3.7. Dendrogram of the results of cluster analysis of food habits of smooth and winter flounder grouped by size and site of capture.

Stomach fullness index at SQ108 decreased from spring to summer for both species and then showed little change into the autumn (Figure 3.8). At MIDGB, neither species showed significant seasonal changes in stomach fullness index (Figure 3.9). At both sites, winter flounder consistently had significantly higher index values than smooth flounder.

Niche Overlap and Niche Breadth

At SQ108, prey abundance increased as the year progressed, with autumn values greater than double the spring values (Figure 3.10). This increase in prey abundance was due in large part to an increase in the abundance of *S. benedicti*. The dietary overlap between smooth and winter flounder was relatively low in the spring (0.47) but increased in the summer (0.70) and remained at that level into the autumn (0.70) (Figure 3.10). The habitat overlap showed the same trend as the dietary overlap but at a lower level, reaching a peak of 0.44 (Figure 3.10) during the summer. Both species of flounder showed little seasonal change in niche breadth. Niche breadth was about equal for both species and remained narrow through all seasons (Figure 3.11), indicating that both species were relative specialists in this habitat.

Prey abundance at MIDGB showed little seasonal change (Figure 3.12). Values of prey abundance were about the same as those for SQ108 in the spring but fell to about one-half

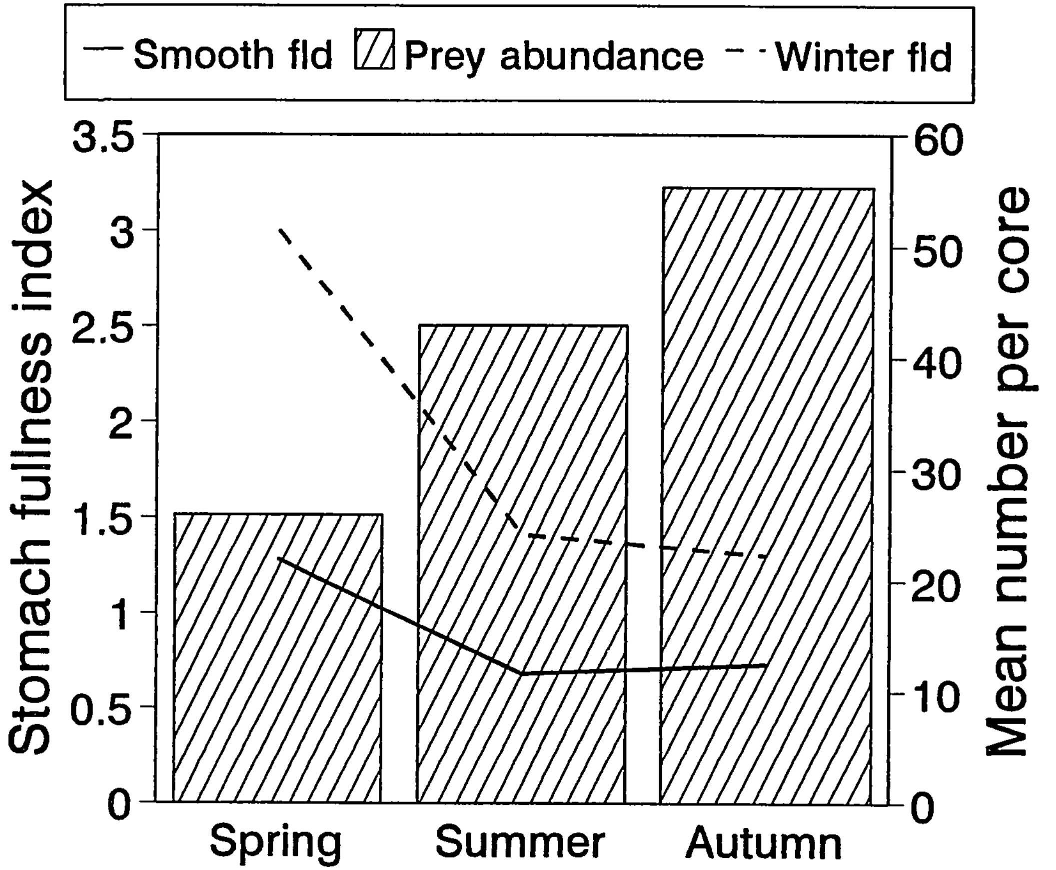

Figure 3.8. Stomach fullness index for smooth and winter flounder and prey abundance at site SQ108 during three seasons.

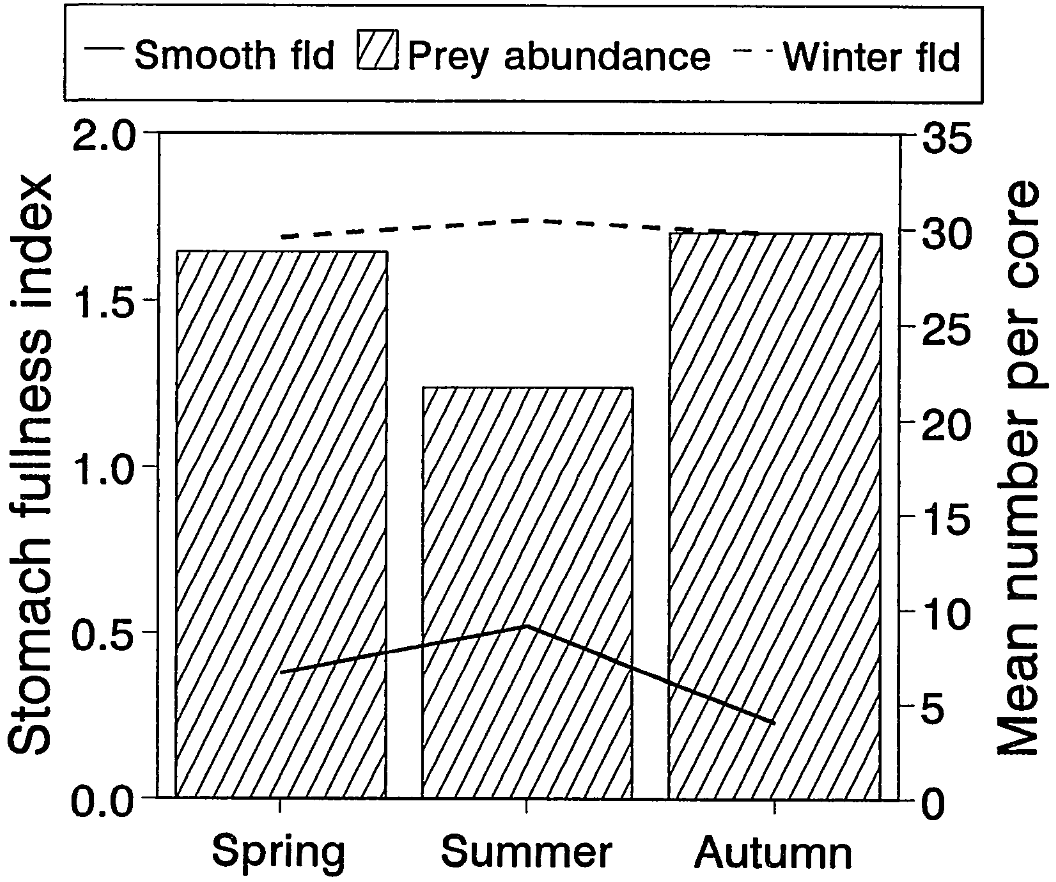

Figure 3.9. Stomach fullness index for smooth and winter flounder and prey abundance at site MIDGB during three seasons.

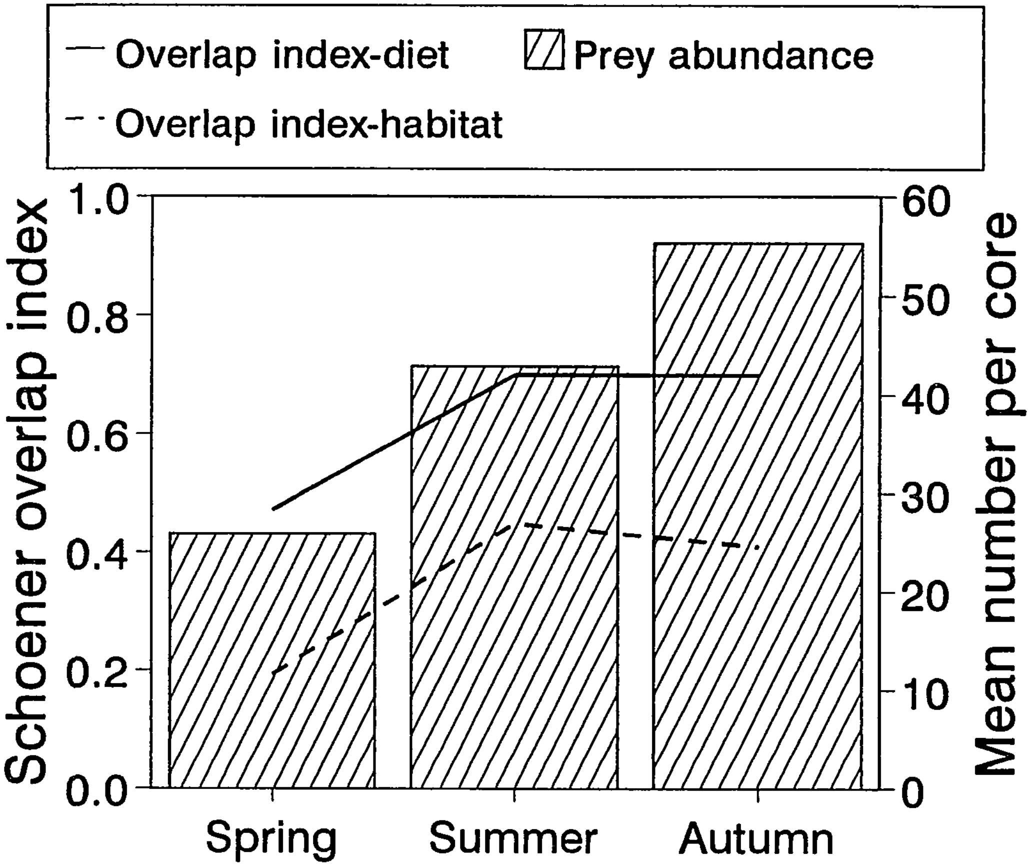

Figure 3.10. Dietary and habitat use overlap between smooth and winter flounder and prey abundance at site SQ108 during three seasons.

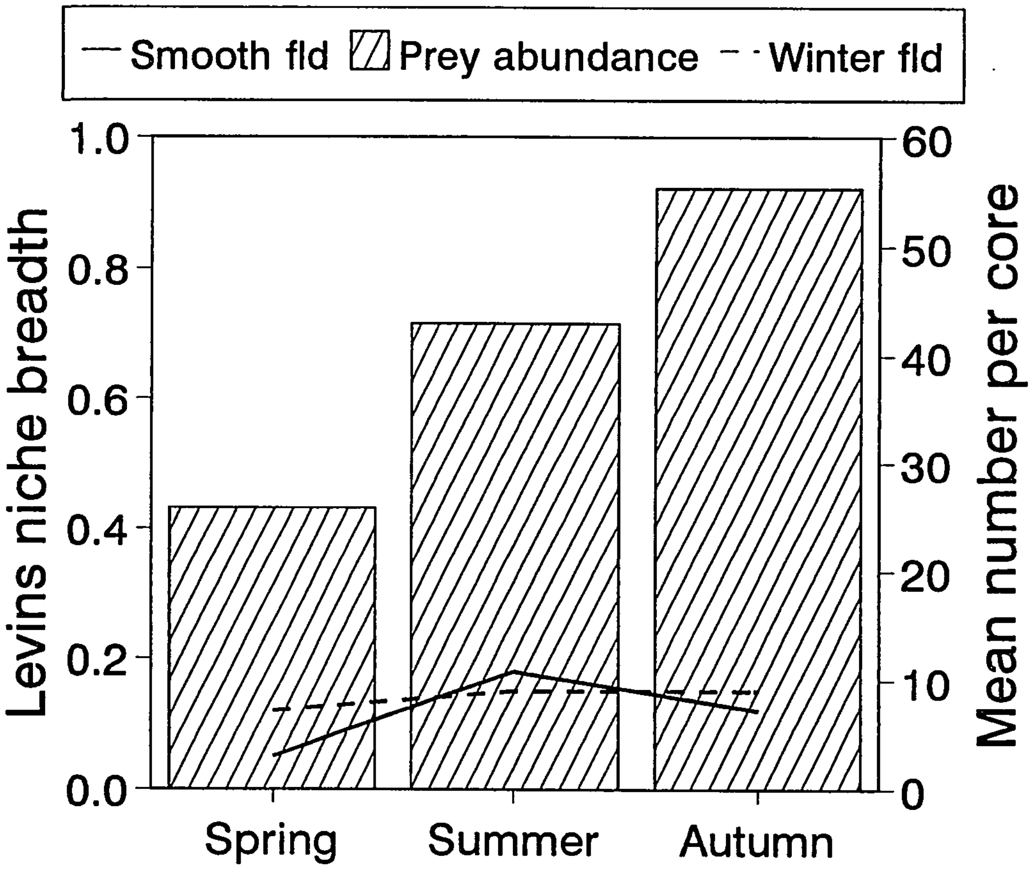

Figure 3.11. Dietary niche breadth for smooth and winter flounder and prey abundance at site SQ108 during three seasons.

of the values of prey abundance at SQ108 in the summer and autumn. Dietary overlap also showed little seasonal change (Figure 3.12), maintaining an overlap value of about 0.60 throughout the sampling period. Niche breadth measures changed little over the seasons (Figure 3.13) and were similar between species and with values from SQ108.

Discussion

Food Habits

Winter flounder have been shown to prey on a wide variety of species including polychaetes, amphipods, isopods, and pelecypods. They appear to be opportunistic feeders, eating whatever is locally available (Pearcy, 1962; Richards, 1963; Mulkana, 1966; MacPhee, 1969; Frame,1972), although they tend to concentrate on a few prey items even though many prey species may be available (Tyler, 1972). Far less information is available for smooth flounder but evidence indicates they feed on similar prey types (Laszlo, 1972; Imrie and Daborn, 1981; Scully, 1983). Scully (1983) found that smooth flounder from a salt marsh habitat in Nova Scotia preyed heavily on S. benedicti and siphons from M. balthica. In the present study, S. benedicti and M. balthica were, overall, the most important prey to both flounder species. Streblospio benedicti is a small, tube-dwelling polychaete. It is abundant in the shallow portions of estuaries on mud or sandy-mud bottom. It feeds by

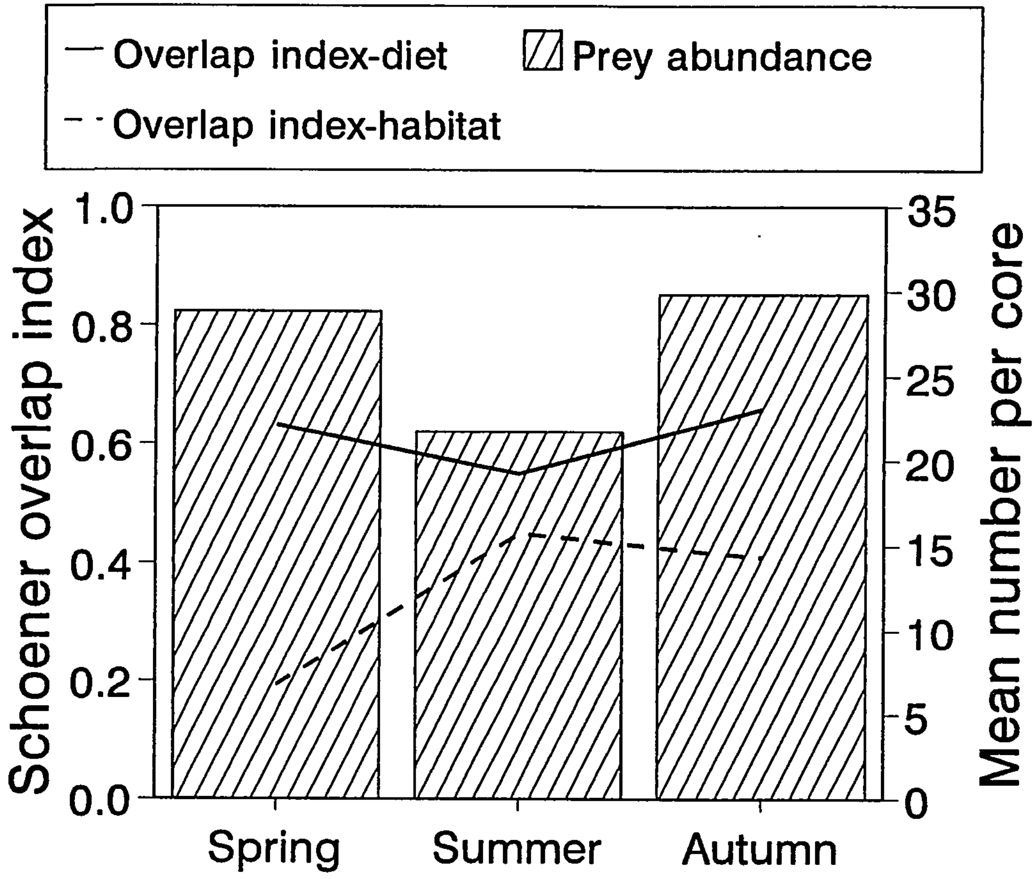

Figure 3.12. Dietary and habitat use overlap for smooth and winter flounder and prey abundance at site MIDGB during three seasons.

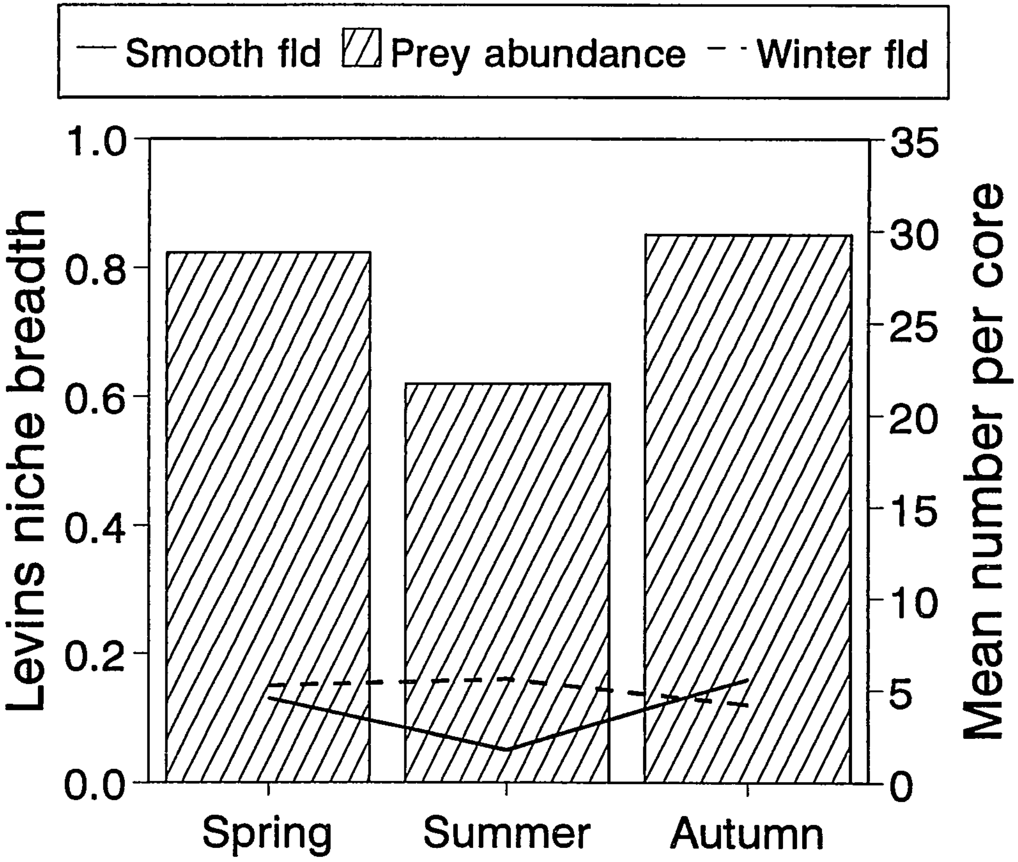

Figure 3.13. Dietary niche breadth for smooth and winter flounder and prey abundance at site MIDGB during three seasons.

sweeping its palps along the bottom and ingests the material that sticks to the palps (Gosner, 1978). This behavior apparently makes it vulnerable to predation by smooth and winter flounder. *M. balthica* is an estuarine bivalve which deposit feeds by snaking its long inhalant siphon along the bottom and vacuuming organic debris (Gosner, 1978). This behavior makes it vulnerable to predation also and explains the presence of only siphons in flounder stomachs. The young of plaice, *Pleuronectes platessa* were found to prey heavily on *M. balthica* siphons in the Wadden Sea (Kuipers, 1977)

Both species showed a general trend to prey on larger prey types with increasing body size while dropping smaller prey from their diet. Similar results have been seen for winter flounder in other studies (Pearcy, 1962; Richards, 1963; Mulkana, 1966; Keats, 1990) and for other flatfish species (Kuipers, 1977; Grossman,1980; Marrin, 1983; Carter et al., 1991). Feeding on the largest prey possible relative to their gape size may provide an energetic advantage by minimizing search activity and number of prey captures needed to ingest a given amount of food. Changes in prey preferences with increasing size also decreases the the possibility of intraspecific competition (Schoener, 1974). Ontogenetic shifts in feeding have been found in a large number of animals (Werner and Gilliam, 1984). Because of these ontogenetic shifts, the complete analysis of interactions between two species can be enormously complex.

Ivlev's electivity index indicated that the two flounder species exhibited very similar selection of food items from the benthos. It is important to keep in mind that this index can have severe biases. It assumes that what occurs in the benthic core samples is representative of what is available to the flounder. It is almost certainly true that not all of the benthic organisms are represented in their true abundance. This is particular true of the more mobile animals such as M. balthica which are poorly represented in the cores but were a major prey item for both species. In addition, what the researcher perceives as available is not necessarily what is actually available to the flounder. This may be the case for the oligochaetes. Although they were extremely abundant in the core samples, particularly at SQ108, they never occurred in the stomach samples. It may be that the flounder are not actively avoiding this prey type, but rather, oligochaetes are not accessible to flounder because of their behavior. This is probably also true for G. gemma which were very abundant in the cores from the intertidal site, GBFLATS, but were not present in stomach samples. G. gemma filter feeds rather than deposit feeds like M. balthica, making it less vulnerable to predation. The dominance of M. balthica in the stomachs of smooth flounder from GBFLATS likely reflects their abundance at this intertidal site even though they are poorly represented in the cores. M. balthica tend to dwell deeper than the other prey types occuring in the cores and so may be poorly sampled by the coring device used. It is also possible that M. balthica are patchily distributed and so are not sampled representively by the cores. The biases inherent in the index mean interpretation of the results for a species should be done with caution. Use of the index to compare relative selectivities between smooth and winter flounder is less biased because it is a comparison of relative selectivities rather than the true selectivities. This comparison shows that the two species are very similar in their prey selection with a few exceptions.

Cluster analysis indicated little separation of the species by diet. The most important factor affecting the composition of the stomach contents in these two flounders was the site at which it was captured. This reflects the differences in prey types available at the sites.

The decrease in the Stomach Fullness Index from spring into the later seasons seen at SQ108 is contrary to what would be expected based on prey abundance. It may be that digestion proceeds faster in the warm summer and autumn temperatures, but flounder species have been found to have fuller stomachs in the warmer seasons (Pearcy, 1962), probably due to increased feeding rates. The reduction in SFI coincides with an increase in the number of winter flounder at SQ108, suggesting that increased competition for food may play a role in summer and autumn, although the combined abundance of both species is lower in summer and autumn than in spring due to the lowered abundance of smooth flounder. There was also a species difference in SFI, with winter flounder always exhibiting fuller stomachs. This may reflect a species difference in the rate of digestion. It may also reflect a difference in the time of feeding for the two flounders. Winter flounder and other pleuronectid species have been found to be diurnal, visual feeders (Pearcy, 1962; De Groot, 1964; Hempel, 1964; Verheijen and De Groot, 1967; Olla et al., 1969; MacDonald and Waiwood, 1987). For winter flounder, the time of sampling coincided with the time of feeding. Nothing is known of the periodicity of feeding in smooth flounder but it is likely to be similar to the other pleuronectids. However, if they did have a nocturnal or crepuscular feeding pattern, that would explain the difference in stomach fullness. The difference in SFI may also indicate a difference in energetic requirements between the species. All winter flounder included in this analysis were juveniles. Energy requirements are very high at this period of their life and so they require a high feeding rate. Smooth flounder mature at under 100 mm TL (Armstrong and Starr, 1994) and so a large percentage of the smooth flounder were adults and presumably had lower energy requirements, resulting in a lower relative rate of feeding as compared to the winter flounder sampled.

Measures of resource use overlap are simply indications of the similarity in which two species utilize a resource. They can not be taken by themselves as a measure of competition (Sale, 1974). However, careful interpretation of the pattern of overlap in response to changing levels of the shared resource can provide insights into the relationship between the species. In a review of 30 studies, Schoener (1982) found that resource overlap was generally least when resources were reduced and high when resources were abundant. He interpreted the results as evidence for interspecific competition during lean times. Wiens (1989, 1993) stressed that this is only evidence for competition if resources can be shown to be limiting. The reduction in diet overlap between smooth and winter flounder at SQ108 in the spring is consistent with the pattern expected if interspecific competition were present. Prey abundance is lower at this time of year compared to summer and autumn, although there is no data to suggest it was below some critical resource-limitation threshold (Wiens, 1993). In addition to prey abundance being lower in the spring, the density of smooth flounder was at a seasonal high, reaching two to three times higher than summer and autumn values. At the same time, however, the abundance of winter flounder was very low. The relative abundances of the two species indicate that intraspecific competion should have been more likely than interspecific competition. Intraspecific competition is believed to result in niche broadening (Svärdson, 1949; Wiens, 1989; Smith, 1991). The observed pattern of no seasonal change in niche breadth suggests that intraspecific competition was not important. Because intraspecific competition must be present for interspecific competition to occur (Wiens, 1989), the lack of evidence for intraspecific competition means interspecific competition could not be occurring. This contradicts the evidence for interspecific competition seen in the diet overlap data. Niche breadth was relatively narrow for both species indicating they are feeding specialists. Other studies have indicated that these species feed on a wide variety of prey (see reviews in Klein-MacPhee, 1978; Buckley,1989), so the narrowness of the niche breadth seen here is the result of the paucity of prey types available and the relative abundance of a few prey types rather than true trophic specialization.

Armstrong (Section I) found that the center of abundance for smooth flounder underwent a seasonal upstream movement from SQ108 to SQ51 in late summer and autumn. At the same time, winter flounder moved into SQ108 from lower in the estuary. The movement of winter flounder into SQ108 during summer and autumn was associated with three favorable conditions related to salinity, density of smooth flounder, and abundance of prey. In late summer and early autumn, salinity was at a seasonal high mean of about 15‰. Prior to that time, salinity was lower than that which winter flounder can physiologically tolerate (Armstrong, Section II). Smooth flounder density in summer and autumn was at a low level compared to spring because of the upriver movement to SQ51. Finally, prey abundance is much higher in summer and autumn than in spring. As a habitat, SQ108 is metabolically costly to winter flounder in the spring because of low salinity. As this habitat becomes more physiologically benign with increasing salinity, there is a concurrent decrease in the density of a potential competitor and a greater prey abundance than at MIDGB. Because the relative cost of iono- and osmoregulation is about the same for SQ108 and MIDGB when salinity is seasonally high (Armstrong, Section II), it is energetically favorable for winter flounder to move into SQ108. It appears that in this particular habitat, the profitability of utilizing this habitat is an interaction of physical and biotic factors. There are no data on prey availability for the oligohaline site, SQ51, so it is not known what role that played in the upriver movement of smooth flounder with increasing salinity. By moving upriver, smooth flounder remain in lower salinity water from which winter flounder are excluded because of physiological constraints. The lower salinity portion of the estuary is consequently acting as a refugium from competition with winter flounder. Beamont and Mann (1984) suggested a similar scenario for the flounder, Platichthys flesus. It is impossible to say if the evolutionary adaptation which allows for partitioning of the upper estuary between these closely related flounder is the result of physiological character displacement resulting from past competition, or if the two species were simply pre-adapted for different salinities when they became sympatric in evolutionary history. Unfortunately, little is known of the evolutionary histories of either species.

Overall, smooth and winter flounder showed more segregation by habitat than by diet. Schoener (1974) found that resource partitioning by habitat was less important than by food in aquatic animals, although when all ecosystems were considered, habitat segregation was most common. Ross (1986) found that resource partitioning in fishes was more common by food than by habitat. Both these studies found that temporal partitioning of resources was relatively rare. The findings of partitioning by habitat for smooth and winter flounder may be the result of the unique characteristics of the upper portions of estuaries where these two species co-exist. Prey species are generally less diverse than in freshwater and coastal systems and therefore there is less opportunity to trophically diversify. On the other hand, habitat diversity is high because of the physical gradients present, the primary one being salinity. It is along this axis that smooth and winter flounder partially segregate within Great Bay Estuary.

Although this study provides suggestive evidence that competition may occur between smooth and winter flounder, there have been studies that indicate that competition should not be important in such an environment. Evans (1983) demonstrated that food resources are not limiting in shallow, soft-bottom temperate waters. Ross (1986) found a general pattern of studies showing less evidence of species interactive effects on community structure in harsher environments. Examination of the impact of juvenile flatfishes on the abundance of their prey has indicated that their effect is generally insignificant (Shaw and Jenkins, 1992) or insufficient to reduce prey levels to a point where they become limiting (Kuipers, 1977). Schlosser and Toth (1984) suggested interspecific competition may be relatively unimportant in structuring communities in temporally variable environments. In contrast, Thorman (1982) found that competition was seasonally important in estuarine fish populations in Sweden.

It is important to note that there may be interactions with other species that were not considered within the scope of this study. Important species that potentially share resources with these flounder species and co-occur at least seasonally include white perch, Morone americanus, tomcod, Microgadus tomcod, grubby, Myoxocephalus aeneus, and the horseshoe crab, Limulus polyphemus. Further studies need to examine resource utilization by these species in order to better assess community level species interactions in Great Bay Estuary.

Summary

Previous to this study, little was known about the potential for interactions between smooth and winter flounder. These two flounder species were reported to both occur in estuaries north of Cape Cod, and that was the extent of the information available on the overlap in resource use.

This study has demonstrated a moderate degree of resource partitioning between smooth and winter flounder in Great Bay Estuary, New Hampshire. Additionally, the use of resources was shown to be seasonally dynamic. Smooth flounder had a center of abundance in the oligo-mesohaline portion of the estuary while the center of abundance for winter flounder was in the meso-polyhaline portion. Both species showed a generalized up-estuary movement from spring into autumn. Smooth flounder showed distinct habitat partitioning by size, with the smallest individuals occurring in the shallowest water. For smooth flounder, the intertidal mud flat habitat is an important nursery area for the young-of-year. Winter flounder demonstrated little habitat partitioning by size, and showed little use of the intertidal mud flat habitat.

Resource partitioning is prevalent among fish species and descriptions of partitioning are common in the literature (Ross, 1986), but the mechanism of segregation is less commonly studied. This study has demonstrated that the primary cause of segregation in habitat use was differences between the species in salinity tolerances. Both species were found to occur in Great Bay Estuary at salinities that were found experimentally to be the least energetically costly. The result of this segregation along the salinity gradient was a significant reduction in the potential for interactions between the species.

Partitioning along the food dimension was much less than for habitat. Smooth and winter flounder generally preyed on similar food types, as expected based on their similarity in morphology. Differences in food habits were greater between the estuarine sites than between the flounder species. Observations of overlap in food use at SQ108 suggested that interspecific competition might have been important during the spring at this site but observations of niche breath and prey abundance suggest that food was not a limiting factor at SQ108 or at MIDGB.

Although smooth and winter flounder are sympatric from Newfoundland to Cape Cod, this study has shown that, because of different physiological adaptations, they are only partially syntopic within that range. Seasonal changes in resource use were shown for both species and this illustrates the importance of conducting ecological studies on a time scale that will incorporate these changes. This is especially important in a dynamic system such as an estuary.

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