Fish and macroinvertebrate community structure and habitat use patterns in salt marsh creeks of southern New Jersey, with a discussion of marsh carbon export

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ABSTRACT OF THE DISSERTATION

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Faunal composition, abundance, biomass and size structure of fishes and macroinvertebrates were described from polyhaline intertidal and subtidal marsh creek habitats in a southern New Jersey estuary. New Jersey marsh creeks support a rich fauna, including 64 species of fishes, 13 invertebrates and the diamondback terrapin. Although estuarine species numerically dominant the fauna, a more diverse assemblage of species utilize the creeks primarily as a nursery for young-of-the-year (YOY). Abundance, biomass and faunal composition were strongly seasonal with peaks in May and August. Variation in community structure was found among creeks of different size and within creeks along a mouth-to-headwater gradient. Many species which utilize marsh creeks appear to undergo passive or active tidal movements. Creek morphology is hypothesized to influence community structure directly through the mediation of tidal dynamics, and indirectly through the mediation of tidal and diel changes in physical conditions along the creek gradient. Fish and decapod species assemblages, and abundances, were strongly influenced by diel period suggesting diel movements. Summer flounder, *Paralichthys dentatus*, growth, foraging habits and temporal patterns of habitat use were assessed. Summer flounder grew rapidly and appear to undergo tidal foraging movements into the creeks. Patterns in growth and seasonal emigration of fifteen fishes were examined in detail. Most species grew very rapidly and exhibited well defined pulses of emigration from the creeks. Major emigration pulses of YOY from the creeks occurred from July through September. Two types of emigration patterns were evident: 1) emigration at a specific size (size dependent emigration), and 2) seasonal emigration independent of size. Patterns in abundance and growth of YOY fishes in New Jersey marsh creeks strongly suggest that seasonal migration of fishes constitutes a major pathway of energy export from the marsh into coastal waters. Recent research on patterns of marsh creek community structure and mechanisms of energy exchange between the marsh and marine waters are reviewed. Ontogenetic migrations and cyclic foraging movements are the two major types of animal movements which result in energy exchange between the marsh and adjacent habitats.

Acknowledgments and Dedication

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This dissertation is dedicated to my family

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General Introduction

A growing body of evidence suggests that salt marsh creeks are one of the most important nursery habitats for fish and decapods within an estuary. Additionally, many researchers during the last decade have begun to suggest that fish and invertebrates may serve as important vectors of energy exchange among estuarine and coastal marine habitats, through seasonal migrations. However few studies have actually attempted to examine mechanisms of energy exchange between marine and estuarine habitats through fish and invertebrate movements. Further, most information on marsh creek community structure comes from studies in the southeastern and Gulf coast areas of the United States. Only a few studies have been conducted in other areas of the world (chiefly Australia). Studies in the northeastern United States are conspicuously lacking, despite the fact that northeastern estuaries are arguably among the most threatened marine habitats in the country.

The major goals of the research discussed in the following chapters were: 1) to describe the fish and macroinvertebrate fauna of polyhaline marsh creeks in the unaltered marsh habitats of the Great Bay-Little Egg Harbor estuary located in southern New Jersey; 2) to examine patterns of creek habitat use, and 3) to describe mechanisms and patterns of energy export from the creeks. This study was conducted primarily from April-November 1988 and April-October 1989, however, supplemental efforts directed specifically at summer flounder, _Paralichthys dentatus_, were undertaken during 1990.

Chapter 1 presents a description of the fish, macroinvertebrate and turtle fauna of subtidal marsh creeks in a New Jersey estuary. Information on species occurrence, seasonality, abundance, biomass and species size structure is emphasized. Chapter 2 describes spatial variation among and within creeks, based on sampling within subtidal and intertidal creeks. It examines the influence of creek morphology on marsh creek communities and discusses the importance of tidal movements to the communities. Chapter 3 describes diel variation in faunal assemblages and species abundance, and discusses causes of diel movements within the marsh. Chapter 4 examines patterns of marsh creek habitat use by summer flounder, including growth, foraging movements and residency. Chapter 5 examines patterns of growth and seasonal emigration of many of the dominant marsh creek fishes. It emphasizes that fishes that utilize New Jersey marsh creeks as nurseries grow very fast despite a relatively short growing season. It further describes temporal patterns of energy export from the creeks through fish emigration, and compares the relative importance of the dominant species to energy export. The final chapter summarizes this research and reviews literature on selected aspects of marsh community structure, and on mechanisms of energy exchange between estuarine and marine habitats. The main goal of this paper is to place the findings within a broader ecological context, and to assimilate findings from the separate dissertation chapters to present a broader discussion of patterns of marsh community structure and mechanisms of energy exchange between estuarine and marine habitats.

Chapter 1. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass

Abstract

Three polyhaline subtidal marsh creeks in southern New Jersey were sampled with weirs and seines to determine seasonal patterns of use by fishes and macroinvertebrates. Sixty-four species of fish, 13 invertebrates and the diamondback terrapin were collected in 69 weir and 57 seine samples from April-November 1988 and April-October 1989. Average abundance, biomass and faunal composition were strongly seasonal with greatest abundances during spring and summer and peaks in May and August. Sixteen species were represented by all life history stages, including the five most important species by combined ranks of percent frequency, mean abundance and mean biomass. These five species were important during spring, summer and fall and included the fishes *Menidia menidia* and *Fundulus heteroclitus*, the shrimps *Palaemonetes vulgaris* and *Crangon septemspinosa*, and the crab *Callinectes sapidus*. In addition, there were distinct seasonal assemblages of other species which utilized the creeks primarily as young-of-year. Important species in spring collections included the fishes *Clupea harengus*, *Alosa aestivalis*, *Alosa pseudoharengus*, *Pollachius virens* and *Urophycis regia*,

while *Leiostomus xanthurus*, *Pomatomus saltatrix*, *Paralichthys dentatus*, *Mugil curema* and *Strongylura marina* were important in the summer. Fall samples were best characterized by declining abundances of summer species. Thus subtidal marsh creeks in southern New Jersey appear to be valuable nurseries for a variety of species which spawn over the continental shelf, as well as one of the most important habitats for estuarine residents.

Introduction

Numerous investigators have suggested that salt marshes are critically important nurseries for marine fishes and invertebrates (Gunter 1956, 1961, Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Daiber, 1977, Boesch and Turner 1984, Currin et al. 1984, Weinstein 1979). However, most salt marsh studies have concentrated on a single species, or species group, and few have documented the overall faunal composition. Hence, only limited data to evaluate the nursery function of salt marshes are available. Studies of salt marsh communities in the northeastern United States are particularly lacking, although research activity has increased in the last decade (Nixon and Oviatt 1973, Daiber 1977, Werme 1981, Nixon 1982, Talbot and Able 1984, Talbot et al. 1986, Teal 1986, Sogard and Able 1991).

The salt marsh may be divided into several important contiguous sub-habitats: 1) irregularly flooded marsh surface, including marsh pools, 2) regularly flooded intertidal marsh surface, 3) intertidal marsh creek, 4) subtidal marsh creek (sensu Hackney et al. 1976, Hackney 1977), and 5) bay-marsh fringe (i.e., shallow bay areas directly bordering the salt marsh).

Because tidal marsh creeks are a primary interface between the salt marsh and open estuarine waters, and they provide fish access to the marsh, numerous researchers have pointed out the need for research into the role of marsh creeks as fish habitat and in energy export from the marsh (Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Bozeman and Dean 1980, Weinstein et al. 1980, Currin et al. 1984, Weinstein 1984, Weinstein et al. 1984). Consequently, subtidal creek communities have been the most extensively examined among salt marsh habitats. These studies have been conducted in several types of marshes in several geographic regions: 1) Mangrove marshes in Australia (Blaber et al. 1985, Blaber 1986); 2) Juncus marshes in Florida (Subrahmanyam and Drake 1975, Subrahmanyam and Coultas 1980) and Mississippi (Hackney 1977, Hackney and de la Cruz 1981); 3) Spartina marshes in Georgia (Hackney and Burbanck 1976, Hackney et al. 1976), Virginia (Richards and Castagna 1970, Smith et al. 1984, Cowan and Birdsong 1985), New Jersey (Sogard and Able 1991) and Massachusetts (Werme 1981, Teal 1985); and, 4) mixed Juncus and Spartina marshes in Georgia (Dahlberg and Odum 1970, Dahlberg 1972) and North Carolina (Keup and Bayless 1964, Weinstein 1979, Weinstein et al. 1980). Most of these subtidal marsh creek studies were concentrated in the southeastern United States, while studies in the northeast have been limited (Werme 1981, Teal 1985, Sogard and Able 1991).

This study is part of a larger effort to describe the community structure and nursery function of the marsh surface, intertidal creek, and subtidal creek sub-habitats within a representative salt marsh system in the northeastern United States. The specific goal was to describe the faunal composition and seasonal abundance patterns of polyhaline marsh creeks in a southern New Jersey salt marsh.

Materials and Methods

STUDY SITES

The study was conducted within the Great Bay - Little Egg Harbor estuarine complex in southern New Jersey (Fig. 1.1). The unaltered marsh in the study area is dominated by the grasses Spartina alterniflora (short form) and Spartina patens and is characteristic of salt marshes in the northeastern United States (Chapman 1960). Tidal creeks are abundant within the study area (Fig. 1.1), with at least 34 primary creeks (opening directly into the bay) and an additional 95 subtidal and intertidal tributaries. The three study creeks were of similar depths (0.5 - 1.0 m mean low tide depth at the mouth), lengths (approximately 1.0 km), and extent (23 - 26 ha subtidal areas), and were closed systems that received freshwater only through local runoff after rainfall.

SAMPLING GEAR AND TECHNIQUES

Sampling was conducted within three subtidal marsh creeks (Schooner, Foxboro and New creeks) over a 3 - 5 day period (sample week) approximately fortnightly from April-November 1988 and April-October 1989 (Fig. 1.1, Table 1.1). During 1988 consecutive day and night tides were sampled from Schooner and Foxboro creeks, while night tides were sampled from all three creeks during 1989 (Table 1.1). Day and night tides were those in which at least the last two hours of flood occurred after sunrise and sunset, respectively.

Fishes, macroinvertebrates and turtles were collected from the subtidal creeks using a weir system developed specifically for use in tidal marsh creeks (Fig. 1.2). The weir was set to block off the mouth of a creek at high tide to capture fishes leaving the creek with the ebb tide. Two wing nets (15.2 m long by 3.0 m high) were used to block off the creek and to lead fish into the rectangular weir (Fig. 1.2). The front of the weir consisted of a polyvinyl chloride (PVC) pipe frame (38 mm diameter) supporting two sets of doors leading into a large fish pen. All netting was 6.4 mm square mesh nylon. Ropes on the steel support poles, and a 6.4 mm chain lining the wings along their entire length, held the weir and wings down to the substrate. Deployment of the weir was begun about 30 minutes before slack high tide and was completed within one hour.

Once set, the weir was allowed to fish over the entire ebb tide. At low tide a removable sliding panel was used to close off the front of the weir to prevent fish from entering the weir as a result of seining operations. The weir was hauled by raising it on ropes above the water line and removing the fish through the cod-end (Fig. 1.2 inset). The weir and wings were removed after each collection so that the steel supporting poles were the only permanent structures remaining in the creeks.

Because the weir is a passive gear which primarily captures animals moving with the tide, seine sampling (Fig. 1.2) was also conducted within the creeks to capture less mobile forms and species/individuals which actively avoid the weir and remain within the creeks. Seine samples were collected in the creek above the weir after the weir was closed off at low tide. During 1988 a block net was stretched across the creek at the head of the wings to contain fishes within the wing area. Then one haul with a bag seine (6.1 m long by 1.2 m high with 3.2 mm mesh) was made inside of the wing area. Additional seine hauls were made on an irregular basis to collect additional length-frequency data on species of special interest. During 1989, seining operations were standardized to a single haul of a larger bag seine without the use of a block net. The seine was large enough (18.3 m long by 1.2 m high with 6.4 mm mesh) to allow the entire area (approximately 100 m^2)

enclosed by the wings to be swept with a single "purse" of the seine.

SAMPLE ANALYSIS

A total of 69 weir and 57 seine samples were collected during the study, however of these some species were not quantified in 15 weir and 5 seine samples (Table 1.1). Catches from weir and seine samples were put on ice and transported back to the laboratory for sorting and identification. However, turtles (*Malaclemys terrapin*) and horseshoe crabs (*Limulus polyphemus*) were immediately culled from the samples and released. For small samples all species of fishes and invertebrates were sorted and enumerated. For large samples the entire sample was sorted once to enumerate economically important species, species of special interest (e.g., *Sardinella aurita*, *Chaetodon ocellatus*), and generally any species present in low abundance which might be missed in subsampling. After the initial sort, all species were enumerated in a subsample of 10-50% by wet weight of the sample. Infrequently much smaller subsamples by percent weight were taken. Total biomass for each species was recorded, except for turtles and horseshoe crabs, which were estimated by multiplying the number collected by the average weight of individuals from a subsample of 16 turtles and 116 horseshoe crabs. Nomenclature and taxonomy follow standard references for fishes (Robins et al. 1980) and invertebrates (Gosner 1979, Williams 1984) of the eastern United States.

Standard lengths (SL) measured to the nearest millimeter (or in some cases total lengths - TL, or disc width -DW) of a subsample of up to one hundred individuals of each fish species were measured. The carapace length (CL) of M. terrapin was measured in the field. Lengths of invertebrates were not taken, so average wet weight (g) was used as a measure of invertebrate size. Average invertebrate weights (sizes) were obtained by dividing the total wet weight of a subsample by the number of individuals in the subsample for each collection and then calculating a mean for all collections.

Water depth, air and water temperature, and salinity were recorded at high tide after the weir had been set and at low tide just prior to hauling the gear. Since high and low tide water temperatures were highly correlated (Chapter 2), the mean of the high and low tide water temperature for each sample was examined for temporal trends.

Mean abundance for each species was calculated for weir and seine samples separately, while fish length and invertebrate size data were pooled from both gears. Abundance and size data were used to classify the life history stages of each species. Because many of the collections made in 1988 did not quantify the abundance of all species, collections from 1989 were emphasized in the description of faunal composition and seasonality. To identify the dominant species utilizing the subtidal creeks, the paired weir and seine samples from 1989 were pooled into combined gear collections (n=24) and percent frequency, mean abundance, mean biomass and ranks for each of these variables were determined for all species. All species occurring in at least 50% of the samples plus any additional species which were ranked within the top 10 by abundance or biomass were considered dominant. An index of overall species importance was determined, for each of the twenty species selected by the above criterion, by summing the three rank scores for each species and then ranking the sum over all twenty species.

Dominant species within spring (April-June), summer (July-September) and fall (October-December) seasons were determined for each gear with data combined from night samples from 1988 and 1989 (N=39 weir and 39 seine samples). Samples which were not fully quantified were excluded from this analysis. Because of sampling bias between weir and seine, and differences in seine methods between years, the data was standardized to mean percent relative abundance per sample.

Annual variation in the ten most abundant species collected in night weir samples during the summers of 1988 and 1989 was tested with an Analysis of Variance (ANOVA) with year, month and creek class variables based on Log (x+0.5) transformed abundances. Annual variation of the abundances of seine collected fauna could not be tested because of differences in seine gear and techniques between years.

Results

PHYSICAL CHARACTERISTICS

Creek water temperature averaged 19 (0.7 SE) C and ranged 8-28 C (Table 1.2). Night water temperature was lowest in the spring and peaked in August (Fig. 1.3a). Salinity ranged from 23‰ to 33‰ and averaged 29 (0.3 SE)‰ (Table 1.2). No seasonal salinity trends were apparent, but salinity was slightly lower during 1989 than 1988 with means of 28‰ (0.3, range=23-30‰) and 31‰ (0.2, r=30-33‰), respectively. Mean tidal depth range was 0.8 m (0.04 SE, Table 1.2).

TOTAL ABUNDANCE AND BIOMASS

An average of 15,388 (6,733 SE) animals was collected per combined gear sample during night tides in 1988 and 1989 (n=39). Overall abundance of the subtidal creek fauna was strongly seasonal (Fig. 1.3). Trends for both years and gears were similar with major peaks occurring in late July and August when water temperatures were greatest. Smaller peaks occurred for both gears in late May, and again for weir samples in late June and early July during 1989, the only year with adequate sampling prior to July.

Abundances in seine samples exhibited some tendency to rise again in the fall after the sharp decline in early September (Fig. 1.3).

Total biomass averaged 62 (22 SE) kg sample^{-1} for combined gear collections during 1989 night tides (n=24). Total biomass exhibited a strikingly similar seasonal pattern to total abundance during 1989 (Fig. 1.3) except for the extremely high mean in late May weir samples. The May peak was due to collections of large numbers of mated pairs of adult horseshoe crab, Limulus polyphemus, while the August peak was due to large catches of the fish Menidia menidia.

FAUNAL COMPOSITION

Approximately 600,000 fishes of 64 species representing 36 families were collected within the subtidal creeks during the study (Table 1.3). Nearly 80,000 invertebrates of 13 species were dominated by decapod crustaceans. Two hundred and twenty six turtles, Malaclemys terrapin, were also collected. The total number of species per combined gear sample ranged from 14 to 27 and averaged 19.6 (0.5 SE) during night tides (n=39).

Twenty of the 70 species collected during 1989 were considered most representative of the subtidal marsh creek fauna based on combined estimates of percent frequency, mean abundance and mean biomass for combined gear samples

(Table 1.4). Menidia menidia was the top ranked species by all three measures and was ranked first in overall importance. Another fish Fundulus heteroclitus was the second most important species followed by the shrimp Palaemonetes vulgaris and the crab Callinectes sapidus. The fish Clupea harengus was highly ranked by abundance and biomass, but occurred infrequently, while the horseshoe crab Limulus polyphemus and fish Cynoscion regalis were highly ranked only for biomass. The turtle, M. terrapin, occurred frequently and was the third ranked species by biomass.

Most of the sixteen species represented by all life history stages from early YOY to adults were commonly collected (Table 1.3), including the five most important species during 1989 (Table 1.4). An even greater component of the fauna (38 species) occurred primarily, or exclusively as young-of-year (YOY), twelve of which were common and apparently use the creeks as nurseries (common >1.0 sample^{-1}, Table 1.3). Six of these were the fishes Pomatomus saltatrix, Mugil curema, Paralichthys dentatus, Pseudopleuronectes americanus, and Mustelus canis, which were among the twenty most representative species for 1989 (Table 1.4). Other notable fishes occurring primarily as YOY included Pollachius virens, Alosa aestivalis, Brevoortia tyrannus, Sardinella aurita, Leiostomus xanthurus, and Sphyraena borealis. A smaller component of the fauna (14 species) occurred exclusively as adults, three of which were common (Limulus polyphemus, and the fishes Anchoa hepsetus and Lucania parva). Additionally, the fishes Anchoa mitchilli, Gasterosteus aculeatus and Cynoscion regalis, and turtle Malaclemys terrapin occurred primarily as adults (Table 1.3).

Seasonality

Although many species occurred throughout the spring, summer and fall study period, distinct seasonal faunal assemblages in the creeks were identified. The fishes Menidia menidia and Fundulus heteroclitus, and shrimp Palaemonetes vulgaris were among the dominant species for all seasons and both gears, while the shrimp Crangon septemspinosa was dominant during all seasons except for weir samples in the fall (Fig. 1.5). The fish Anchoa mitchilli was important in all seasons in weir samples, but was not important in any season for seine samples. Except for these dominant species, the spring fauna was otherwise strikingly different from summer and fall faunas (Fig. 1.5). Fishes such as Alosa aestivalis, Alosa pseudoharengus, and Clupea harengus were prevalent in the spring, as were Gasterosteus aculeatus, Pollachius virens and Urophycis regia (all YOY except G. aculeatus; Table 1.3). Summer collections contained a diverse assemblage of quite different species, including YOY Pomatomus saltatrix, Paralichthys dentatus, Strongylura marina and Mugil curema, while fall samples were best characterized by declining abundances of summer species (Fig. 1.4, 1.5). A few faunal differences did appear in the fall when YOY crabs Ovalipes ocellatus, shrimp Palaemonetes vulgaris, and fishes Fundulus heteroclitus, Fundulus majalis, Anchoa mitchilli and Menidia beryllina became briefly more abundant.

While many species contributed to the spring and summer peaks in total abundance, a few were clearly responsible for the magnitude of the peaks. The major summer peak was due to a large influx of YOY of the fish Menidia menidia in July (seine) and to their subsequent migration out of the creeks when they reached a size of 60-80 mm TL in early August (weir, Fig. 1.3, 1.4). The fishes Clupea harengus and Fundulus heteroclitus made up the largest contribution to the May peak in abundance from seine samples, while the shrimp Crangon septemspinosa, and fishes Fundulus heteroclitus and Clupea harengus were most responsible for the May peak in abundance from weir samples (Fig. 1.4). The June-July peak in weir abundance was due mainly to large catches of adult shrimps Palaemonetes vulgaris and Crangon septemspinosa. Extremely large unquantified catches of these two species were also recorded during the same period in 1988 (a crude number volume^{-1} estimate indicates numbers of >100,000 individuals sample^{-1}). The small increase in fall seine samples was primarily due to increased abundances of YOY fish Anchoa mitchilli, shrimps Palaemonetes vulgaris and Crangon septemspinosa and the crab Callinectes sapidus (Fig. 1.4, 1.5).

Seven of the ten most abundant species underwent sharp declines just prior to the August peak of Menidia menidia (Fig. 1.4). Only Callinectes sapidus exhibited peak abundance simultaneously with Menidia menidia. However, the abundances of several seasonally transient predators, Paralichthys dentatus, Strongylura marina and Pomatomus saltatrix peaked during the period of peak Menidia menidia catches. The less abundant predators Sphyraena borealis and Cynoscion regalis also first appeared during this period.

Annual variation

Although the summer fauna of the marsh creeks was very similar between years, the abundances of four species varied significantly between years (Table 1.5). Based on weir samples, Leiostomus xanthurus and Paralichthys dentatus were the only species not among the top ten by abundance for both years. Of the nine species among the top ten for both years, only Pomatomus saltatrix and Callinectes sapidus were significantly more abundant in 1989. In general, total fauna abundance and the abundances of most individual species tended to be greater in 1989 (Fig. 1.3, 1.4; Table 1.5). Although abundances could not be directly compared for seine samples between years, the overall faunal composition was very similar.

Discussion

SEASONAL ABUNDANCE AND BIOMASS

Although a comparison of absolute abundance and biomass data reported by other researchers was not possible because of differences in sampling techniques and methods, it is clear that the study creeks support a very high abundance of fishes and invertebrates. In fact, recent quantitative comparisons of several estuarine habitats in New Jersey, including eelgrass and subtidal creeks, found the highest fish densities in marsh creeks (Sogard and Able 1991, Wilson, Able and Heck personal observation). It should be noted, however, that although studies in salt marsh habitats from Florida to Massachusetts generally report a strong seasonality of fauna, few studies provide data on seasonal patterns in total faunal abundance or biomass in marsh creeks (Subrahmanyam and Coultas 1980, Smith et al. 1984).

Seasonal patterns in faunal abundance in New Jersey marsh creeks were similar to those reported for polyhaline marshes in other regions. Spring (March-April), summer (August-September) and fall (November) peaks in total abundance were reported in a New England tidal embayment (Nixon and Oviatt 1973), in a pattern similar to my samples (Fig. 1.3). In Virginia, a major peak in fish abundance occurred in May followed by a smaller peak in July in one creek and August for a second creek (Smith et al. 1984). In Florida, seasonal peaks in abundance occurred in March and July-August, but were highly variable between years (Subrahmanyam and Coultas 1980). Thus, although the timing of peak abundance can exhibit spatial and annual variation in a particular study, strong seasonal peaks are typical. Such seasonal patterns in abundance within estuaries have been attributed to seasonal shifts in faunal composition, immigration-emigration from estuaries, and predator-prey interactions (Nixon and Oviatt 1973, Subrahmanyam and Coultas 1980, Haedrich 1983).

FAUNAL COMPOSITION

Patterns of Utilization

The high diversity and abundance of YOY and juvenile fishes in the study creeks (Table 1.3, 1.4) strongly suggests this habitat is an important nursery ground for a large number of marine species. Further, marsh creeks also appear to be equally important habitats within the estuary for estuarine residents. Estuarine residents numerically dominated the fauna, based on these sampling techniques, and polyhaline subtidal marsh creeks are undoubtedly critically important habitats for the fishes *Menidia menidia* and *Fundulus heteroclitus*, the shrimp *Palaemonetes vulgaris*, and the crab *Callinectes sapidus* (Table 1.3, 1.4). Several other estuarine residents utilized marsh creeks extensively for restricted seasonal periods, including the fishes *Cyprinodon variegatus* (July), and *Gobiosoma bosci* (July-November). Other studies have also found marsh creeks to be dominated by estuarine residents (Richards and Castagna 1970, Nixon and Oviatt 1973, Subrahmanyam and Coultas 1980, Weinstein et al. 1980, Smith et al. 1984).

As is the case for most estuaries (Haedrich 1983) seasonal transients made up mostly of YOY and juveniles of marine species were the most diverse component of the fauna collected (Table 1.3). Notable among these were the crab *Ovalipes ocellatus* and the fishes *Pomatomus saltatrix*, *Mugil curema*, *Strongylura marina*, *Paralichthys dentatus*, *Mustelus canis* and *Clupea harengus* (Table 1.3). However, several seasonal transients occurred in the creeks primarily as adults, including the horseshoe crab *Limulus polyphemus*, and fishes *Gasterosteus aculeatus*, *Anchoa mitchilli*, and *Cynoscion regalis*.

A significant component of the fauna were visitors from continental shelf and southern waters, as has been previously reported for New Jersey estuaries (Milstein and Thomas 1976). At least 15 less abundant species from the subtidal creeks fall into this category (including the crab *Callinectes similis*, and fishes *Selene vomer*, *Lutjanus griseus*, *Chaetodon ocellatus*, *Gobionellus boleosoma*, *Aluterus* spp., and *Monacanthus hispidus*). Finally, several oligohaline estuarine fishes (*Menidia beryllina*, *Morone americanus* and *Trinectes maculatus*) were collected in small numbers (Table 1.3).

Seasonality

The seasonal pattern in total abundance resulted from the superimposed individual abundance patterns of the dominant species, although it mainly reflected the seasonal abundance pattern of *Menidia menidia* (Fig. 1.3, 1.4). With *M. menidia* excluded, the major peak in total abundance would have been during June-July.

A comparison between gears of the temporal abundance patterns of dominant species suggests seasonal movement patterns. Since the weir is a passive gear, it primarily captures species which are moving out of the creeks with the tides (passively or actively), while the seine captures species which remain in the creeks to avoid the weir, as well as those which do not move with the tides. Therefore, while a species is resident within the creek it will be primarily collected by the seine. However, during periods of seasonal movements a species is more susceptible to the weir. A transition from residency to seasonal migration, then, may be suggested by a temporal shift in peak catches between gears. For example, peak weir catches which follow a sharp decline in seine catches suggest seasonal emigration from the creek. Contrastingly, peak catches in seine samples following a decline in weir catches suggest immigration into the creeks.

A pattern indicating emigration from the creeks is exhibited by the shrimps *Palaemonetes vulgaris* and *Crangon septemspinosa* during the late spring-early summer, and by the fish *Menidia menidia* during summer (Fig. 1.4). Other studies have shown that adult *Crangon septemspinosa* migrate from shallow estuarine to deeper estuarine and offshore waters with the onset of high water temperatures in July (Price 1961, Haefner 1979, Modlin 1980). Similarly a strong decline in the abundance of *Palaemonetes pugio* and *Palaemonetes* spp. in July have been reported in other marshes, but has been attributed to predation by fishes (Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Welsh 1975, Sikora 1977, Subrahmanyam and Coultas 1980). Large catches of resident YOY *Palaemonetes vulgaris* and *Crangon septemspinosa* in fall seine catches are the result of increased susceptibility to the seine with growth. The sudden, dramatic increase and decline in *Menidia menidia* abundance in weir samples appears to have been due to mass migrations of YOY out of the creeks, and may be a prelude to the late fall estuarine/offshore migration described by others for northeastern estuaries (Conover and Ross 1982, Bengston 1984). A pattern of high weir catches followed by high seine catches, indicating immigration into the creeks, was exhibited by the fishes *Fundulus heteroclitus* and *Fundulus majalis* during the spring. Spring immigration of

Fundulus heteroclitus into a shallow tidal embayment was similarly reported in a New England marsh (Nixon and Oviatt 1973).

The blue crab, Callinectes sapidus, exhibited both types of patterns. I observed initially high seine catches of juveniles in the early spring followed by a peak in weir catches in June, indicating movement out of the creeks. However, weir catches of YOY (and of adults) peaked in August and then declined throughout the fall, while catches of YOY in seine samples continued to rise throughout the summer and fall (Fig. 1.4), indicating seasonal movement of YOY into the creeks. Thus YOY appear to move into the creeks during late summer through fall where they remain resident until they migrate out of the creeks as juveniles in the spring. Other marsh creek studies have reported this seasonal migration pattern for Callinectes sapidus (Hines et al. 1987, Mense and Wenner 1989).

A comparison of abundance patterns among species reveals two trends suggesting strong interspecific interactions. First, seven of the ten most abundant species underwent dramatic declines in July (Fig. 1.4). Second, a number of seasonally transient predators first appeared, or exhibited maximum abundances, during the August peak in Menidia menidia abundance (including adult Callinectes sapidus and Cynoscion regalis, and YOY Pomatomus saltatrix, Paralichthys dentatus, Strongylura marina, and Sphyraena borealis). Many of the dominant marsh residents, such as *Fundulus heteroclitus* and *Palaemonetes vulgaris*, may have declined as a result of predation by seasonal transients like *Pomatomus saltatrix* and *Strongylura marina*, or as a result of migration into other areas not sampled by my gear (upper creek or deeper bay regions) to escape predation. However, marsh residents may have migrated into other areas to avoid competition with the extremely high summer abundances of *Menidia menidia*. Alternatively, the disappearance of many of the marsh residents in August may simply have been due to a response to high water temperatures (Fig. 1.3a).

Differences between summer catches between 1988 and 1989 may have been partly due to differences in water temperatures between the years (Fig. 1.3). In fact, 50 year record low inshore water temperatures were recorded for 1988 (J. Eberwine, National Weather Service, Atlantic City, NJ) and I measured temperatures as low as 9 C within the study area in August 1988 when temperatures are normally above 20 C, suggesting that the lower abundances of typical summer fauna during 1988 may have been due to depressed water temperatures (Table 1.5, Fig. 1.3a).

Geographical comparison

The fauna of the polyhaline subtidal marsh creeks studied in New Jersey is broadly similar to that of subtidal creeks in other regions of the eastern United

States, although there is a pronounced decrease in shared fauna with more southern regions. Unfortunately, many of the published studies of marsh creeks do not report the overall faunal composition of the subtidal creeks separately from other habitats examined, and only rarely report a complete list of fauna.

To my knowledge only one study of marsh creek communities has been conducted north of New Jersey (Werme 1981, Teal 1985). All eleven species recorded in Werme's snorkeling survey, including the three most abundant species, *Menidia menidia*, *Fundulus heteroclitus* and *Fundulus majalis*, are common to New Jersey.

Previous subtidal creek studies in New Jersey used throw trap or drop cylinder/suction sampling techniques which are highly biased towards small epibenthic forms (Sogard and Able 1991, Wilson, Able and Heck personal observation) and, hence, collected far fewer species than my study. I collected all 16 species taken by Sogard and Able (1991) and 17 of 21 species taken by Wilson, Able and Heck (personal observation). *Menidia menidia*, *Fundulus heteroclitus*, *Gobiosoma bosci*, *Anchoa mitchilli* and *Fundulus majalis* were among the dominant fishes and *Palaemonetes vulgaris*, *Crangon septemspinosa*, *Pagurus longicarpus*, and *Callinectes sapidus* were among the dominant decapods (Sogard and Able 1991, Wilson, Able and Heck personal observations). The dominant fauna collected in these previous studies, then, was most similar to that collected in my seine samples, and dissimilar to the weir samples (Fig. 1.5).

The faunal composition of subtidal creeks in North Carolina and Virginia is strikingly similar to that for New Jersey. I collected 79% (11 of 14) of the species reported from one Virginia trawl survey (Smith et al. 1984) and 17 of the 19 dominant species collected in a second Virginia seine and trawl study (Richards and Castagna 1970). I collected 54% (30 of 56) of the fishes and invertebrates reported in a more comprehensive seine study in North Carolina marsh creeks (Weinstein 1979, Weinstein, et al. 1980). They report a similarly high diversity of 58 species (compared to 78 species herein), while most other studies report from 10-40 species. More importantly, the five most abundant species, *Anchoa mitchilli*, *Leiostomus xanthurus*, *Mugil curema*, *Menidia menidia* and *Fundulus heteroclitus* collected in a polyhaline creek by Weinstein (1979) were among the most abundant species in New Jersey.

Many species collected in New Jersey marsh creeks are also common to western Florida and Mississippi marsh creeks (Subrahmanyam and Drake 1975, Hackney 1977, Subrahmanyam and Coultas 1980; Hackney and de la Cruz 1981). However, many of the dominant species in my collections are replaced by closely related sibling species in the south (e.g., *Fundulus similis* replaces *F. majalis* and *F. grandis* replaces *F. heteroclitus*). At least 32% of the fishes collected in Florida (15 of 47) were collected in New

Jersey (Subrahmanyam and Coultas 1980). In fact, their five most abundant species, or their sibling counterparts, (*Anchoa mitchilli*, *Leiostomus xanthurus*, *Fundulus similis*, *Fundulus grandis*, and *Cyprinodon variegatus*), were among the most abundant species collected in this study.

It seems clear from this comparison that many of the dominant marsh creek species have a very wide geographic distribution, (particularly estuarine resident species such as *Fundulus heteroclitus*, *Fundulus majalis*, *Menidia menidia*, *Palaemonetes vulgaris*, *Gobiosoma bosci*, *Cyprinodon variegatus*, etc.). Many of the transient nursery species also have wide distributions (*Mugil curema*, *Leiostomus xanthurus*, *Strongylura marina*, etc.), or are replaced by closely related species in adjacent regions (e.g. *Brevoortia tyrannus* vs. *B. patronus*).

Conclusion

Marsh creek faunal composition, abundance and biomass are strongly seasonal in southern New Jersey, with peaks of abundance and biomass occurring in May and August. These marsh creeks support a very diverse fauna, made up both of typical estuarine residents and of YOY of a variety of species which spawn over the continental shelf. Further, many of the dominant species collected in New Jersey marsh creeks are YOY and juveniles of economically important species in the Mid-Atlantic Bight. The abundance of YOY and juveniles in the creeks and prevalence of the habitat in southern New Jersey, strongly suggests that marsh creeks are a significant nursery habitat for many marine species in the adjacent Mid-Atlantic Bight. It is noteworthy that many of the dominant marsh creek species have wide geographic distributions despite important differences in dominant marsh vegetation (*Juncus*, *Spartina*, mixed) tidal flood regimes (diurnal, semidiurnal, high marsh, low marsh) and other factors.

Table 1.1. Sampling effort by year, gear and month. Numbers in parentheses indicate additional samples where the abundances of some species were not quantified.

	1988						1989		
	Day			Night			Night		
Month	Weir	Seine	Number of creeks sampled	Weir	Seine	Number of creeks sampled	Weir	Seine	Number of creeks sampled
April	---	---	0	(2)	---	1	3	1	2
May	1 (1)	---	1	1	---	1	3	3	2
June	1 (1)	(1)	2	(2)	(1)	1	3	3	2
July	5 (1)	2 (2)	2	6 (1)	5 (1)	2	6	6	3
August	3 (1)	4	2	2 (2)	2	2	5 (1)	6	3
September	3	4	2	2 (2)	4	2	5	5	3
October	2	2	1	2	2	1	1	1	1
November	(1)	1	1	---	1	1	---	---	0
Totals	15 (5)	13 (3)	2	13 (9)	14 (2)	2	26 (1)	25	3

Table 1.2. Mean temperature, salinity and water depth at the mouth of the subtidal creeks for 64 weir samples taken from July-November 1988 and April-October 1989 (tidal range = high tide - low tide).

			Seasonal range		
High tide	Mean	SE	Minimum	Maximum	Sample size
Air temperature	19	0.9	3	32	61
Water temperature	18	0.6	8	28	62
Salinity	30	0.2	24	32	61
Depth (m)	1.4	0.05	0.8	2.0	60
Low tide					
Air temperature	18	0.8	3	31	61
Water temperature	19	0.7	8	28	64
Salinity	29	0.3	23	33	61
Depth (m)	0.7	0.03	0.2	1.2	57
Tidal range					
Air temperature	0.6	0.5	-13	8	59
Water temperature	-1.1	0.4	-8	6	60
Salinity	0.8	0.2	-2	7	59
Depth (m)	0.8	0.03	0.3	1.4	57

Table 1.3. Abundance and size (length for fishes and turtles, weight for invertebrates) summary statistics of macrofauna collected within three subtidal marsh creeks during 1988 (day andnight) and 1989 (night). Mean abundance (SE) and total number (sum) for each species were determined for each gear, while mean sizes (SE) were determined from pooled data. The fifth and ninetyfifth percentiles (P5-P95) for size were determined and used to classify the dominant life history stages for each species (yoy=young-of-year, juv=subadult, adu=adult, all=all stages).

	Abundance							
Group	Weir		Seine		Size			Life
Species	Mean (SE)	Sum	Mean (SE)	Sum	Mean (SE)	P5-P95	N	Stages
Invertebrates								
Illex illecebrosus	0.1 (0.1)	8	0.3 (0.3)	15	103 (33)g	3-140	4	yoy,adu
Limulus polyphemus	3.2 (1.9)	206	0	0	1624 (82)g	1261-1982	18	adu
Palaemonetes vulgaris	414 (194)	24849	790 (107)	41888	0.4 (0.04)g	0.2-0.6	82	all
Crangon septemspinosa	183 (86)	11180	145 (28)	7850	0.3 (0.02)g	0.1-0.5	66	all
Penaeus aztecus	0.01 (0.01)	1	0.02 (0.02)	1	4.2 (2.4)g	2-7	2	yoy
Pagurus longicarpus	1.9 (0.9)	118	1.3 (0.5)	69	0.3 (0.03)g	0.2-0.7	22	all
Callinectes sapidus	20 (4)	1201	24 (5)	1304	35 (5)g	0.1-141	102	all
Callinectes similis	0.1 (0.1)	6	0.04 (0.04)	2	3 (0.9)g	0.3-71	5	yoy
Carcinus maenus	0.4 (0.2)	25	0.5 (0.2)	26	39 (10)g	15-71	5	juv,adu
Ovalipes ocellatus	4 (2)	246	0.1 (0.1)	6	5 (2.6)g	0.1-32	12	yoy,adu
Cancer irroratus	0.2 (0.1)	11	0	0	26 (13)g	13-39	2	yoy
Libinia dubia	0.1 (0.1)	4	0	0	95 (26)g	68-121	2	adu
Libinia emarginata	0.1 (0.04)	4	0	0	114 (44)g	70-201	3	adu
Fishes								
Mustelus canis	1.6 (0.7)	110	0.3 (0.2)	17	410 (5)TL	320-493	113	yoy
Raja eglanteria	0.01 (0.01)	1	0	0	695 DW	---	1	adu
Anguilla rostrata	1.0 (0.3)	66	0.6 (0.2)	32	417 (14)TL	199-618	103	juv,adu
Conger oceanicus	0.01 (0.01)	1	0.02 (0.02)	1	295(36)TL	223-331	3	juv
Alosa aestivalis	2.2 (1.8)	149	0.5 (0.3)	26	91 (0.6)SL	80-101	162	yoy
Alosa mediocris	0	0	0.02 (0.02)	1	290 SL	---	1	adu

Table 1.3. Continued.

Group Species	Abundance				Size			Life Stages
	Weir		Seine					
	Mean (SE)	Sum	Mean (SE)	Sum	Mean (SE)	P5-P95	N	
Alosa pseudoharengus	0.7 (0.3)	48	0.2 (0.1)	11	87 (2)SL	59-111	64	yoy
Alosa sapidissima	0.04 (0.04)	3	0.2 (0.2)	10	115 (13)SL	95-154	4	yoy
Brevoortia tyrannus	2.2 (0.8)	150	0.9 (0.5)	51	54 (2)SL	33-101	167	yoy
Clupea harengus	26 (25)	1813	113 (112)	6444	62 (0.4)SL	51-75	329	yoy
Sardinella aurita	1.0 (0.4)	70	0.2 (0.1)	9	45 (0.8)SL	35-56	62	yoy
Anchoa hepsetus	12 (11)	784	0.02 (0.02)	1	77 (0.9)TL	67-84	50	adu
Anchoa mitchilli	161 (55)	9824	23 (9)	1243	65 (0.3)TL	40-82	1441	all
Synodus foetens	0	0	0.02 (0.02)	1	89 SL	---	1	yoy
Opsanus tau	0.2 (0.1)	15	0.5 (0.2)	30	89 (6)SL	36-165	50	all
Pollachius virens	2.8 (1.5)	192	0.02 (0.02)	1	63 (2)SL	42-92	122	yoy
Merluccius bilinearis	0.01 (0.01)	1	0	0	72 SL	---	1	yoy
Urophycis sp.	0	0	0.02 (0.02)	1	49 SL	---	1	yoy
Urophycis regia	0.6 (0.3)	39	0	0	144 (4)SL	96-193	39	yoy
Strongylura marina	5 (1)	347	3 (2)	180	140 (2)BL	76-218	545	all
Cyprinodon variegatus	1.5 (0.6)	97	21 (14)	1110	35 (0.4)TL	28-43	212	all
Fundulus heteroclitus	211 (82)	12432	546 (220)	28935	56 (0.3)TL	34-84	2788	all
Fundulus majalis	6 (2)	372	31 (11)	1669	72 (1.2)TL	36-129	634	all
Lucania parva	0.05 (0.03)	3	1.1 (0.9)	106	30 (0.6)TL	25-36	44	adu
Membras martinica	0.02 (0.02)	1	0	0	98 TL	---	1	adu
Menidia beryllina	0.4 (0.3)	23	0.2 (0.2)	11	52 (4)TL	33-61	23	all
Menidia menidia	5080 (3336)	289568	4198 (1171)	222489	68 (0.2)TL	29-103	9620	all
Apeltes quadracus	0.2 (0.1)	15	0	0	42 (1.5)SL	35-55	15	adu
Gasterosteus aculeatus	2.4 (1.6)	168	0.02 (0.02)	1	52 (0.7)SL	22-60	170	yoy,adu

Table 1.3. Continued.

Group	Abundance							
	Weir		Seine		Size			
Species	Mean (SE)	Sum	Mean (SE)	Sum	Mean (SE)	P5-P95	N	Life Stages
Hippocampus erectus	0.3 (0.2)	21	0	0	1.4 (0.1)g	1-1.9	9	adu
Syngnathus fuscus	0.1 (0.04)	10	5.5 (1.4)	302	109 (2)SL	70-163	208	all
Morone americanus	0.03 (0.02)	2	0	0	273 (3)SL	270-276	2	adu
Centropristis striata	0.06 (0.03)	4	0.02 (0.02)	1	67 (13)SL	42-115	5	yoy,juv
Pomatomus saltatrix	21 (4)	1441	2.8 (0.7)	158	97 (1)SL	48-168	1699	yoy
Rachycentron canadum	0.01 (0.01)	1	0.02 (0.02)	1	63 (8)SL	55-71	2	yoy
Caranx hippos	0.9 (0.4)	61	0.3 (0.2)	19	86 (4)SL	30-129	80	yoy
Selene vomer	0.06 (0.04)	4	0	0	33 (5)SL	28-47	4	yoy
Trachinotus falcatus	0.03 (0.03)	2	0	0	20 (1)SL	19-21	2	yoy
Lutjanus griseus	0	0	0.1 (0.1)	6	31 (1)SL	26-35	6	yoy
Unknown gerreid	0	0	0.1 (0.04)	4	35 (4)SL	23-50	7	yoy
Stenotomus chrysops	0.04 (0.03)	3	0	0	99 (4)SL	89-113	6	yoy
Bairdiella chrysoura	0.1 (0.1)	8	0.1 (0.1)	6	84 (4)SL	55-102	14	yoy
Cynoscion regalis	0.6 (0.2)	43	0	0	389 (18)SL	139-521	41	yoy,adu
Leiostomus xanthurus	169 (46)	11654	18 (6)	1006	68 (0.5)SL	40-98	2889	yoy
Menticirrhus saxatilis	0.04 (0.03)	3	0	0	273 (10)SL	257-290	3	adu
Chaetodon ocellatus	0.01 (0.01)	1	0	0	15 SL	---	1	yoy
Tautoga onitis	0.1 (0.05)	10	0.5 (0.2)	30	58 (3)SL	31-90	45	yoy
Mugil cephalus	0.03 (0.02)	2	0.2 (0.2)	12	113 (7)SL	68-174	15	yoy
Mugil curema	7.8 (3.5)	538	29 (19)	1580	72 (1)SL	27-109	1007	yoy
Sphyraena borealis	2.6 (1.6)	180	6.6 (5.2)	378	103 (1)SL	69-142	291	yoy
Ammodytes americanus	0.01 (0.01)	1	0	0	95 SL	---	1	adu
Gobionellus boleosoma	0	0	0.1 (0.1)	6	29 (3)SL	14-35	6	all

Table 1.3. Continued.

Group Species	Abundance							
	Weir		Seine		Size			Life Stages
	Mean (SE)	Sum	Mean (SE)	Sum	Mean (SE)	P5-P95	N	
Gobiosoma bosci	0.1 (0.04)	6	21 (5)	1180	21 (0.3)SL	12-33	553	all
Scomberomorus sp.	0.03 (0.02)	2	0	0	48 (5)SL	43-53	2	yoy
Prionotus evolans	0.1 (0.1)	10	0.1 (0.04)	4	132 (19)SL	16-245	17	all
Paralichthys dentatus	5.2 (1.5)	359	0.04 (0.02)	2	206 (3)SL	165-250	289	yoy
Scophthalmus aquosus	0.01 (0.01)	1	0	0	23 SL	---	1	yoy
Pseudopleuronectes americanus	1.5 (0.3)	104	2 (0.5)	112	78 (2)SL	56-98	305	yoy
Trinectes maculatus	0.04 (0.3)	3	0	0	127 (10)SL	117-136	2	adu
Aluterus spp.	0.1 (0.1)	7	0	0	53 (6)SL	38-77	7	yoy
Monacanthus hispidus	0.1 (0.1)	7	0.02 (0.02)	1	28 (5)SL	15-53	8	yoy
Sphoeroides maculatus	0.1 (0.05)	5	0.02 (0.02)	1	81 (7)SL	55-110	8	yoy
Chilomycterus schoepfi	0.03 (0.02)	2	0	0	35 SL	---	1	yoy
Turtles								
Malaclemys terrapin	3.3 (0.5)	228	0.1 (0.1)	7	159 (2)CL	115-203	226	juv,adu
Total invertebrates	663 (286)	27786	965 (123)	51161				
Total fishes	5767 (3333)	328711	5041 (1182)	267175				
Total animals	6654 (3470)	365961	6006 (1160)	318343				

Table 1.4. Summary statistics and overall rank for all species occuring in at least 50% of the samples and any additional species ranked within the top ten by abundance or biomass (g) for combined gear collections made during 1989 (N=24). Overall rank was obtained by ranking the sum of the ranks of percent frequency, mean number, and mean biomass for each species.

Species	Percent frequency	Rank	Mean number	(SE)	Rank	Mean biomass	(SE)	Rank	Overall rank
Palaemonetes vulgaris	100	1	1256	456	3	548	244	10	3
Crangon septemspinosa	100	1	562	215	4	251	113	16	5
Fundulus heteroclitus	100	1	1418	561	2	2971	937	4	2
Menidia menidia	100	1	15266	9576	1	33018	20870	1	1
Callinectes sapidus	96	5	61	10	9	1763	392	6	4
Pomatomus saltatrix	83	6	28	9	11	1254	554	8	6
Mugil curema	79	7	79	51	7	448	161	12	7
Anchoa mitchilli	75	8	164	77	6	299	116	15	9
Fundulus majalis	75	8	67	23	8	381	130	13	9
Malaclemys terrapin	75	8	5	1	17	4354	13	3	8
Ovalipes ocellatus	67	11	9	4	14	72	22	20	15
Strongylura marina	67	11	14	5	12	300	119	14	12
Pseudopleuronectes americanus	63	13	3	1	20	29	12	27	19
Paralichthys dentatus	54	14	12	4	13	1918	588	5	11
Mustelus canis	50	15	2	1	23	470	184	11	16
Cyprinodon variegatus	50	15	46	33	10	31	22	26	17
Syngnathus fuscus	50	15	1	0	29	2	0	43	20
Limulus polyphemus	29	23	7	5	16	11252	7834	2	14
Cynoscion regalis	33	21	1	0	28	1462	509	7	18
Clupea harengus	25	24	340	336	5	882	876	9	13

Table 1.5. Annual variation in the mean (SE) abundances of the ten most abundant species collected in night weir samples during the summers (July-Sept.) of 1988 (n=11-15) and 1989 (n=11-12).

	Mean (SE)		
Species	1988	1989	ANOVA
Menidia menidia	5126 (3062)	17718 (17079)	ns
Palaemonetes vulgaris	544 (376)	597 (526)	ns
Leiostomus xanthurus[1]	433 (223)	8 (4)	***
Anchoa mitchilli	420 (223)	51 (29)	ns
Fundulus heteroclitus	291 (204)	145 (112)	ns
Pomatomus saltatrix	17 (4)	51 (15)	*
Crangon septemspinosa	17 (14)	221 (216)	ns
Mugil curema	11 (7)	29 (7)	ns
Callinectes sapidus	6 (3)	46 (12)	***
Strongylura marina	5 (2)	17 (7)	ns
Paralichthys dentatus[1]	0.6 (0.3)	26 (6)	***

$^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

[1] not in the top ten for both years

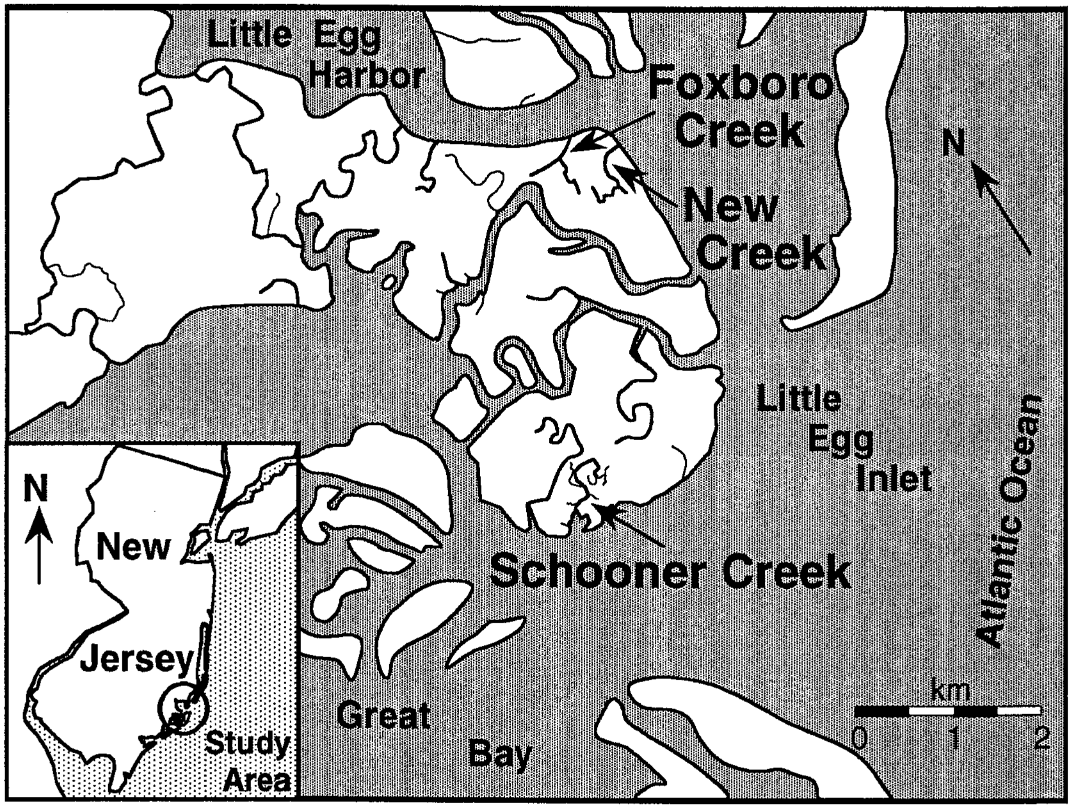


Figure 1.1. Great Bay-Little Egg Harbor estuarine complex and study creeks in southern New Jersey.

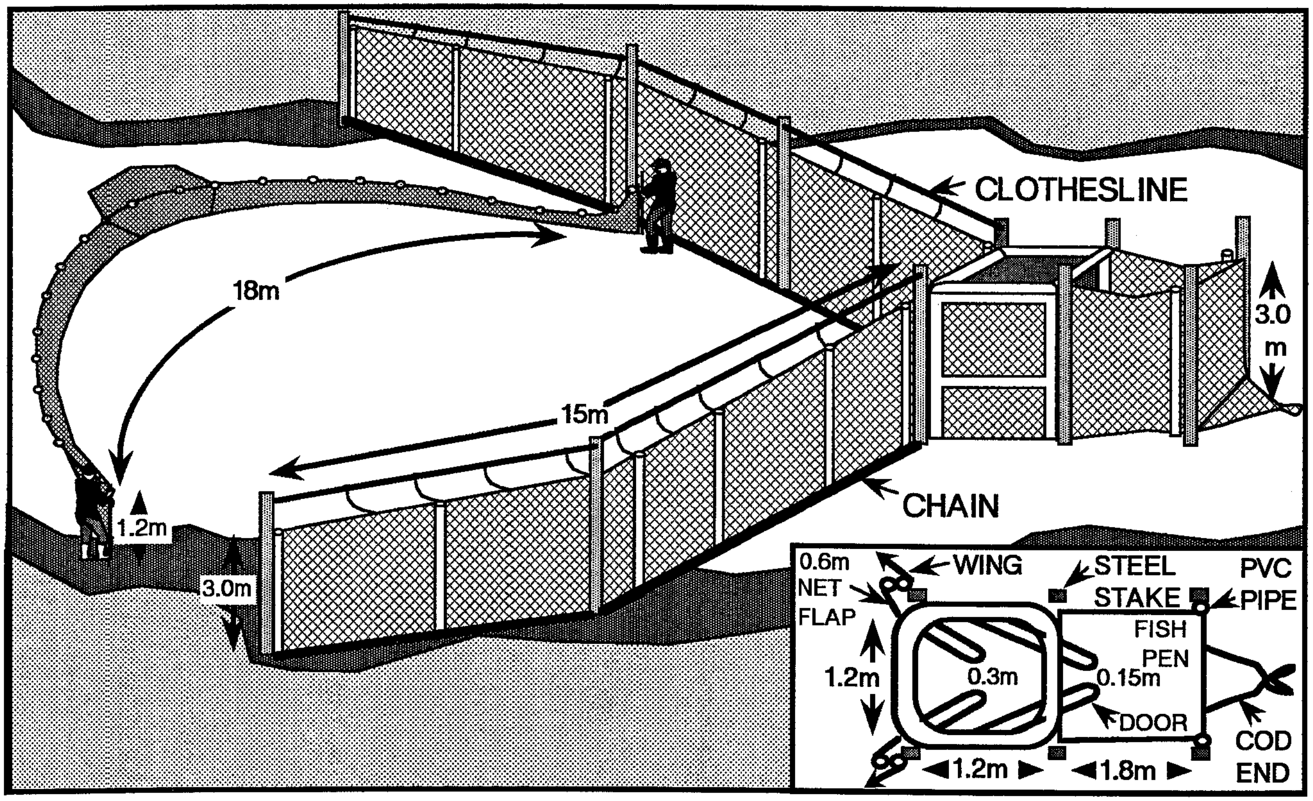


Figure 1.2. Diagram of the fish weir and seine methodology (not to scale). Inset: schematic illustration of the weir from an overhead view.

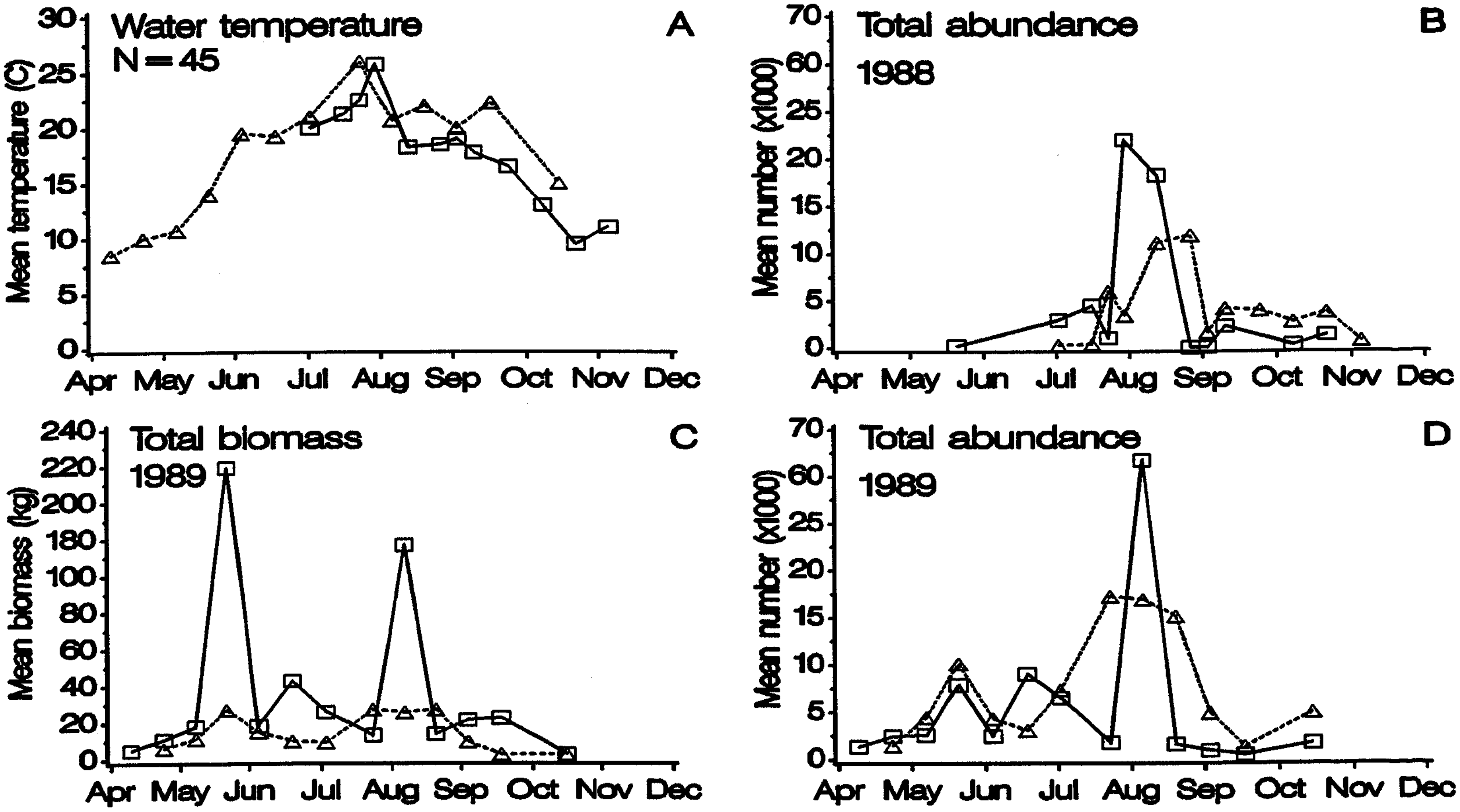


Figure 1.3. Average weekly temperature, faunal abundance and biomass in the study creeks for night samples: A) Water temperature by year (1988=squares, n=18), (1989=triangles, n=27); B) Total abundance by gear in 1988 (weir=squares, n=13, and seine=triangles, n=14); C) Total biomass by gear in 1989 (n=26, 25, respectively); D) Total abundance by gear in 1989 (n=26, 25, respectively). Note scale breaks in B-D.

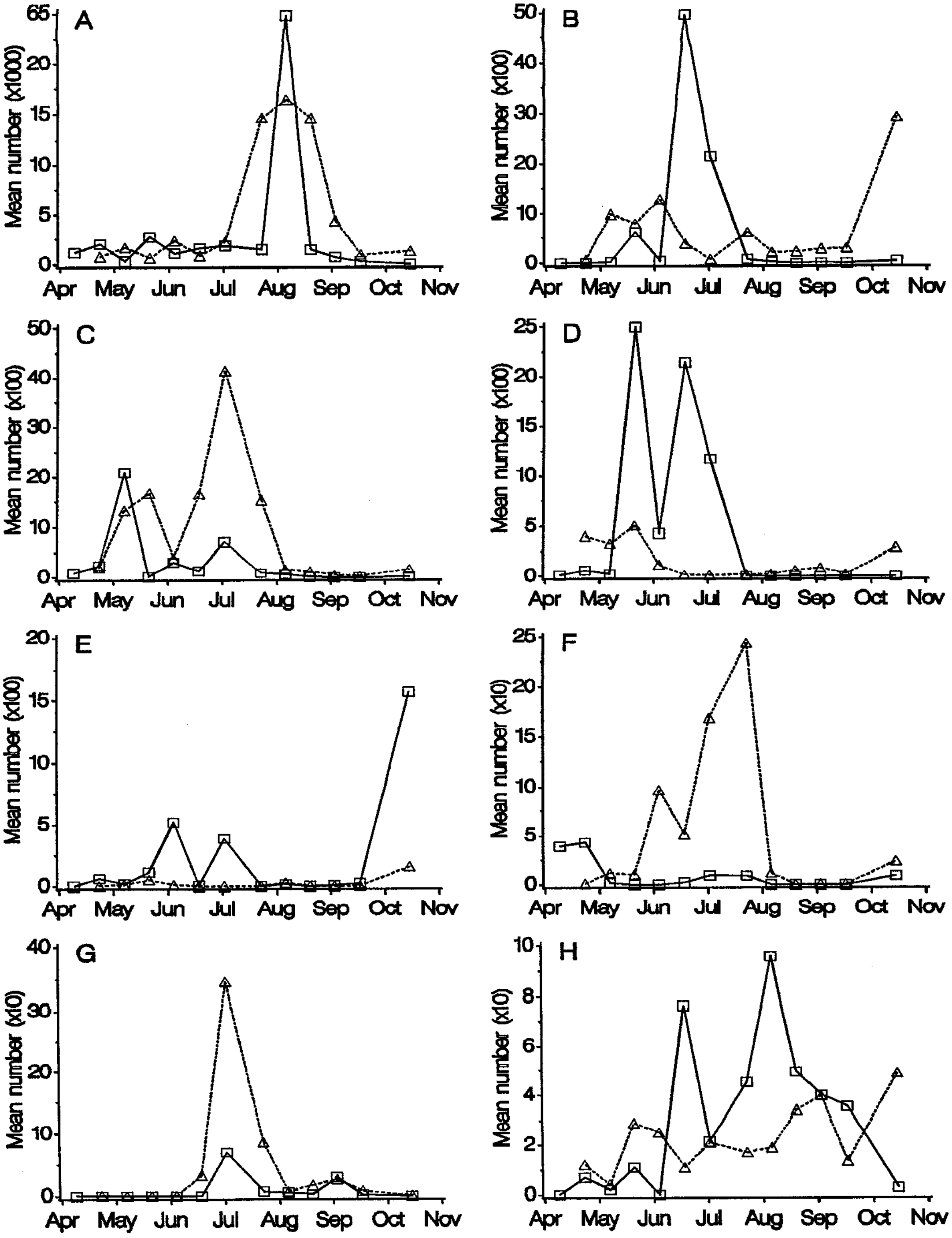


Figure 1.4. Weekly mean abundances by gear of eight of the most abundant species collected during 1989 (weir=squares, n=26, seine = triangles, n=25): A) *Menidia menidia*, B) *Palaemonetes vulgaris*, C) *Fundulus heteroclitus*, D) *Crangon septemspinosa*, E) *Anchoa mitchilli*, F) *Fundulus majalis*, G) *Mugil curema*, and H) *Callinectes sapidus*.

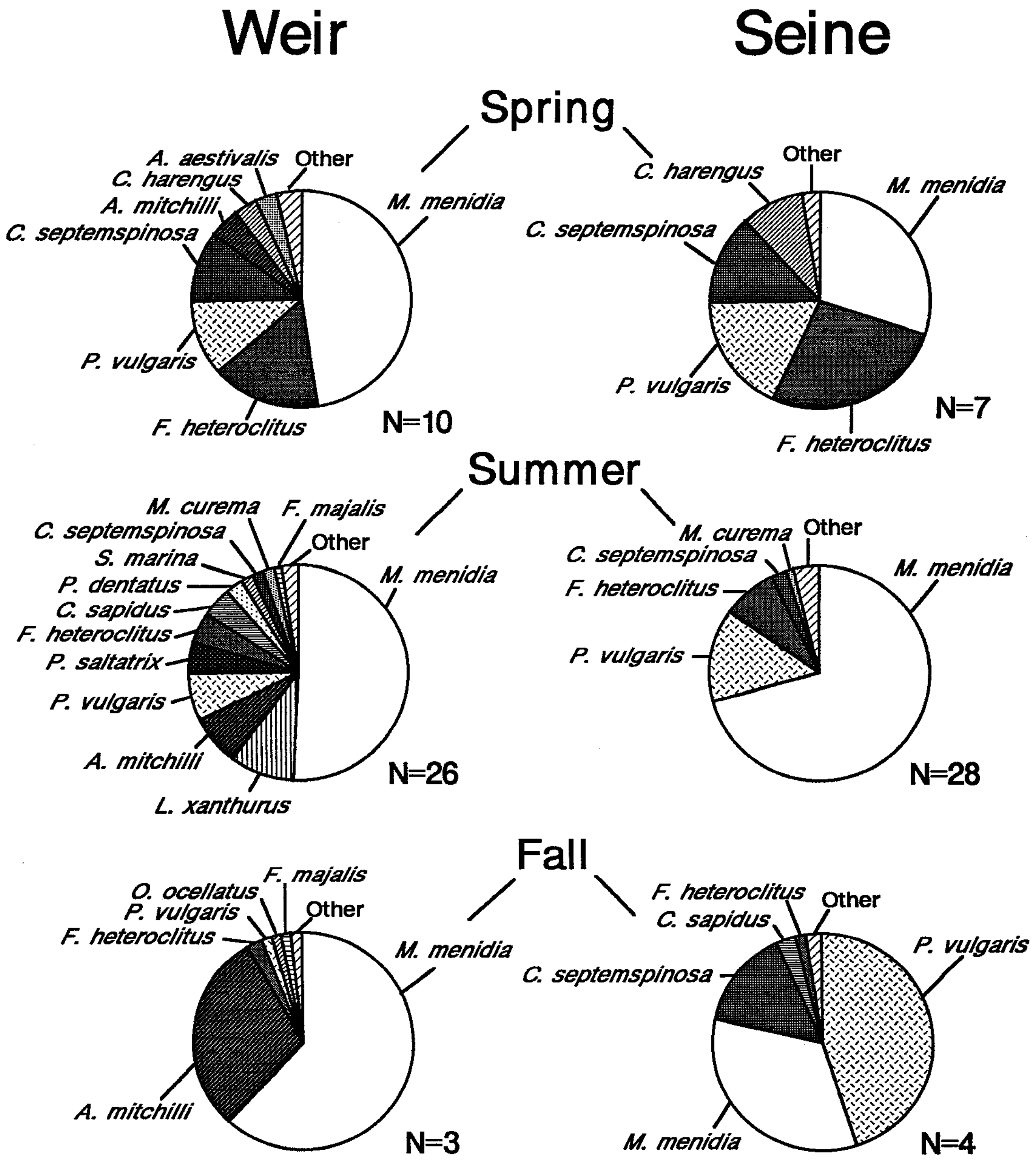


Figure 1.5. Mean percent relative abundance of all species >1% by season and gear. Spring=April-June, summer=July - September, fall=October-December.

Chapter 2. Spatial variation in salt marsh creek communities: influence of tides and creek morphology

Abstract

Three polyhaline subtidal marsh creeks and two intertidal marsh creeks in southern New Jersey were sampled with weirs and seines to examine spatial variation in fauna among, and within, marsh creeks. Among-creek spatial variation in fauna was examined by comparing weir and seine samples (n=27) taken at the mouths of three subtidal creeks from April-October 1989. Within-creek variation was examined by comparing intertidal weir samples from two intertidal tributaries of a subtidal creek (n=13) with subtidal weir (n=6) and seine (n=7) samples from the subtidal creek during July-October 1989. Strong differences in community structure, as measured by species relative abundances, were found among and within creeks. Among-creek differences appear to be more strongly related to creek size than to creek location. Creek size denotes an array of creek morphological characteristics such as length, depth, and flood area. Within-creek differences suggest that community structure differs between upper and lower regions of creeks, and between intertidal and subtidal habitat. Comparison among subtidal weir and seine samples, and intertidal weir samples, further suggests that many species undergo tidal movements (passive or active)

within marsh creeks. It is hypothesized that creek size strongly influences the prevalence of tidal movements in the communities, with virtually all species/individuals undergoing tidal migration in intertidal creeks, while progressively fewer species/individuals migrate as creek size increases. Creek morphology is hypothesized to influence community structure in two major ways, 1) directly through the regulation of tidal dynamics, and 2) indirectly through the regulation of tidal and diel changes in physical conditions along a mouth-to-headwater creek gradient.

Introduction

Although numerous recent studies have suggested that marsh creeks are important nursery habitats for marine fishes and invertebrates (Bozeman and Dean 1980, Weinstein et al. 1980, Currin et al. 1984, Weinstein 1984, Weinstein et al. 1984, Cowan and Birdsong 1985, Teal 1985, Blaber 1986, Sogard and Able 1991, Chapter 1), little is known of factors which regulate marsh creek communities. Weinstein et al. (1980) sampled tidal creeks and other shallow marsh habitats throughout Cape Fear Estuary, North Carolina and reported that fauna appeared to be strongly influenced by estuarine salinity gradients and substrate characteristics. Studies have also shown that distinct faunal assemblages can form along a mouth-to-headwater creek gradient (Hackney et al. 1976, Weinstein and Brooks 1983, Smith et al. 1984). Similarly, species assemblages and abundances of nekton utilizing the intertidal marsh surface have been found to be strongly affected by gradients of creek order (*sensu* Harrell and Dorris 1968), with greatest nekton abundance at creek headwaters (Rozas and Odum 1987, Hettler 1989). McIvor and Odum (1988) compared nekton utilizing depositional and erosional marsh creek banks and found highest fish densities along depositional banks.

In this study I examine factors which structure fish and macroinvertebrate communities in marsh creeks located in a southern New Jersey estuary. Fauna use of subtidal and intertidal marsh creeks are compared in order to gain a better understanding of how differences in tidal patterns effect marsh creek use patterns. The specific goals of this study are: 1) to examine among-creek and within-creek spatial variation in fauna of salt marsh creeks in New Jersey, and 2) to examine the nature and extent of tidal movements in these habitats.

Materials and Methods

STUDY AREA

The study was conducted within the Great Bay - Little Egg Harbor estuarine complex in southern New Jersey (Fig. 2.1). Fishes were collected from two intertidal and three subtidal polyhaline (22-30‰) marsh creeks during 1989 with a weir system (Chapter 1). Foxboro, Schooner and New creeks were subtidal, approximately 930 m, 1160 m, 1390 m in length, 23,000 m^2, 24,000 m^2, 26,000 m^2 in area, and were located 2.3 km, 1.3 km and 2.0 km from Little Egg Inlet, respectively (Fig. 2.1a). Each creek had a single connection with the bay and received freshwater only through local runoff, and hence, the criteria of tidal creeks (Hackney et al. 1976). The two intertidal tributaries of Schooner Creek, designated "Lower" and "Upper" creeks, were approximately 110 m, 150 m in length, 1500 m^2, 3300 m^2 in flood area, and were located 73 m and 730 m from the mouth of Schooner Creek, respectively (Fig.

2.1b).

SAMPLING GEAR AND METHODOLOGY

Schooner, Foxboro and New creeks were sampled over a three day period approximately fortnightly from April-October 1989 (n=27). Lower and Upper creeks were sampled simultaneously from July-October 1989 (n=13) on alternate weeks from subtidal sampling. All sampling was begun on night high tides. Night tides were those in which at least the last two hours of flood occurred after sunset.

During subtidal creek sampling a weir was set to block off the mouth of a creek at high tide and captured fishes leaving the creek with the ebb tide (see Chapter 1). Two wing nets (15.2 m long by 3.0 m high, with 6.4 mm mesh) were used to block off the mouth of the creek and to lead fishes into the weir (1.2 m wide by 3.0 m long, by 3.0 m high, with 6.4 mm mesh). Deployment of the weir was begun about 30 minutes before slack high tide and was completed within one hour. At low tide fish were removed from the weir through a cod-end.

Because the weir is a passive gear which primarily captures animals moving with the tide, seine sampling was also conducted within the creeks to capture less mobile forms and species/individuals which actively avoid the weir and remain within the creeks. A single haul of a bag seine (18.3 m long by 1.2 m high, with 6.4 mm mesh) was made in the creek above the weir after it had been closed off at low tide. The seine was large enough to completely enclose and "purse" in the approximately 100 m^2 area between the wings (Chapter 1).

The intertidal creeks were sampled with a smaller and more simplified weir (1.2 m wide by 1.8 m long weir, with 4.6 m long by 1.2 m high wings). Due to gear limitations the intertidal weir used at Lower Creek had 6.4 mm mesh, while that used at Upper Creek had 3.2 mm mesh (all wings had 3.2 mm mesh). The intertidal creek weirs were set at high tide in about fifteen minutes and were hauled at low tide when the creek had completely drained except for a small run-off channel.

All samples were put on ice and transported back to the laboratory for sorting and identification. However, turtles (Malaclemys terrapin) and horseshoe crabs (Limulus polyphemus) were immediately culled from the samples and released. For small samples, all species of fishes and macroinvertebrates were sorted and enumerated. For large samples the entire sample was sorted once to enumerate economically important species, species of special interest, and generally any species present in low abundance which might be missed in subsampling. After the initial sort, all species were enumerated in a subsample of 10-50%, by wet weight, of the sample.

During subtidal creek sampling water depth, air and water temperature and salinity were taken at the weir location at high tide after the weir had been set and at low tide just prior to hauling the gear. Tidal ranges in physical variables were calculated as the difference between high and low tide values. Because the intertidal creeks were nearly dry at low tide, physical data were collected from the main channel of the subtidal creek directly off of the intertidal creek mouth (stations 1 & 2; Fig. 2.1b). Physical data from the Schooner Creek subtidal weir and from the Lower Creek intertidal weir samples were taken in the same location (station 1; Fig. 2.1b).

SAMPLE ANALYSIS

Among-creek spatial variation

A comparison among creeks and between tide stages of natural logarithm-transformed (ln) physical data (air temperature, water temperature, salinity and depth) was made using a MANOVA and profile analysis (Harris 1985) with high tide and low tide response variables. Profile analysis was performed to examine interactions between tide stage and creek. Three hypotheses were tested 1) H_1 - response profiles are parallel (no interaction between tide and creek), 2) H_2 - response profiles are coincidence (means pooled over tides are equal among creeks), and 3) H_3 - response profiles are flat (tide means are equal). Simple Pearson correlations among physical factors were also determined (Sokal and Rohlf 1981).

A MANOVA with two transformed (ln+0.5) response variables (abundance in weir and seine) for each species was used to test for both univariate and multivariate differences in species abundances among creeks. Profile analysis was performed on species with significant creek effects to examine interactions between gear and creek effects. Here the hypotheses are, 1) H_1 - no interaction between gear and creek, 2) H_2 - means pooled over gear are equal among creeks, and 3) H_3 - gear means are equal. The latter analysis was not performed because the direct comparison of log transformed abundances among gears was not considered useful. However, the MANOVA analysis was repeated on transformed (arcsine square root) relative abundance data to enable a direct comparison among gears. Here, I report only the results of the test of H_3 because I am only interested in relative abundance differences between subtidal weir and seine samples (other effects are reported in the MANOVA on logarithm transformed abundance data described above).

While the above analyses provide information on spatial and gear differences for each individual species, I also used canonical discrimination analysis (CDA) to examine spatial variation in faunal assemblages among creeks and gears (Pielou 1984, Harris 1984, SAS Institute Inc. 1988). This analysis was performed on transformed (arcsine square root) relative abundance data. Average relative abundance for each species for weir and seine samples was determined by dividing the number of animals collected (sum of all invertebrates, fish and turtles in the sample) for each sample and computing a mean for all samples. The CDA was performed on data grouped by creek and gear (six groups), and on data grouped by creek separately for each gear (three groups, two analyses). Because of the large number of species only the ten most abundant species from each group were entered in the CDA. Pearson correlations of the original transformed variables with the derived canonical variables were calculated to determine which species contributed most to the group discrimination (Harris, 1985). Finally, canonical correlation analysis (CCA, Harris 1985, SAS Institute Inc. 1988) was performed separately for each gear to determine, 1) physical variables which most influence fauna collected by a gear, and 2) species which are most influenced by the measured physical variables.

Within-creek spatial variation

A comparison of the faunal compositions of catches in Schooner Creek subtidal weir and seine, and Lower and Upper creek intertidal weirs, was made to examine within-creek faunal variations. Samples taken from July-October 1989 were used in this comparison. The intertidal creek weirs, like the subtidal creek weirs, passively collect natant fauna moving out of the intertidal creek with the tide.

Since the subtidal creek serves as the low tide refuge for the intertidal fauna, I consider the comparison between intertidal creeks to be a comparison of fauna between upper and lower regions of Schooner Creek (within-creek comparison). A comparison of the intertidal weir samples with the subtidal weir and seine samples was also used to delineate fauna which tends to be restricted to subtidal portions of the creek from that which uses both subtidal and intertidal areas. Mean abundance and relative abundance of species for these four collection groups (subtidal weir, seine, Lower Creek and Upper Creek intertidal weirs) were determined. To compare community assemblages among groups, CDA was performed on arcsine transformed relative abundance data using the ten most abundant species from each collection group.

Results

PHYSICAL CHARACTERISTICS

While all three subtidal creeks exhibited similar water temperatures and salinities, morphological differences were apparent. Depth profiles of Schooner and New creeks indicated numerous deep water holes (2-3 m) throughout their lengths, while the smaller Foxboro Creek lacked deep holes entirely (Fig. 2.2). Unlike the other two creeks, Foxboro Creek was deepest at the mouth, where its low tide depth ranged from 0.2 to 0.6 m (8 to 28 inches, Table 2.1). Depth variables (high and low tide depth, and tidal depth range) were significantly different among creeks. It is clear that both the larger creeks had substantially more water volume at low tide than Foxboro Creek. Other physical factors were very similar among subtidal creeks which averaged 19 C and 28‰ during the sampling period (April-October). However, small, but significant, differences in high tide water temperature and low tide salinity were observed among the creeks (Table 2.1).

Physical variables measured in the subtidal creek sampling exhibited intercorrelations and tidal influences. A significant drop in salinity (mean=1.7‰, maximum=6‰, $p<0.01$) was observed between high and low tide. Although mean water temperature was not significantly different between high and low tide, water temperatures rose as much as 7 C and dropped as much as 6 C from high to low tide. Tidal range in water temperature and salinity tended to be greatest at Foxboro Creek and least at New Creek. High and low tide water temperatures were highly correlated with air temperatures and with each other (Table 2.2). Salinity was negatively correlated with water temperature and with water depth. Tidal salinity range was positively correlated with tidal depth range.

During intertidal creek sampling salinity and water depth within the main channel of Schooner Creek were significantly lower at the Lower Creek compared to the

Upper Creek location (Table 2.1). Depth was the only variable significantly different between high and low tide (H_3: $p \leq 0.0001$). However, salinity dropped an average of 3‰ (maximum 7‰) from high to low tide (which was significant at $\alpha=0.1$). No spatial or tidal effects on water temperature were observed.

AMONG-CREEK FAUNAL VARIATION

Among-subtidal-creek spatial variation in fauna resulted mainly from differences in abundances. Only *Sphyraena borealis* was restricted to a single creek (Schooner Creek, Table 2.3). However, *Clupea harengus* and *Mustelus canis* were rare outside of Foxboro Creek. Six of the 15 most abundant (based on combined subtidal weir and seine samples) subtidal creek species, including the shrimp *Palaemonetes vulgaris*, crab *Callinectes sapidus*, turtle *Malaclemys terrapin* and fishes *Anchoa mitchilli*, and *Mugil curema*, exhibited significant multivariate differences (i.e., based on both subtidal weir and seine response variables) in abundance among the three subtidal creeks (Table 2.3). Additionally, several fishes exhibited univariate differences (i.e., based on a single gear response variable) in abundance among creeks, including *Fundulus heteroclitus* in seine samples, and *Mustelus canis* and *Sphyraena borealis* in weir samples. In general Foxboro Creek tended to have the highest abundance for many species, including F. heteroclitus, P. vulgaris, C. septemspinosa, C. harengus, M. curema, C. sapidus, Cyprinodon variegatus, P. saltatrix, S. marina and M. canis. Schooner Creek had higher abundances of M. menidia, A. mitchilli, Gobiosoma bosci, Alosa aestivalis and S. borealis. New Creek had higher abundances of F. majalis. Strongylura marina and M. terrapin exhibited significant interactions between gear and creek.

Foxboro Creek weir samples contained the most diverse assemblage of dominant species (mean relative abundances of ≥1%), and exhibited the greatest difference between weir (12 species) and seine (6 species) samples, while New Creek had the least diverse dominant species assemblage, and the least difference between weir (6 species) and seine (5 species) samples (Table 2.4).

Significant among-creek differences in species assemblages captured by subtidal weirs were indicated by the canonical discrimination analysis (Fig. 2.3). Significant creek differences were not found for the seine samples. Weir samples cluster in a pattern which parallels creek size, with Schooner Creek intermediate to the smaller Foxboro Creek and larger New Creek (Fig. 2.3). This pattern is particularly striking since Foxboro and New creeks are located only 300 m apart, while Schooner Creek is located nearly 6 km away (Fig. 2.1). The first canonical variable (can1), therefore, appears to separate the creeks by size, rather than location. Pearson correlations of individual species with the derived canonical variables indicates that three fishes were most strongly influence by creek size (Fig. 2.3). Menidia menidia was positively correlated with can1 (indicating increased relative abundance in subtidal weir samples from larger creeks), while P. saltatrix and S. marina were negatively correlated with can1 (indicating increased relative abundance in smaller creek weir samples).

COMPARISON OF SUBTIDAL WEIR AND SEINE

The composition and relative abundances of dominant fauna caught in subtidal weir and seine samples differed markedly. Five of the dominant species (Alosa aestivalis, Paralichthys dentatus, Pomatomus saltatrix, Anchoa mitchilli, Fundulus majalis) exhibited significant differences in relative abundance among gears (Fig. 2.4). Additionally, relative abundances of less abundant species including, the crab Ovalipes ocellatus, turtle M. terrapin and fish Gasterosteus aculeatus were significantly greater in subtidal weirs, while the fish G. bosci was significantly greater in seines ($p<0.05$).

Canonical discrimination analysis on data grouped both by creek and gear (subtidal weir and seine) revealed a significant interaction between creek and gear on the fauna assemblage (Table 2.5, Fig. 2.5). This analysis illustrates three trends: 1) fauna from subtidal weir and seine samples can be discriminated, 2) within a gear, fauna clusters in a pattern which parallels creek size, and 3) there is an interaction between gear and creek such that weir and seine samples from the smallest creek (Foxboro) discriminate strongly, those from Schooner Creek exhibit intermediate discrimination, and there is little discrimination between gears at New Creek (Fig. 2.5). In other words, the smaller the creek the greater the differences between assemblages in seine and weir samples. This analysis also indicates that among-creek spatial variation in species assemblages are most pronounced in weir samples.

An examination of species correlations with the derived canonical variables from the gear by creek CDA can be used to identify species correlations with collection groups (Table 2.5). For example, _L_. _polyphemus_, _S_. _marina_, _C_. _sapidus_ and _M_. _canis_ are positively correlated with can1 and negatively correlated with can2, indicating a correlation with Foxboro Creek weir samples (compare Table 2.5 & Fig. 2.5). Thirteen species were significantly correlated with the first canonical variable (can1), while 10 species were significantly correlated with the second canonical variable (can2).

The strongest pattern in the gear by creek CDA is the separation of weir and seine samples primarily by can1. When species are ordered by their correlations with can1 they tend to fall into three groups: 1) species with positive correlations indicating high susceptibility to the subtidal weir (11 species), 2) species with no correlation (10 species), and 3) species with negative correlations indicating high susceptibility to the seine (M. menidia, G. bosci, F. majalis, and F. heteroclitus). The first and third group are designated the weir and seine assemblage, respectively (Table 2.5). Species which are correlated with can1, but are not correlated to can2 appear to be most influenced by gear (M. terrapin, P. saltatrix, P. dentatus, O. ocellatus, L. xanthurus, P. americanus and G. bosci), while species correlated to both canonical variable are strongly influenced both by gear and creek (L. polyphemus, S. marina, C. sapidus, M. canis, A. mitchilli, and M. menidia).

CORRELATION BETWEEN PHYSICAL AND BIOLOGICAL DATA

Although the canonical correlation analyses of species relative abundances with physical data should be viewed with caution because of the small sample sizes, they do provide some interesting insights on the influence of physical conditions on marsh creek fauna. The CCA on weir samples suggests that tidal ranges in salinity and water temperature had the greatest influence on species relative abundances, although the overall squared correlation was only significant at $\alpha=0.1$ (Table 2.6). Additionally, the CCA suggests that Crangon septemspinosa, S. marina, C.

sapidus and A. mitchilli were most strongly influenced by physical conditions. Species with a high positive correlation with the derived canonical variable were positively correlated with tidal range in salinity and negatively correlated with tidal range in water temperature.

Catches in seine samples were highly significantly correlated with physical variables. Menidia menidia was positively correlated with water temperature variables and negatively correlated with tidal ranges in salinity and water depth. Crangon septemspinosa exhibited the opposite pattern.

WITHIN-CREEK FAUNAL VARIATION

Although faunal assemblages were similar among Schooner Creek collection groups (groups=subtidal weir, subtidal seine, Lower Creek and Upper Creek intertidal weirs, see Materials and Methods), each group exhibited some striking differences, suggesting within-creek differences in community structure and/or habitat use. Menidia menidia was the most abundant faunal component in all four collection groups (Table 2.7). Five other species P. vulgaris, F. heteroclitus, C. sapidus, M. curema and C. septemspinosa were also in the top ten for all groups. Each group lacked some species which were dominant in one or more of the other groups (e.g. A. mitchilli, S.

borealis, and *O. ocellatus* were absent from Upper Creek, but present in all other groups). *Fundulus luciae* and *Menidia beryllina* were unique to Upper creek.

Lower and Upper creek intertidal weir samples discriminated strongly from each other and from Schooner Creek subtidal weir and seine samples (Table 2.8, Fig. 2.6). Correlations of species relative abundances with the derived canonical variables suggest that *F. majalis*, *F. heteroclitus* and *C. sapidus* were strongly correlated with Lower Creek, while *S. marina*, *G. bosci*, *M. menidia*, *L. xanthurus* and *P. dentatus* tended to correlate with subtidal weir and seine samples. *Fundulus luciae* and *Menidia beryllina* were most correlated with Upper Creek intertidal weir samples.

Based on these analyses, species which appear to depend most on the use of intertidal creeks included: *C. variegatus*, *F. luciae*, *M. beryllina*, *M. curema*, *F. majalis* and *F. heteroclitus*. However, differences between the intertidal creeks (Table 2.7,2.8) apparently result from the preference of some species for upper or lower regions of Schooner Creek (e.g., *S. borealis*, *G. bosci*, *F. majalis* for the Lower Creek area, and *F. luciae*, *M. beryllina* for the Upper Creek area) suggesting that community structure changes between locations within the creek.

The specific comparison of the Schooner Creek subtidal weir and seine samples and Lower Creek intertidal weir samples (taken a few meters apart, and with gears of equal mesh size) helps distinguish species which utilize both subtidal and intertidal microhabitats from those which are restricted to the subtidal creek itself (Table 2.7,2.8, Fig. 2.6). Gobiosoma bosci was rare in both the subtidal and intertidal weirs, but was common in the seine samples suggesting it primarily uses subtidal habitat and is relatively non-mobile. Fundulus majalis, Fundulus heteroclitus, C. sapidus and C. variegatus were strongly correlated with Lower Creek intertidal weir samples (Table 2.8, Fig. 2.6), but were also abundant in the seine samples and apparently extensively use both subtidal and intertidal habitats. Although M. menidia was abundant in all groups, it was typically most abundant in the seine samples suggesting some preference for subtidal habitat (Table 2.7). Finally, A. mitchilli, P. saltatrix, P. dentatus and O. ocellatus were abundant only in subtidal weir samples, and appear to make limited use of intertidal habitat.

Discussion

Spatial variation in community structure in this study was due primarily to differences in species abundances (Table 2.3), rather than to differences in both species composition and abundance (Keup and Bayless 1964, Weinstein et al. 1980). A strong effect of location within the estuary on subtidal marsh creek communities was not apparent during this study, although previous studies have reported community variation among creeks distributed along an estuarine salinity gradient (Keup and Bayless 1964, Weinstein et al. 1980). The lack of similar location effects during this study results from the close spatial proximity among the three subtidal creeks, and their similar proximity to Little Egg Inlet (1.3-2.3 km, Fig. 2.1). The among-creek variation in salinity and other physical conditions observed during this study were on a much smaller scale (26-29‰, Table 2.1) than those reported by Keup and Bayless (1964, 0-12‰) or Weinstein et al. (1980, 2-25‰).

The among-creek spatial variation in community structure observed during this study, therefore, appeared to be more strongly related to differences in creek size than to location within the estuary. This conclusion is supported by the CDA on subtidal weir samples which suggests that creek fauna can be discriminated based on creek size, rather than creek location, at least on the spatial scale examined during this study (see my comments under results, Fig. 2.3).

The within-creek spatial variation observed during this study results both from differences between subtidal and intertidal habitats, and differences between upper and lower regions of the creek (Fig. 2.6), and agrees well with previous studies. These previous studies either provide evidence of community differences among marsh habitats (e.g., subtidal creek, intertidal marsh surface, and marsh ponds, see my comments in Chapter 1, Subrahmanyam and Drake 1975, Subrahmanyam and Coultas 1980, Werme 1981, McIvor and Odum 1988), or provide evidence of community changes between locations within the creek (Hackney et al. 1976, Weinstein 1979, Weinstein and Brooks 1983, Rozas and Hackney 1984, Smith et al. 1984, Rozas and Odum 1987, McIvor and Odum 1988, Hettler 1989). The influence of location within a creek on community structure has variously been described as occurring along a mouth-to-headwater creek gradient (Hackney et al. 1976, see my comments below and Fig. 2.7), along a marsh creek coenocline (Weinstein 1979, Weinstein and Brooks 1983, Smith et al. 1984), or along a marsh creek order gradient (Rozas and Odum 1987, Hettler 1989).

INFLUENCE OF CREEK MORPHOLOGY

I believe that both the influence of creek size and of within-creek location on marsh creek community structure, reported herein and by others (Hackney et al. 1976, Weinstein and Brooks 1983, Smith et al. 1984, Rozas and Odum 1987, Hettler 1989), may be related to creek morphology and tidal dynamics. Therefore, I provide below a conceptual model of how creek morphology may influence community structure, borrowing heavily from concepts presented by Hackney (Hackney et al. 1976, Hackney 1977). Research in subtidal salt marsh habitats is greatly hampered by the lack of such a framework to understand how habitat characteristics can influence abiotic and biotic regulation of aquatic communities.

Creek morphology can influence fauna composition and abundance in at least two major ways: 1) directly through the regulation of tidal dynamics, and 2) indirectly through regulation of changes in physical conditions along a creek gradient (Fig. 2.7,2.8).

REGULATION OF TIDAL DYNAMICS

In Figure 2.7 cross-sectional and longitudinal profiles from three locations along a diagrammatic tidal marsh creek are illustrated. Profiles at A, B, and C can be considered either from different locations within one creek, or from creeks of different size. Tidal drainage of a creek is defined, herein, as the extend to which a creek is emptied with each tide; that is, as the ratio of subtidal to intertidal volume. Intertidal creeks are completely drained on each tide, while the increasing subtidal volumes of larger creeks reflects less complete drainage.

To illustrate how within-creek and among-creek variation in communities can both result from similar effects of creek morphology, consider profiles A through C (Fig. 2.7) as representing profiles at different locations within a single creek. The proportion of subtidal to intertidal creek volume decreases moving up the creek gradient (progressing from lower to upper regions), indicating an increasing degree of tidal drainage of the creek bed, until the creek becomes completely intertidal in its upper-most reaches. Under these conditions, species which do not undertake tidal movements along the subtidal creek gradient would tend to become more concentrated towards the creek headwaters, due to the decreasing volume of subtidal water. Additionally, the tendency to undertake tidal movements would increase moving up the creek gradient, because of the increasing tidal drainage. Ultimately, in the intertidal headwaters of the creek (at location C, Fig. 2.7) all components of the fauna are forced to tidally migrate, except those adapted to live in the marsh surface water, or to bury in the mud (e.g., Fundulus heteroclitus larvae, etc., Kneib 1984). Contrastingly, moving down the creek gradient fewer species/individuals would tend to make tidal movements along the subtidal creek gradient, because of the greater ratio of subtidal to intertidal volume, and resulting lower extent of tidal drainage. Similar patterns would be expected among creeks of different size. While most species would be forced to undergo tidal movements in a creek the size of C, progressively fewer species would undergo tidal movements as creek size increased to that of B and A. Hence, many species were captured in the subtidal weir at Foxboro Creek, which exhibited the greatest degree of tidal drainage (i.e, least subtidal volume, for a similar flood area of approx. 23,000-26,000 m^2, Fig. 2.2), and progressively fewer species were captured at Schooner and New creek weirs (Table 2.4).

The observed interaction between subtidal creek and sampling gear (weir and seine) may also have resulted from differences in tidal drainage among creeks (Fig. 2.5, Table 2.4,2.5). The shallow Foxboro Creek is much more completely drained at low tide than the other two subtidal creeks (Fig. 2.2), and more of the fauna is forced out with the tides and captured in the weir. In New Creek, which drains less and has a greater subtidal volume, fewer species/individuals are forced to leave the creek and weir and seine samples are more similar. In the latter case (New Creek), weir and seine assemblages are virtually identical and reflect only the most abundant marsh species (Table 2.4). Larger species such as P. saltatrix, P. dentatus, S. marina which are important in Foxboro and Schooner creeks, make up less than 1% of the catch at New Creek. The more complete drainage at Foxboro Creek also accounts for the higher weir abundances of many small species otherwise abundant only in the seine at the other two subtidal creeks (and in the intertidal weirs), including F. heteroclitus and P. vulgaris (Table 2.3).

Differences in tidal drainage among creeks, and along a creek gradient, have important implications for studies designed to determine habitat use and secondary production patterns. Because of the decreasing subtidal volume, animals would become increasingly crowded at low tide moving up the creek gradient (assuming equal high tide marsh densities). Species can respond to these conditions by either adapting to tolerate temporary crowding at low tide, or by migrating down the creek to less crowded areas. If animals do not migrate down the creek, a gradient in low tide densities would occur along the creek, with increasing densities toward the creek headwaters. Such concentration effects may partially account for reports of higher fish densities in upper creek regions compared to lower creek regions (Weinstein 1979, Rozas and Odum 1987, Hettler 1989), as well as reports of higher densities in creek habitat relative to other estuarine habitats (Sogard and Able 1991). Weinstein (1979) found higher low tide densities of juvenile fishes in the upper reaches of marsh creeks relative to lower reaches, and suggested that "marshes fill up backwards during recruitment... accumulating in great numbers in the upper reaches of creeks and gradually decreasing in densities downstream." While further research may confirm this finding, the same patterns might alternatively result from the simple concentration effects I describe above. Researchers are cautioned to carefully consider possible concentration effects, and other effects related to marsh hydrography, when attempting to compare densities among marsh habitats. The recent practice of quantifying flume catches in terms of "marsh frontage (i.e., length of creek bank, McIvor and Odum 1986)" rather than by high tide marsh area is particularly cautioned.

REGULATION OF PHYSICAL CONDITIONS

As depicted in Figure 2.8, gradients in physical conditions can form along creeks as a result of interactions between the influences of the adjacent bay waters, atmospheric conditions, and terrestrial conditions (Dewitt and Daiber 1973, Hackney et al. 1976, Daiber 1977). Generally, because of the decreasing depth and water volume, and increasing distance from the bay, physical conditions are increasingly influenced by atmospheric and land conditions moving up the creek, while bay conditions have an increasing influence moving down the creek. Additionally, bay conditions have their greatest influence at high tide and atmospheric/land conditions at low tide (Hackney et al. 1976, Daiber 1977). Over a diel and tidal cycle, conditions become increasingly variable (with greater maxima and minima values) moving up the creek gradient, being maximal in intertidal areas, but become more stable moving down the creek, being minimal in the bay. Therefore, in addition to the physical gradient formed along the creek at any given time, a gradient in environmental variability along the creek is formed over the diel and tidal cycle.

Consideration of Figure 2.7 and 2.8, suggest that the strength of these gradients would be partly a function of creek size. Further, a small creek would tend to exhibit conditions similar to a comparable section of a larger creek. For example, one would predict that a small creek with a longitudinal profile similar to B in Fig. 2.7 would exhibit similar conditions as the upper section of a larger creek corresponding to B. Therefore, one would expect to find similar species assemblages between the small creek and upper section of the larger creek. However, some faunal differences might result from the influence of creek length, or distance of a sample location from the creek mouth. For example, bay species which invade creeks during high tide stages may occur in a small creek the size of C in Figure 2.7, but not in the upper reach (with profile as in C) of a larger creek because the distance from the creek mouth.

The differences in fish and macroinvertebrate communities observed between the Upper and Lower creek tributaries of Schooner Creek during this study (Table 2.7, 2.8, Fig. 2.6) may have resulted from this type of gradient in environmental conditions along Schooner Creek. A more extensive study of physical conditions within Schooner Creek suggests that strong gradients in dissolved oxygen concentration (D.O.), turbidity, and gradients in the magnitude of diel variation in D.O., turbidity, and water temperature do occur, but are strongly seasonal (Rountree and Able, unpublished data).

Although, the importance of tidal gradients in environmental conditions in structuring intertidal communities are well known for rocky and sandy shores, and have been the subject of more recent research in salt marshes (see reviews by Kneib 1984, Gibson 1986), researchers have generally failed to recognize their role in the shallow subtidal marsh. However, in an important study, Hackney et al. (1976) and Hackney (1977) found that species abundances and assemblages changed along a creek gradient (mouth-to-headwaters) in response to tidal and diel gradients in physical conditions. Later studies have found similar changes in marsh creek fauna, but do not discuss possible physical causes (Weinstein 1979, Weinstein and Brooks 1983, Smith et al. 1984). A future emphasis on research examining the response of subtidal marsh communities, which consist of many highly motile species, to tidal gradients in environmental conditions is needed before it will be possible to understand how communities in marsh ecosystems are regulated and structured.

SPECIES ASSEMBLAGES

Marsh creek fauna can be categorized by habitat use based on a comparison among subtidal weir, seine and intertidal weir samples (Table 2.7, 2.8). Species which appear to be primarily restricted to subtidal areas include

G. bosci, P. dentatus, A. mitchilli and O. ocellatus. The relatively high abundance of M. menidia in the seine samples also suggests it depends primarily on subtidal areas, agreeing with Werme (1981). Other species exhibited extensive use of intertidal areas (F. heteroclitus, F. majalis, C. variegatus, P. vulgaris, etc.). Similar categories of fishes and invertebrates based on abundances within marsh creek habitats have been reported previously (Subrahmanyam and Drake 1975, Subrahmanyam and Coultas 1980, Werme 1981).

Because of the dynamic tidal nature of marsh creek habitat, and the observed differences in species assemblages between weir and seine samples, it is tempting to categorize marsh creek fauna into tidal migrant and tidal resident species. It is clear from the conceptual model of creek habitat I presented above, however, that the prevalence of tidal movements is a function of creek size and the degree of tidal drainage, with most species forced to tidally migrate in intertidal creeks and progressively fewer species forced to migrate in progressively larger subtidal systems. Hence, the categorization of fauna into tidal migrants and residents is somewhat arbitrary and is probably highly site specific. In other words, while all species using intertidal creeks would have to be characterized as tidal migrants, many of the same species many not exhibit tidal movements within larger subtidal creeks.

Categorization of fauna into migrants and residents within a given habitat, however, can provide insight into the response of species to tidal changes in the environment. I suggest that many of the species in the weir assemblage (see my comments under Results; Fig. 2.4, Table 2.5), particularly those which were poorly represented in seine samples, are either passive or active tidal migrators (e.g., *M. terrapin*, *P. saltatrix*, *P. dentatus*, *O. ocellatus*, *L. xanthurus*, and *P. americanus*; see my comments in Results). That is, they utilize the subtidal creeks primarily during flood tide stages. The turtle, *M. terrapin*, is clearly a passive tidal migrator within the creeks, as I have often observed individuals passively drifting in and out of creeks with the tides. Subrahmanyam and Drake (1975) similarly grouped tidal creek fauna into permanent residents, nursery species, and tidal foraging species based on their abundance in high and low tide seine samples. Further, several of the species falling into the "weir" assemblage have been reported to undergo tidal movements in other marshes, supporting my interpretation of the weir assemblage as tidal migrants. *Strongylura marina* is listed as a tidal forager by Subrahmanyam and Drake (1975). Both *L. xanthurus* (Hodson et al. 1981, Archambault 1987 cited in Billheimer and Coull 1988) and *P. americanus* (Olla et al. 1969, Tyler 1971, Wells et al. 1973) have been shown to undergo tidal foraging movements into intertidal and shallow subtidal areas. *Callinectes sapidus* on the other hand has been shown to undergo tidal movements into subtidal marsh creeks to obtain a molt refuge (Hines et al. 1987), though others have suggested tidal foraging movements (Kneib 1982, Ryer 1987, Fitz and Wiegert 1991). Most strikingly, recent telemetry studies of P. dentatus in Schooner Creek confirm that it undergoes regular tidal movements (Szedlmayer and Able in prep), which appear to be foraging movements (Chapter 4).

The canonical correlation analysis (Table 2.6) indicates that abundance of species caught in the subtidal weir are partially dependent on the magnitude of tidal changes in physical conditions in the creeks. Catches in weir samples were most correlated with tidal changes in water temperature and salinity, suggesting that species in the weir assemblage may undergo tidal movements in response to tidal changes in these variables. This finding is particularly interesting in light of the growing body of evidence that fishes and other aquatic organism frequently respond to sublethal changes in conditions by moving to maintain a narrow range of preferred physiological conditions (Rozin and Mayer 1961, Brett 1971, Beitinger et al. 1975, Beitinger 1976, Reynolds and Casterlin 1976, Major 1978, Clark and Green 1991). In fact, Olla and Studholme (1978) report P. saltatrix (which I list among the weir assemblage, Table 2.5) exhibits behavioral thermoregulatory movements under laboratory conditions. However, these correlations may also reflect other tidal changes in variables not regularly measured during this study (such as dissolved oxygen concentration), but known to undergo large, potentially stressful, tidal and diel fluctuations in marsh creek and other shallow estuarine habitats (Nixon and Oviatt 1973, Dewitt and Daiber 1973, Hackney et al. 1976, Daiber 1977, Müller 1978, Breitberg 1988, Portnoy 1991, pers. observ.).

Species captured mainly in seine samples, such as _G_. _bosci_ and _F_. _majalis_ might be considered tidal residents of the subtidal creeks (Fig. 2.4, Table 2.3,2.4). Designation of "seine" assemblage species was less clear because of seasonally high catches in the weir. For example, the fishes _C_. _variegatus_, _F_. _heteroclitus_, _M_. _curema_, _M_. _menidia_ and shrimp _P_. _vulgaris_ were normally more abundant in seine samples (Table 2.3), but were extremely abundant in weir collections during certain times of the year, apparently as a result of seasonal movements (Chapter 1 and 5). In contrast to the correlation of weir catches with tidal change in salinity and temperature, seine catches appear little affected by tidal changes in these variables, but were highly correlated with high and low tide water temperature (Table 2.6), suggesting seasonal, rather than tidal effects. However, seine catches were negatively correlated with tidal depth range suggesting an influence of tidal drainage (i.e, abundances in seine samples were reduced with increasing tidal depth range, because more individuals are "flushed" out of the creeks).

Conclusions

Among-creek spatial variation in subtidal marsh creek communities appears to be strongly influenced by creek size, while within-creek variation in communities suggests differences between locations along a mouth-to-headwater creek gradient. Comparison between subtidal weir, subtidal seine and intertidal weir samples suggests that species can be categorized into different habitat use patterns, with some species abundant in all habitats, and some exhibiting greater use of subtidal or intertidal habitats. Additionally, many species appear to undergo some form of tidal movements which may be regulated by the extent of tidal drainage of the creek. For example, most species are forced to undergo tidal movements in intertidal creeks, while fewer species exhibit tidal movements in progressively larger subtidal creeks. It is proposed, therefore, that the tendency of a given species to undergo tidal movements is directly related to the tidal dynamics of a particular site, and, hence, is a highly plastic behavior. The patterns illustrated, herein, suggest each species has a basic distribution resulting both from a response to gradients in physical conditions, and from the effects of the tidal dynamics of the creek. However, species interactions such as competition, risk of predation, etc., may also influence species distributions (McIvor and Odum 1988, Chapter 3). For example, a species may be restricted to intertidal creeks at high tide, even though it could occur subtidally in the absence of competition or predation pressures. Mechanisms regulating the distributions of animals in tidal creeks, therefore, parallel those regulating other intertidal habitats, being controlled by balances between physiological tolerances/preferences, predations pressures, and competitive interactions (Connell 1961, Kneib 1984). However, the highly motile fauna of marsh creeks have the option of moving (actively or passively) between areas in response to changes in physical conditions, in contrast to sessile communities (Connell, 1961). The conceptual model of creek morphology and tidal dynamics presented herein, provides a framework for understanding spatial variation in marsh communities. It predicts that creeks of similar size and morphology should exhibit similar community structure, and that fauna assemblages at specific locations within different marsh creeks should be comparable based on their locations along creek gradients.

Table 2.1. Mean temperature (C), salinity (‰) and depth (cm) measured at the mouths of three subtidal (April-October 1989) and two intertidal (July-October 1989) salt marsh creeks located in a southern New Jersey estuary. Tidal range in physical conditions was determined as the difference between high and low tide values. Maximum and minimum values are given in parentheses (minimum,maximum). Variables which exhibited significant (*p≤0.05, **p≤0.01, ***p≤0.001, ns=nonsignificant) differences among subtidal, or between intertidal creeks are indicated under the ANOVA column. Multivariate analyses of creek and tide effects are reported in the text.

	Subtidal creek				Intertidal creek		
Physical variable	Foxboro	Schooner	New	ANOVA	Lower	Upper	ANOVA
High tide							
Air temperature	19 (11,26)	17 (3,23)	17 (9,24)	ns	20 (8,23)	19 (6,23)	ns
Water temperature	19 (10,25)	18 (8,25)	20 (9,28)	*	20 (12,23)	21 (11,24)	ns
Salinity	29 (26,30)	28 (24,30)	29 (27,30)	ns	29 (26,30)	27 (22,29)	***
Depth	109 (90-120)	184 (155-200)	114 (100,123)	***	205 (165,230)	159 (123,175)	***
Low tide							
Air temperature	19 (14,24)	16 (6,26)	17 (8,23)	*	19 (9,23)	19 (12,23)	ns
Water temperature	20 (11,25)	18 (9,27)	20 (11,26)	ns	21 (11,24)	21 (10,24)	ns
Salinity	27 (26,28)	26 (23,30)	28 (26,30)	*	25 (22,28)	23 (20,26)	ns
Depth	46 (23,55)	91 (60,115)	71 (55,80)	***	91 (80,100)	58 (50,80)	***
Tidal range							
Air temperature	0.7 (-3,3)	0.8 (-5,5)	0.2 (-3,2)	ns	0.4 (-1,3)	-0.6 (-6,4)	ns
Water temperature	-1.1 (-7,3)	-0.1 (-4,6)	0.0 (-4,2)	ns	-0.3 (-4,3)	0.0 (-1,1)	ns
Salinity	1.2 (-2,4)	2.3 (0,5)	1.0 (0,2)	ns	3.6 (2,6)	3.0 (0,7)	ns
Depth	63 (40,84)	93 (65,138)	43 (25,61)	*	114 (65,140)	100 (43,125)	ns
Sample size	9	12	6		7	5	

Table 2.2. Pearson correlation coefficients among physical variables measured fortnightly from April-October 1989 within three subtidal marsh creeks located in southern New Jersey.

	High tide				Low tide				Tidal range			
	Air (C)	Water (C)	‰	cm	Air (C)	Water (C)	‰	cm	Air (C)	Water (C)	‰	cm
High tide												
Air temperature (C)	-	-	-	-	-	-	-	-	-	-	-	-
Water temperature (C)	0.84^{***}	-	-	-	-	-	-	-	-	-	-	-
Salinity (‰)	-0.47^{*}	-0.61^{**}	-	-	-	-	-	-	-	-	-	-
Depth (cm)	ns	ns	ns	-	-	-	-	-	-	-	-	-
Low tide												
Air temperature (C)	0.90^{***}	0.82^{***}	-0.61^{***}	ns	-	-	-	-	-	-	-	
Water temperature (C)	0.90^{***}	0.89^{***}	-0.50^{**}	ns	0.90^{***}	-	-	-	-	-	-	-
Salinity (‰)	ns	ns	0.50^{*}	-0.44^{*}	ns	ns	-	-	-	-	-	-
Depth (cm)	ns	ns	ns	0.73^{**}	ns	ns	ns	-	-	-	-	-
Tidal range												
Air temperature (C)	0.46^{*}	ns	ns	ns	ns	ns	ns	ns	-	-	-	-
Water temperature (C)	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	-	-
Salinity (‰)	ns	-0.43^{*}	0.57^{**}	0.48^{*}	ns	ns	-0.43^{*}	ns	ns	-0.43^{*}	-	-
Depth (cm)	ns	-0.42^{*}	ns	0.78^{***}	ns	ns	-0.39^{*}	ns	ns	ns	-0.58^{**}	-

$^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$, ns=nonsignificant

Table 2.3. Comparison of mean abundance by gear of the fifteen top species among three subtidal creeks located in a southern New Jersey salt marsh. Additional species exhibiting significant variation among creeks are also included. Univariate analysis of variance (ANOVA) was used to test for differences among creeks within each gear. Multivariate analysis of variance (MANOVA) was used to test for creek main effects based on data from both gears (see text for a complete design description). Profile analysis was conducted for species exhibiting a significant overall creek effect in the MANOVA. Hypotheses tested with profile analysis were H_1: gear profiles are parallel (no gear by creek interaction), and H_2: Means pooled over gears are equal among creeks (no creek effect).

	Subtidal weir				Subtidal seine				MANOVA		
Species	Foxboro	Schooner	New	ANOVA: Creek effect	Foxboro	Schooner	New	ANOVA: Creek effect	Main effect	H_1	H_2
Menidia menidia[a]	877	17922[a]	2194	ns	2302	9859[a]	8021	ns	ns		
Fundulus heteroclitus	631	83	229	ns	2205	353	559	*	ns		
Palaemonetes vulgaris	1744	142	36	*	660	595	64	ns	*	ns	*
Crangon septemspinosa	982	83	193	ns	69	151	74	ns	ns		
Clupea harengus	189	1.4	0	ns	716	0	0	ns	ns		
Anchoa mitchilli	54	221	118	*	14	15	2	*	*	ns	*
Mugil curema	5.6	7.3	0	ns	37.8	10.4	0.6	**	**	ns	*
Fundulus majalis	4.9	5.0	16.2	ns	50.3	35.5	138	ns	ns		
Callinectes sapidus	61.1	12.5	45.8	**	34.4	15.6	16.4	ns	*	ns	*
Pomatomus saltatrix	43.8	19.6	7.7	ns	5.2	2.5	0	ns	ns		
Strongylura marina	21.2	1.2	2.3	*	1.1	10.8	0.4	**	***	*	***
Paralichthys dentatus	15.4	14.3	5.8	ns	0.1	0	0.2	ns			
Ovalipes ocellatus	5.2	9.5	9.8	ns	0.1	0.3	0.2	ns			
Alosa aestivalis	1.0	11.6	0.2	ns	2.1	0.6	1.2	ns			
Malaclemys terrapin	5.0	1.5	8.2	*	0.3	0	0.2	ns	*	**	*
Gobiosoma bosci	0.1	0.1	0.2	ns	2.6	7.7	1.2	***	**	ns	ns
Sphyraena borealis	0	3.8	0	*	0	6.1	0	ns			
Mustelus canis	3.7	0.3	0.8	*	0.6	0	0.2	ns	ns		

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, ns=nonsignificant

[a] with one outlier removed abundance at Schooner Cr. weir=865, seine=6578

Table 2.4. Comparison of dominant (≥1% mean relative abundance) species assemblages between subtidal weir and seine species assemblages among three marsh creeks located in southern New Jersey.

Subtidal weir								
Foxboro Creek (n=9)			Schooner Creek (n=11)			New Creek (n=6)		
	Mean	(SE)		Mean	(SE)		Mean	(SE)
Menidia menidia	27.3	(6.5)	*Menidia menidia*	55.0	(10.4)	*Menidia menidia*	82.1	(6.3)
Palaemonetes vulgaris	15.3	(7.7)	*Anchoa mitchilli*	12.8	(7.9)	*Fundulus heterocitus*	6.1	(2.4)
Fundulus heteroclitus	13.7	(9.5)	*Palaemonetes vulgaris*	8.2	(3.4)	*Crangon septemspinosa*	3.3	(2.9)
Callinectes sapidus	9.3	(4.7)	*Crangon septemspinosa*	4.4	(1.9)	*Callinectes sapidus*	2.7	(1.1)
Crangon septemspinosa	8.7	(4.4)	*Fundulus heteroclitus*	4.2	(1.4)	*Anchoa mitchilli*	2.1	(1.8)
Pomatomus saltatrix	7.2	(3.9)	*Paralichthys dentatus*	2.9	(2.3)	*Palaemonetes vulgaris*	1.0	(0.6)
Strongylura marina	4.6	(2.2)	*Mugil curema*	2.9	(2.9)	Other	2.7	
Paralichthys dentatus	3.2	(1.3)	*Alosa aestivalis*	2.8	(2.8)			
Anchoa mitchilli	2.4	(1.1)	*Pomatomus saltatrix*	1.5	(0.7)			
Clupea harengus	2.4	(2.4)	*Callinectes sapidus*	1.3	(0.6)			
Mugil curema	1.2	(0.5)	Other	4.0				
Ovalipes ocellatus	1.0	(0.7)						
Other	3.7							
Subtidal seine								
(n=9)			(n=11)			(n=5)		
Menidia menidia	47.5	(12.3)	*Menidia menidia*	60.8	(9.3)	*Menidia menidia*	83.6	(7.1)
Fundulus heterocitus	26.4	(9.3)	*Palaemonetes vulgaris*	18.6	(6.0)	*Fundulus heteroclitus*	10.6	(5.2)
Palaemonetes vulgaris	13.3	(3.5)	*Fundulus heterocitus*	9.4	(4.7)	*Fundulus majalis*	2.8	(1.8)
Clupea harengus	7.1	(7.0)	*Crangon septemspinosa*	9.1	(5.3)	*Crangon septemspinosa*	1.0	(0.5)
Mugil curema	1.8	(0.8)	Other	2.7		*Cyprinodon variegatus*	1.0	(0.7)
Crangon septemspinosa	1.0	(0.5)				Other	1.0	
Other	2.9							

Table 2.5. Results of canonical discrimination analysis on 1989 relative abundance data grouped by creek and gear (three creek by two gears = *six groups, N=51). Pearson correlation coefficents of* original variables on the canonical variables are given.

Species	Can1	Can2	Designated Assemblage
Malaclemys terrapin	0.54^{***}	-0.09	Weir
Pomatomus saltatrix	0.53^{***}	-0.21	
Limulus polyphemus	0.49^{***}	-0.36^{**}	
Strongylura marina	0.48^{***}	-0.45^{**}	
Paralichthys dentatus	0.48^{***}	-0.04	
Callinectes sapidus	0.45^{**}	-0.30^{*}	
Ovalipes ocellatus	0.45^{***}	0.12	
Leiostomus xanthurus	0.45^{**}	0.14	
Mustelus canis	0.43^{**}	-0.32^{*}	
Anchoa mitchilli	0.35^{*}	0.30^{*}	
Pseudopleuronectes americanus	0.35^{*}	-0.20	
Gasterosteus aculeatus	0.20	0.39^{**}	
Alosa pseudoharengus	0.14	0.30^{*}	
Crangon septemspinosa	0.14	-0.05	
Alosa aestivalis	0.13	0.23	
Sphyaena borealis	0.12	0.30^{*}	
Mugil curema	0.03	-0.21	
Clupea harengus	-0.03	-0.20	
Palaeomonetes vulgaris	-0.06	-0.28^{*}	
Cyprinodon variegatus	-0.16	-0.18	
Syngnathus fuscus	-0.17	-0.03	
Fundulus heteroclitus	-0.26	-0.27	Seine
Fundulus majalis	-0.26	0.07	
Gobiosoma bosci	-0.28^{*}	-0.19	
Menidia menidia	-0.31^{*}	0.39^{**}	
Squared canonicical correlation	0.86^{***}	0.79^{*}	

Wilk's lambda among group difference $F = 1.9^{***}$

$^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

Table 2.6. Canonical correlation analyses of species relative abundance in subtidal weir (squared canonical correlation=0.92, p=0.07, n=26) and seine (squared canonical correlation=0.99, p<0.001, n=25) samples with physical variables for data collected from three subtidal marsh creeks from April-October 1989. Pearsons correlations between the original transformed (arcsine square root) species and physical variables (ln) with the derived canonical variables (V1 for species variables, and W1 for physical variables) are given.

Species variable	Correlation with V1	Physical variable	Correlation with W1
	Subtidal weir samples		
Crangon septemspinosa	0.46^{*}	Tidal range in salinity	0.40^{*}
Menidia menidia	0.37^{a}	High tide water depth	0.15
Clupea harengus	0.33	Low tide water depth	0.13
Palaemonetes vulgaris	0.21	High tide salinity	0.13
Fundulus heteroclitus	0.11	Tidal range depth	0.09
Mugil curema	-0.07	Low tide water temperature	0.07
Pomatomus saltatrix	-0.19	High tide water temperature	-0.25
Paralichthys dentatus	-0.26	Low tide salinity	-0.27
Strongylura marina	-0.53^{**}	Tidal range in water temperature	-0.65^{***}
Callinectes sapidus	-0.53^{**}		
Anchoa mitchilli	-0.64^{***}		
	Subtidal seine samples		
Menidia menidia	0.50^{*}	Hight tide water temperature	0.89^{***}
Stongylura marina	0.25	Low tide water temperature	0.72^{***}
Mugil curema	0.25	Tidal range water temperature	0.38
Fudulus majalis	0.20	Low tide salinity	0.07
Callinectes sapidus	0.01	Low tide depth	0.03
Cyprinodon variegatus	0.03	High tide depth	-0.29
Anchoa mitchilli	-0.02	High tide salinity	-0.43^{*}
Fundulus heteroclitus	-0.13	Tidal range depth	-0.44^{*}
Palaemonetes vulgaris	-0.29	Tidal range salinity	-0.52^{**}
Clupea harengus	-0.32		
Crangon septemspinosa	-0.75^{***}		

$^{a}p=0.06$, $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$

Table 2.7. Mean abundance (SE) of the ten dominant species from each of four collection groups taken from Schooner Creek during night flood tides fortnightly from July-October 1989 (N=26).

	Subtidal				Intertidal			
Species	Weir		Seine		Lower Creek Weir		Upper Creek Weir	
Menidia menidia[a]	32057	(31290)	14803	(7069)	740	(267)	13995	(11166)
Anchoa mitchilli	293	(257)	22	(22)	2	(2)	0	(0)
Palaemonetes vulgaris	103	(63)	693	(381)	52	(24)	794	(307)
Pomatomus saltatrix	32	(12)	3	(2)	1	(<1)	4	(1)
Fundulus heteroclitus	31	(17)	149	(57)	310	(217)	766	(516)
Paralichthys dentatus	25	(9)	0	(0)	0	(0)	<1	(<1)
Callinectes sapidus	19	(7)	18	(8)	17	(5)	19	(7)
Ovalipes ocellatus	15	(13)	<1	(<1)	<1	(<1)	0	(0)
Mugil curema	13	(9)	16	(9)	3	(2)	23	(17)
Crangon septemspinosa	8	(8)	72	(37))	1	(<1)	16	(16)
Sphyraena borealis	5	(5)	10	(9)	4	(4)	0	(0)
Leiostomus xanthurus	5	(2)	<1	(<1))	0	(0)	<1	(<1)
Fundulus majalis	2	(2)	25	(14)	8	(3)	2	(1)
Strongylura marina	2	(1)	17	(12)	<1	(<1)	3	(2)
Gobiosoma bosci	0	(0)	12	(6)	<1	(<1)	<1	(<1)
Cyprinodon variegatus	0	(0)	<1	(<1)	1	(<1)	35	(20)
Fundulus luciae	0	(0)	0	(0)	0	(0)	20	(14)
Menidia beryllina	0	(0)	0	(0)	0	(0)	8	(4)
Sample size	6		7		8		5	

[a] With one outlier removed subtidal weir mean=770, seine=10159, Upper Creek weir=2891

Table 2.8. Canonical discrimination analysis on relative abundance data taken from Schooner Creek from July-October 1989 (N=26). Data grouped into subtidal creek weir and seine samples, and Lower and Upper creek intertidal weir samples for the analysis. Pearson correlations of the original transformed (arcsine square root) variables on the derived canonical variables (Can1 and Can2) are given.

Species	Can1	Can2
Strongylura marina	0.30^{a}	0.23
Gobiosoma bosci	0.26	0.19
Menidia menidia	0.25	0.10
Leiostomus xanthurus	0.23	0.06
Paralichthys dentatus	0.20	0.05
Pomatomus saltatrix	0.13	0.05
Anchoa mitchilli	0.13	0.07
Mugil curema	0.12	0.02
Palaemonetes vulgaris	0.09	-0.07
Ovalipes ocellatus	0.08	0.10
Fundulus luciae	0.03	-0.72^{***}
Menidia beryllina	0.03	-0.68^{***}
Crangon septemspinosa	-0.01	0.22
Sphyraena borealis	-0.03	0.17
Cyprinodon variegatus	-0.32^{a}	-0.23
Callinectes sapidus	-0.44^{**}	0.09
Fundulus heteroclitus	-0.47^{**}	-0.21
Fundulus majalis	-0.55^{**}	0.24
Squared canonical correlations	0.97^{**}	0.96^{*}
Among group differences	$F=16^{**}$	

$^{*}P \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$
$^{a}p \le 0.1$

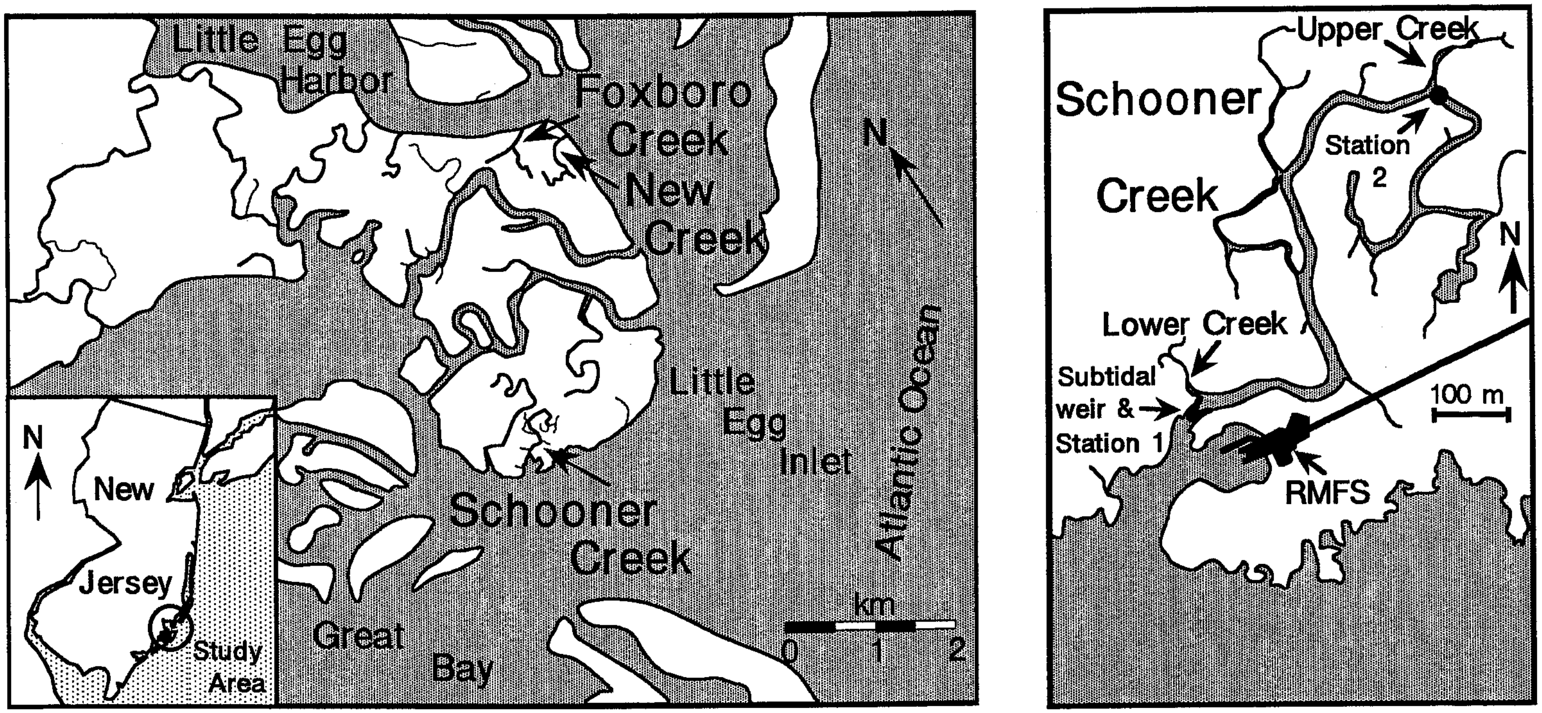


Figure 2.1. Great Bay-Little Egg Harbor estuarine complex and study creeks located adjacent to the Rutgers University Marine Field Station (RMFS) in southern New Jersey. Foxboro, Schooner and New creeks are subtidal salt marsh creeks, while Lower and Upper creeks are intertidal tributaries of Schooner Creek.

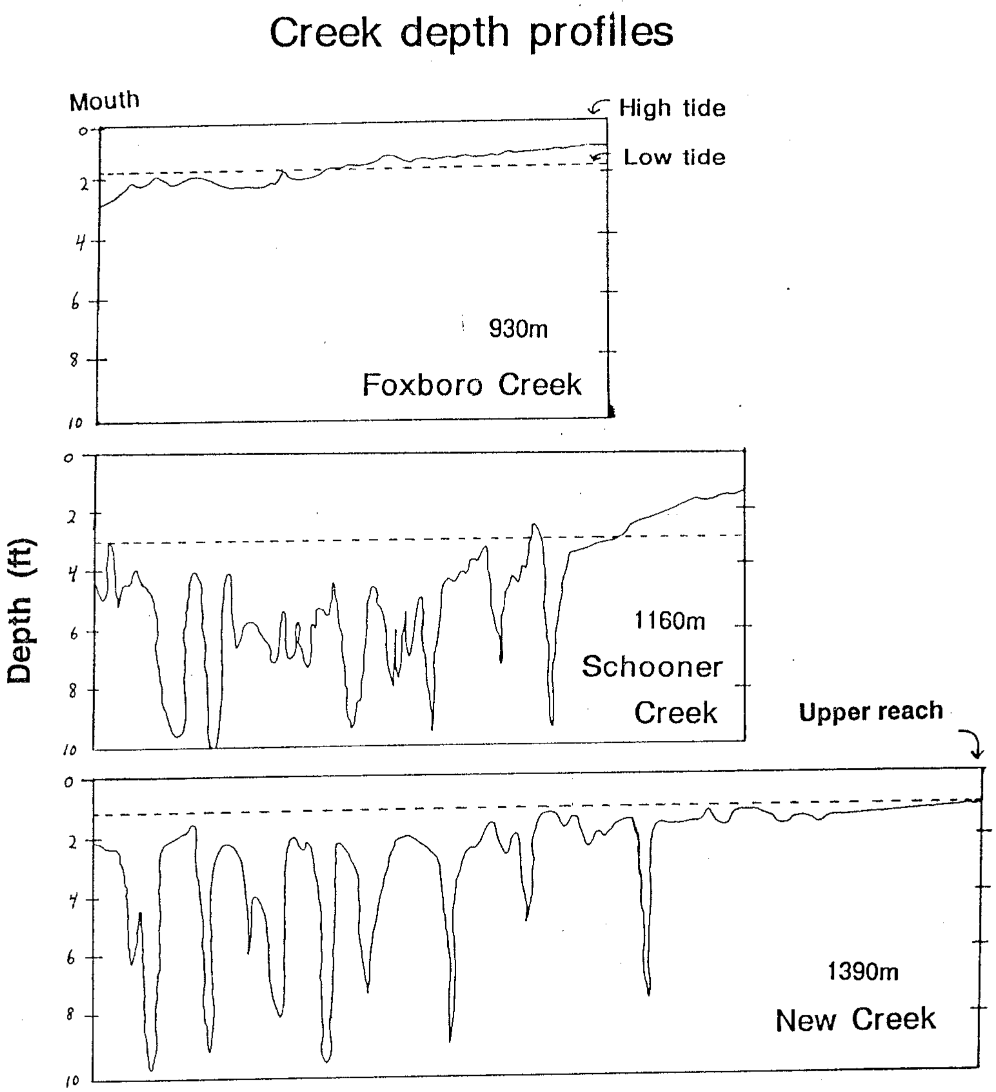


Figure 2.2. Depth profile of Foxboro (A), Schooner (B) and New (C) creeks taken with a fathometer at high tide beginning at the creek mouth and extending to the upper reaches of the creeks. The dashed line represents the mean low tide water depth which was estimated from mean low tide water depth at the creek mouths (see Table 2.1).

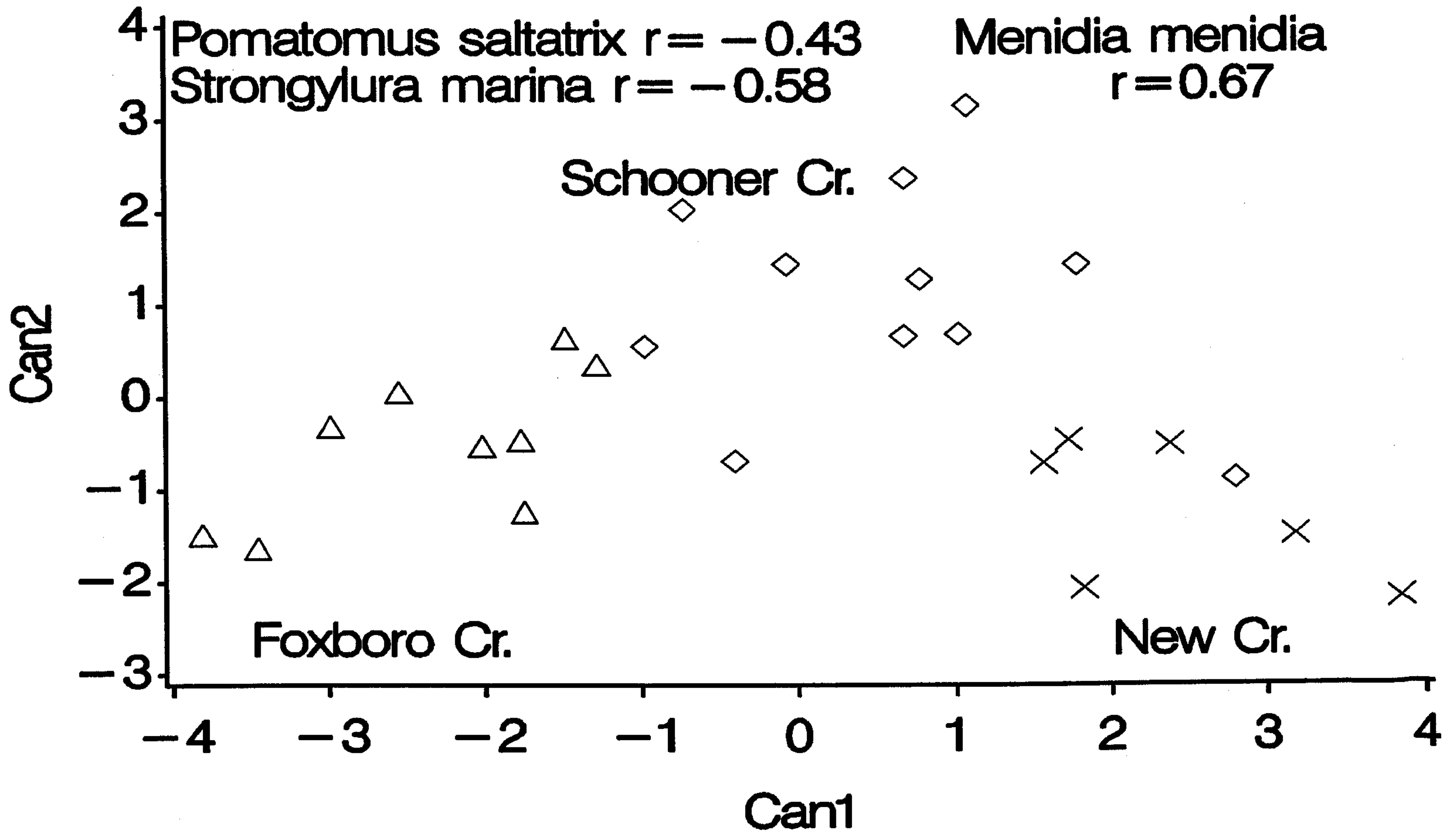
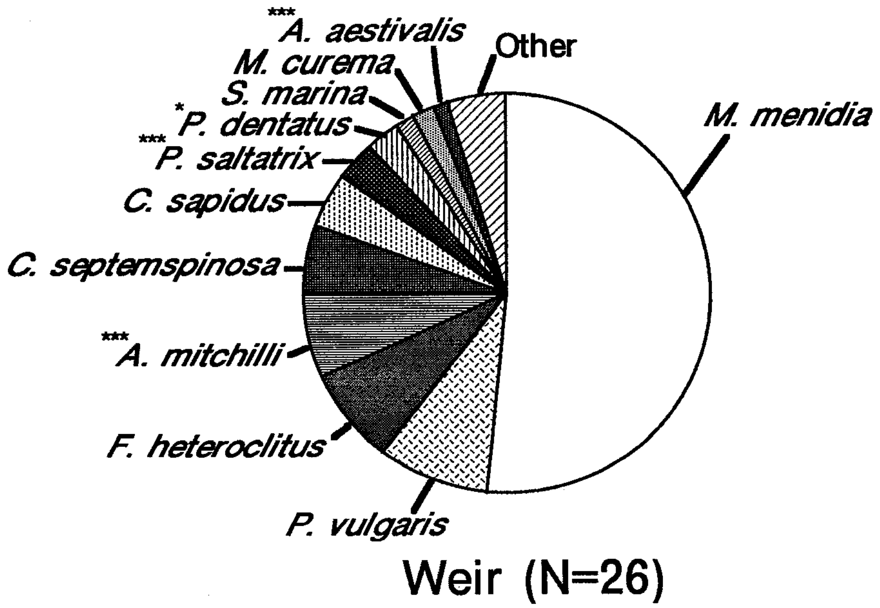


Figure 2.3. Canonical discrimination analysis of species relative abundance data grouped by creek for subtidal weir samples (n=26) collected from April-October 1989. The Wilk's Lambda among group difference test was significant (F=2.56, $p \leq 0.05$). The squared canonical correlations were 0.79 ($p \leq 0.05$) for Can1 and 0.52 (non-significant) for Can2. Species with significant ($p \leq 0.05$) correlations with Can1 are indicated.



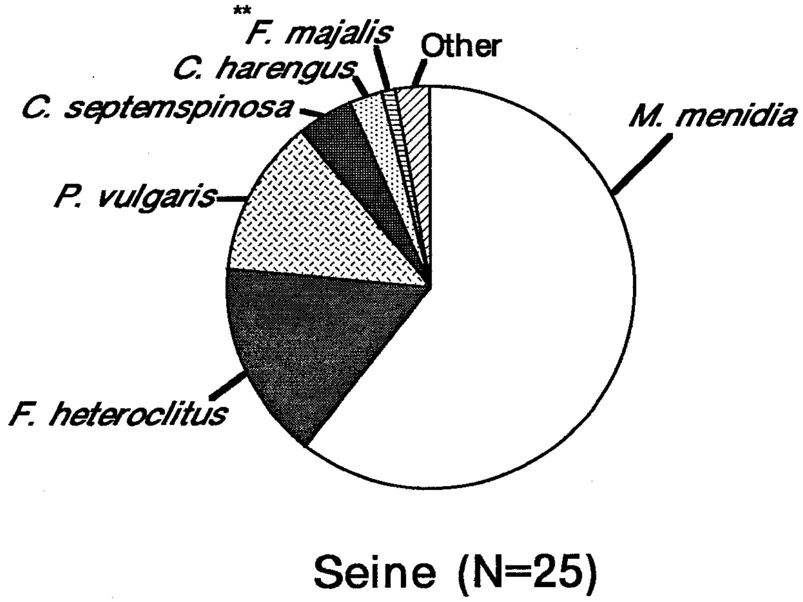


Figure 2.4. Mean percent relative abundance of all species ≥1% for weir (n=26) and seine (n=25) samples pooled over all three subtidal creeks from April-October 1989. Species with significantly higher relative abundances within a gear are indicated (H_3: $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$) based on profile analysis after MANOVA (see text).

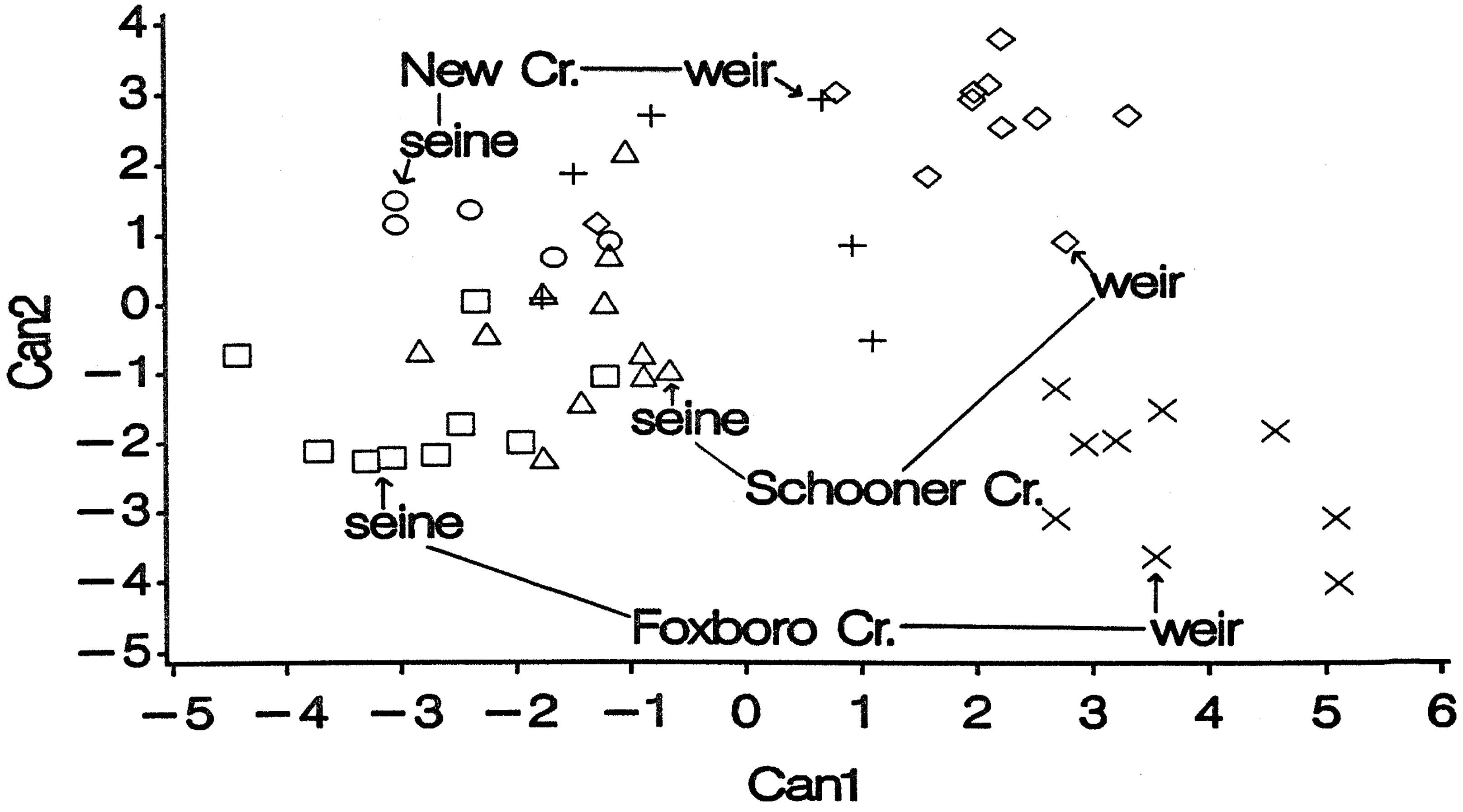


Figure 2.5. Canonical discrimination analysis of subtidal creek species relative abundance data grouped by creek (Foxboro, Schooner and New) and gear (weir and seine), based on 26 weir and 25 seine samples. Statistics are given in Table 2.6.

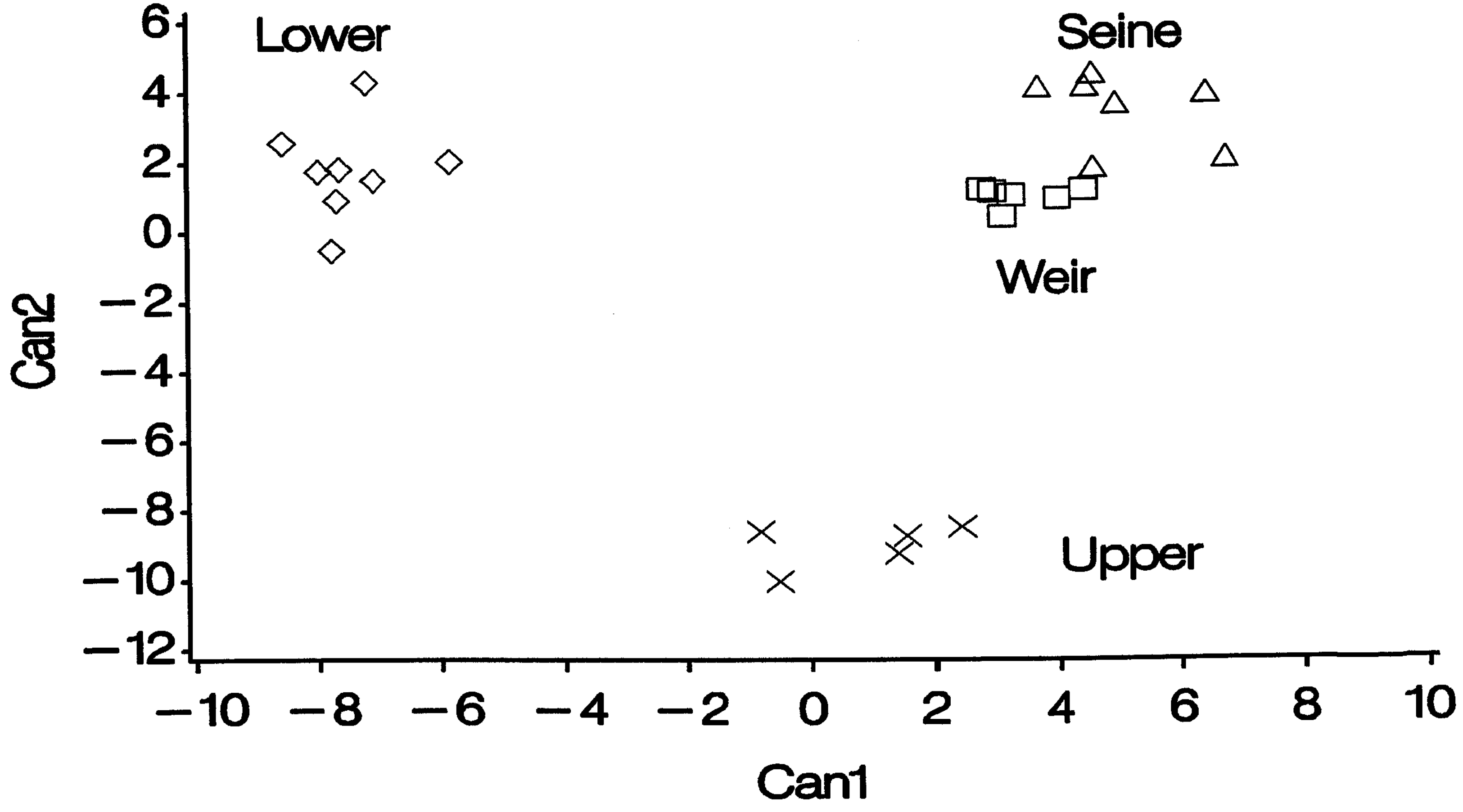


Figure 2.6. Canonical discrimination analysis of species relative abundance data grouped by subtidal weir (squares), subtidal seine (triangles), Lower Creek (diamonds) and Upper Creek (X) intertidal weir collections within Schooner Creek from July-October 1989 (N=26). Statistics are given in Table 2.9.

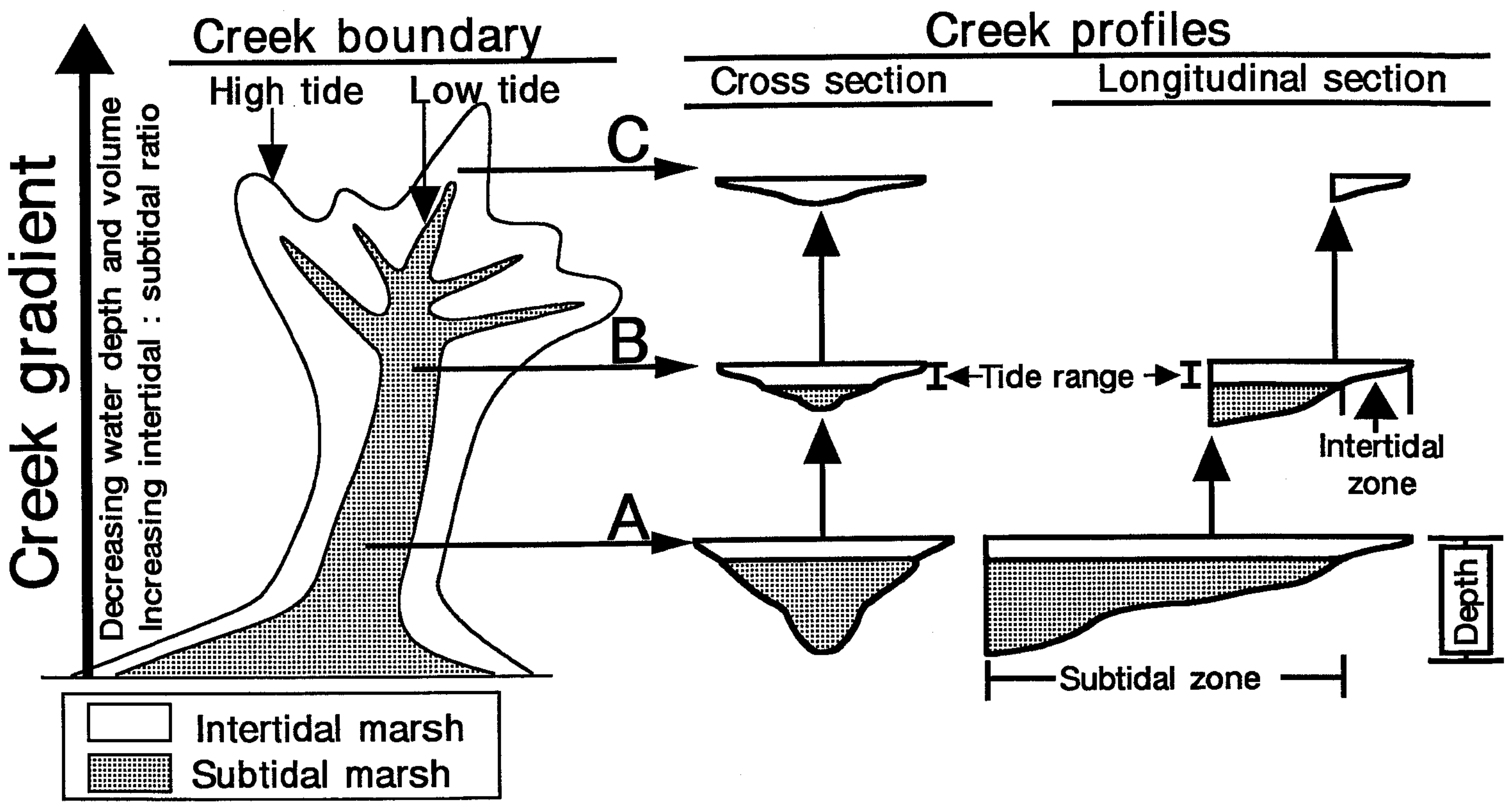


Figure 2.7. Schematic of a hypothetical tidal marsh creek illustrating aspects of creek morphology. Creek boundaries at both high and low tide are shown. Cross sectional and longitudinal profiles at A, B, and C can be considered to be either from three locations within a single creek, or from three different size creeks. Depth, and the ratio of subtidal to intertidal area, decreases along the mouth-to-headwater creek gradient, and from large to small creeks. Tidal drainage is defined, herein, as the extent to which a creek is emptied with each tide, or as the ratio of intertidal to subtidal volume. Tidal drainage, therefore, increases moving up the creek gradient, or from large to small creeks (see text for complete explanation).

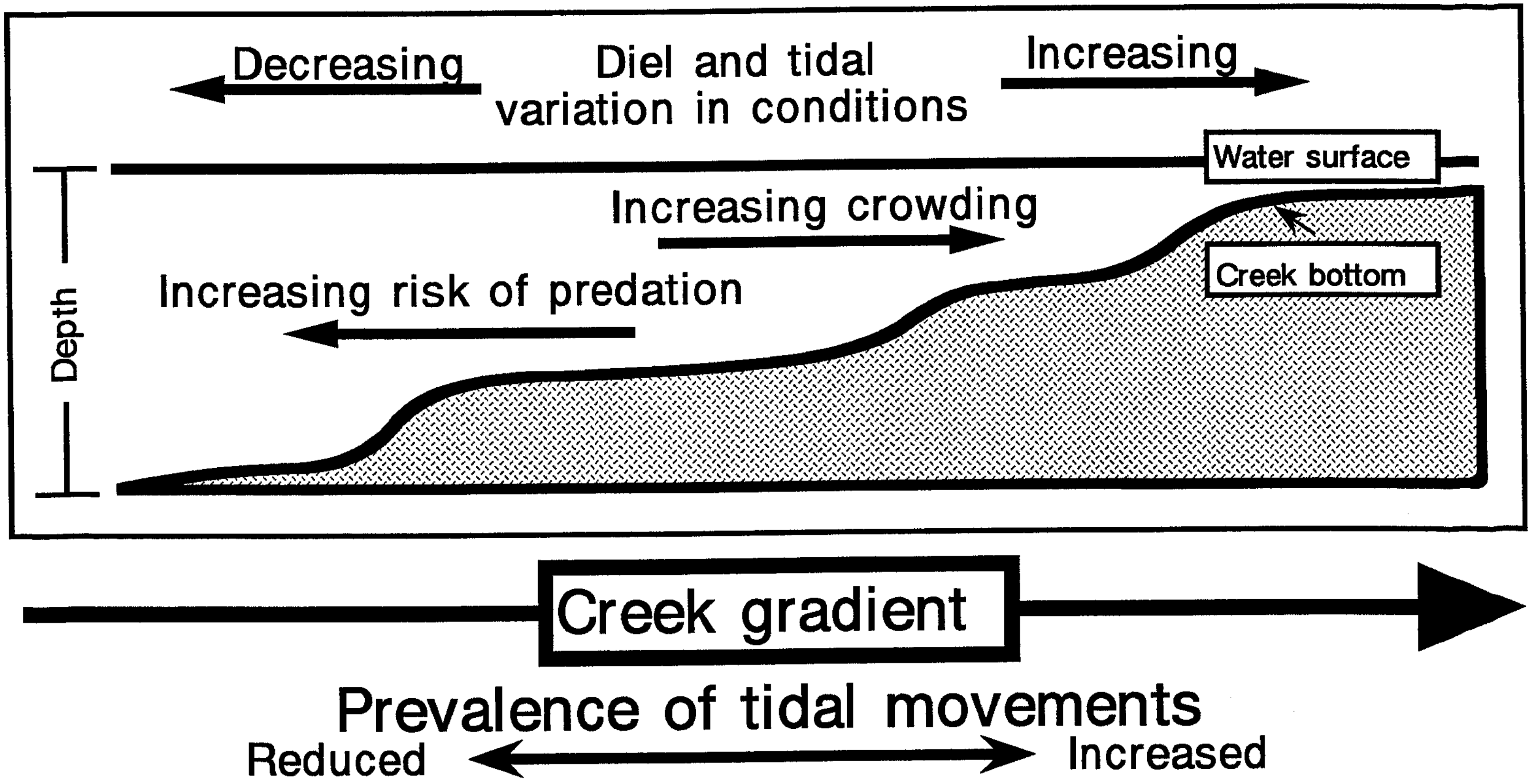


Fig. 2.8. Schematic of hypothetical gradients in physical conditions and biological conditions which may be formed along a creek mouth-to-headwater gradient. Assuming equal high tide densities, crowding at low tide within the subtidal creek would increase moving up the creek gradient. Contrastingly, risk of predation by aquatic predators would increase moving down the creek gradient. Tidal drainage (ratio of intertidal to subtidal volume), and diel and tidal variation in environmental conditions would tend to increase moving up the creek gradient. In response to these gradients the prevalence of tidal movements in the community would be expected to increase moving up the creek gradient (see text for complete explanation).

Chapter 3: Diel variation in decapod and fish assemblages utilizing polyhaline marsh creeks in New Jersey

Abstract

Day versus night variation in fish and decapod abundance and species assemblages were examined to determine diel patterns of marsh creek habitat use in a southern New Jersey estuary. Two subtidal marsh creeks were sampled with weirs from April-November 1988 (n=42) and seines from July-November 1988 (n=33), while two intertidal creeks were sampled with weirs from July-October 1989 (n=28). Fish and decapod species assemblages, as measured by both relative abundance and canonical discrimination analyses, were highly affected by diel period. Total abundance, and abundances of 12 species of fish and decapods exhibited significant diel differences in abundance. Diel patterns in individual species abundances, and in community structure may result from diel changes in environmental conditions within the creeks, and/or from diel use of marsh creeks as refuge or foraging habitats. The most abundant species, _Menidia menidia_, exhibited significantly higher night abundances in subtidal creek weir, seine and intertidal creek weir samples, apparently due to either passive or active nocturnal movements into intertidal and shallow subtidal areas. Since _M. menidia_ is known to be a strongly diurnal forager, feeding largely on

zooplankton, its nocturnal movement into shallow subtidal and intertidal habitats is hypothesized to be a strategy to avoid predation during non-feeding hours. Observed patterns for other species suggest the fauna can be grouped into three general categories: 1) species using subtidal and intertidal creek primarily for refuge during non-feeding periods (e.g., *M. menidia*, *Anchoa mitchilli*), 2) species which use the creeks as diurnal (e.g., *P. saltatrix*) or nocturnal (e.g., *Mustelus canis*) foraging habitat, but tend to avoid the creeks during non-feeding periods, and 3) species which undertake both day and night tidal foraging movements into subtidal (e.g., *Leiostomus xanthurus*), and intertidal habitats (*Fundulus heteroclitus*, *F. majalis*, *Cyprinodon variegatus*). Seasonal and ontogenetic changes in *M. menidia* diel abundance patterns were observed, which may have resulted from seasonal changes in predation pressures, intraspecific competition, or environmental changes.

Introduction

Faunal surveys which include only daytime sampling, have been shown to underestimate fauna abundance, diversity and biomass (see Stoner 1991 and citations therein). Although salt marshes are known to support abundant and diverse communities (see review in Chapter 1), most published studies are based exclusively on daytime fauna surveys (e.g., Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Weinstein 1979, Chapter 1). Therefore, little is known of diel patterns of marsh use by natant fishes and invertebrates. I know of no studies examining diel patterns in subtidal marsh creek communities. However, some studies have been conducted in oligohaline to polyhaline intertidal marsh creeks (Shenker and Dean 1979, Reis and Dean 1981, Rozas and Hackney 1984, Middleton 1986), and on the surface of tidal freshwater marshes (McIvor and Odum 1986, Rozas and Odum 1987). Several of these studies reported diel changes in abundance of select species (Shenker and Dean 1979, Reis and Dean 1981, Rozas and Hackney 1984, Rozas and Odum 1987), or of total fish abundance (McIvor and Odum 1986, Rozas and Odum 1987). Similar reports have been made for other shallow estuarine habitats (McCleave and Fried 1975, Hoese et al. 1968, Livingston 1976, Robertson and Howard 1978, Horn 1980, Robertson 1980, Heck and Thoman 1984, Sogard et al. 1989, Stoner 1991). Most of these marsh and estuarine studies, however, were not directly concerned with diel patterns and few have presented detailed discussions of diel effects (estuary: Robertson and Howard 1978, Robertson 1980, Sogard et al. 1989, Stoner 1991; marsh: Reis and Dean 1981, Middleton 1986).

A comparison of diel abundance patterns can be used to better understand habitat use patterns. Strong diel patterns result either from gear bias related to local activity (e.g., local foraging movements, nocturnal burying, etc.), or from diel movement between habitats (Stoner 1991). In cases where information on diel activity patterns are available, it may be possible to determine whether diel abundance patterns result from movements or local activity. Either conclusion can elucidate patterns of habitat use.

In this study diel patterns in faunal composition and species abundances of fishes and decapods which utilize polyhaline intertidal and subtidal marsh creeks in a southern New Jersey estuary are examined. The primary goals of this study are: 1) to determine if significant diel differences in species assemblages, and/or abundances occur in New Jersey marshes, and 2) to examine diel patterns in species abundance and assemblages in order to elucidate habitat use patterns.

Materials and Methods

STUDY AREA

The study was conducted within the Great Bay - Little Egg Harbor estuarine complex in southern New Jersey (Fig. 3.1). Fishes were collected from two intertidal and two subtidal polyhaline (22-30‰) marsh creeks during 1988 and 1989 with a weir system (Chapter 1). Foxboro and Schooner creeks are subtidal, approximately 930 m and 1160 m in length, 23,000 m^2 and 24,000 m^2 in creek bed area, and are located 2.3 km and 1.3 km from Little Egg Harbor Inlet, respectively (Fig. 3.1). Each creek has a single connection with the bay and receives freshwater only through local runoff. A more detailed description of the morphology of the study creeks is presented in Chapter 2. Lower and Upper creeks are intertidal tributaries of Schooner Creek, which are approximately 110 m and 150 m in length, 370 m^2 and 1110 m^2 in creek bed area, 1500 m^2 and 3300 m^2 in total flood area, and are located 73 m and 730 m from the mouth of Schooner Creek, respectively.

SAMPLING GEAR AND METHODOLOGY

Consecutive day and night tides were sampled from Schooner and Foxboro creeks over a three day period approximately fortnightly from July-September 1988 (n=28). Additional samples were taken from Schooner Creek irregularly from April-June (n=9) and October-November (n=5; Chapter 1). All statistical analyses exclude the irregular samples with the exceptions of the seasonal comparison of day and night abundances, and the *Menidia menidia* cohort analysis. Lower and Upper creeks were sampled simultaneously from July-October 1989 during consecutive day and night tides (n=26). Day and night tides were defined as those in which at least the last two hours of flood occurred after sunrise or sunset, respectively.

Subtidal creeks were sampled with a weir which was set to block off the mouth of a creek at high tide and captured fishes leaving the creek with the ebb tide (see Chapter 1). Two wing nets (15.2 m by 3.0 m, with 6.4 mm mesh) were used to block off the mouth of the creek and to lead fishes into the weir (3.0 m by 1.2 m by 3.0 m high, with 6.4 mm mesh). Deployment of the weir was begun about 30 minutes before slack high tide and was completed within one hour. At low tide fish were removed from the weir through a cod-end.

Because the subtidal creek weir is a passive gear which primarily captures animals moving with the tide, seine sampling was also conducted within the creeks to capture less mobile forms and species/individuals which actively avoid the weir and remain within the creeks. One haul of a bag seine (6.2 m by 1.2 m; 3.2 mm mesh) was made after enclosing the approximately 100 m^2 area between the wings with a block net.

The intertidal creeks were sampled with a smaller and more simplified weir (1.8 m by 1.2 m by 1.2 m high weir, with 4.5 m by 1.2 m wings). Due to gear limitations, the weir used at Lower Creek had 6.4 mm mesh, while that used at Upper Creek had 3.2 mm mesh (all wings had 3.2 mm mesh). The intertidal creek weirs were set at high tide in about fifteen minutes and were hauled at low tide when the creek had completely drained except for a small run-off channel.

All samples were put on ice and transported back to the laboratory for sorting and identification. For small samples all species of fishes and decapods were sorted and enumerated. For large samples the entire sample was sorted once to enumerate economically important species, species of special interest, and generally any species present in low abundance which might be missed in subsampling. After the initial sort, all species were enumerated in a subsample of 10-50% by wet weight of the sample.

During subtidal creek sampling, water depth, air and water temperature, salinity, and secchi depth were taken at the weir location at high tide after the weir had been set and at low tide just prior to hauling the gear. Secchi depth was measured under natural light conditions during both day and night. When the secchi disk was visible on the creek bottom, secchi depth was recorded as water depth. Because the intertidal creeks ran dry at low tide, physical data were collected from the main channel of the subtidal creek directly off of the intertidal creek mouth.

Therefore, physical data from the Schooner Creek subtidal weir and from the Lower Creek intertidal weir samples were taken at the subtidal weir location (Fig. 3.1). Secchi depth was not recorded during intertidal creek sampling.

SAMPLE ANALYSIS

A repeated measures analysis was conducted using a multivariate analysis of variance (MANOVA) model with day and night response variables for each physical factor (e.g., high and low tide water temperatures) and species (Harris 1985, SAS Institute Inc. 1988). The MANOVA was a nested factorial design with month, week(within month), and creek main effects. Diel main effects (the repeated measure) were tested with profile analysis (Harris 1985, SAS Institute Inc. 1988). Only the diel effects are reported, herein. Environmental data were ln(x+15) transformed (15 was added to scale all negative values above zero), while species abundances were ln(x+0.5) transformed for statistical analysis. Separate MANOVAs were performed for subtidal weir and seine species abundances (this was not necessary for environmental data, since weir and seine samples were paired with the same environmental data). Similar MANOVAs were performed on intertidal weir environmental data and species abundances, except that abundances were first converted to density/m^2 by dividing each catch by the creek bed area (370 m^2 and

1110 m^2, for Lower and Upper creeks, respectively). Density estimates were used because the intertidal creeks drain completely, and Upper Creek was approximately three times the size of Lower Creek. The subtidal creeks were more similar in area (23,000 m^2 and 24,000 m^2), and did not drain completely so that catches could not be quantified in terms of density.

While the above analyses provides information on diel differences for each individual species, I also used canonical discrimination analysis (CDA) to examine interactions between spatial and diel variation in faunal assemblages (Pielou 1984, Harris 1985, SAS Institute Inc. 1988). This analysis was performed on transformed (arcsine square root) species relative abundance data. Separate analyses were performed for subtidal weir, seine and intertidal weir samples. The CDA was performed on data grouped by creek (Foxboro and Schooner, or Lower and Upper) and time of day (day or night). Because of the large number of species (i.e., variables), only the ten most abundant (relative abundance) species from each diel group were entered in the analyses. Pearson correlations of the original transformed variables with the derived canonical variables were calculated to determine species variables which contributed most to the group discrimination (Harris, 1985). Average relative abundance for each species was determined by dividing its abundance by the total number of animals collected (sum of all decapods and fishes in the sample) for each sample and computing a mean for all samples.

MENIDIA MENIDIA COHORT ANALYSIS

Fortnightly length frequency histograms for Menidia menidia (Institute of Marine and Coastal Sciences Technical Report, Rutgers University, in prep.) were examined to identify size cohorts. Cohorts were identified by the presence of distinct length modes. After visual examination of the length frequency histograms, each fish length was assigned a cohort designation based on its length at date of capture. Abundance of each size cohort within each sample was then estimated based on the cohort's percent frequency in the sample. Mean abundance within each fortnightly sample week was graphed against the date of the first day of the week.

Results

PHYSICAL CONDITIONS

While environmental variables did not differ significantly between creeks, small, but significant diel differences were found for both subtidal and intertidal data (Table 3.1). Low tide water temperature averaged 3 C warmer during the day than at night. No diel differences were observed at high tide. Water temperature did not change between high and low tide at night, but rose an average of 4 C and 2.5 C during the day for subtidal and intertidal creeks, respectively. Water temperature increased as much as 8 C during the day, and dropped as much as 5 C during the night from high to low tide. Secchi depths were similar between day and night, though slightly greater during the day at high tide. The secchi disk was frequently visible on the bottom at low tide (e.g., at the shallower Foxboro Creek mean low tide depth=0.34 m and mean secchi depth=0.30 m). In fact, the entire creek bed at Foxboro Creek was usually visible during day low tides.

DIEL DIFFERENCES IN SPECIES ASSEMBLAGES

Strong diel differences in species assemblages were found in the three gears (Fig. 3.2). *Menidia menidia* dominated night collections for all gears by relative abundance, while day collections were dominated by *Leiostomus xanthurus* in the subtidal weir, and by *Palaemonetes vulgaris* in both the seine and intertidal weirs. *Palaemonetes vulgaris* was important in all gears and time periods except day subtidal weir samples. The turtle *Malaclemys terrapin*, and fishes *Anchoa hepsetus*, *Caranx hippos* and *P. americanus* were only important in day subtidal weir samples. *Gobiosoma bosci* was only important in day seine samples, while *Mugil curema* was only important in day intertidal weir samples.

Highly significant CDA differences among creek and diel groups were found for all gears (Table 3.2, 3.3; Fig. 3.3, 3.4). For subtidal weir samples day and night samples clustered separately only for Foxboro Creek, while for seine samples day and night groups clustered separately for both creeks. Night intertidal weir samples from both Lower and Upper creek clustered together, while day samples clustered separately from night samples and from each other (Fig. 3.4). Although neither canonical variable should be viewed as solely representing spatial or diel effects, the first canonical variable (can1) tends to separate spatial groups, while the second canonical variable (can2) tends to separate diel groups. Note, however, that day and night samples would cluster separately based on can1 alone.

Correlations of species relative abundances with the derived canonical variables suggest some of the dominant contributors to diel and spatial discrimination among collections. *Strongylura marina* was positively correlated with Foxboro Creek day weir samples. *Fundulus heteroclitus*, *Callinectes sapidus*, *Gobiosoma bosci* and *Palaemonetes vulgaris* were positively correlated, while *Menidia menidia* was negatively correlated, with Foxboro creek day seine samples (Table 3.2). In the intertidal weir collections *Callinectes sapidus*, *Fundulus majalis*, *Fundulus heteroclitus* and *Sphyraena borealis* were positively, while *Palaemonetes vulgaris* and *Menidia beryllina* were negatively, correlated with can1. The positively correlated species tend to be correlated with Lower Creek day samples, while negatively correlated species tend to be correlated with Upper Creek day samples, suggesting diel and spatial interactions. Although the can2 has a low significance level ($\alpha=0.1$, Table 3.3), species positively correlated with can2 tend to be strongly correlated with night samples (*Menidia menidia*), while negatively correlated species (*Palaemonetes vulgaris* and *Callinectes sapidus*) tend to be strongly correlated with day samples.

Canonical discrimination analyses indicate a strong spatial and diel interaction on creek communities. Differences between the two subtidal creeks (Table 3.2, Fig. 3.3) and between the two intertidal creeks (Table 3.3, Fig. 3.4) were much greater during the day than night. Additionally, subtidal seine samples exhibited stronger diel differences in the smaller, and much shallower (Table 3.1) Foxboro Creek compared to Schooner Creek (Table 3.2, Fig. 3.3).

DIEL DIFFERENCES IN SPECIES ABUNDANCES

Ten species, the total number of fish, and total fauna (fishes and decapods) abundance exhibited significant diel differences in subtidal weir samples, while four species, total fish, and total fauna exhibited significant diel differences in seine samples (Table 3.4). Diel difference in total fish and total fauna were largely due to Menidia menidia (Table 3.4). Six species, M. menidia, Mugil curema, Mustelus canis, Opsanus tau, Alosa pseudoharengus and Cynoscion regalis, were more abundant at night, while seven species, Gobiosoma bosci, Pomatomus saltatrix, Pseudopleuronectes americanus, Tautoga onitis, and Pagurus longicarpus, were more abundant during the day. Menidia menidia, Crangon septemspinosa, Pomatomus saltatrix, and total number of fish were significantly more abundant in intertidal weirs at night, while Mugil curema and Menidia beryllina were more abundant during the day (Table 3.5). Total abundances were much greater at night for both subtidal and intertidal creeks (Table 3.4, 3.5).

SEASONAL CHANGES IN DIEL PATTERNS

Seasonal abundance patterns were strikingly different between day and night samples (Fig. 3.5). During July-September night total abundances were greater than day total abundances, particularly for subtidal and intertidal weir samples, however during October and November day total abundances were greater than night total abundances. This pattern resulted largely from changes in the diel abundance pattern of Menidia menidia which dominated the catches (Fig. 3.5).

Comparisons of seasonal patterns between day and night varied greatly among species. Besides M. menidia (Fig.

3.5), important examples of species exhibiting day and night difference in seasonal patterns include Palaemonetes vulgaris, Fundulus heteroclitus (Fig. 3.6). Diel patterns for M. menidia exhibited a strong seasonal reversal in subtidal weir and seine samples with much higher night abundance during July-September followed by higher day abundance during October (Fig. 3.5). Intertidal weir abundances of M. menidia were high only from July-September, at which time day abundances were much lower than night abundances. Day and night abundances of P. vulgaris in subtidal weir samples were similar except during July and August when extreme peaks in night abundance occurred. Contrastingly, day and night abundances of F. heteroclitus in subtidal seines were similar until October when a large peak in day abundance occurred. while its night abundance peaked sharply in July and August while other species such as Pomatomus saltatrix and Leiostomus xanthurus exhibited similar day and night seasonal patterns (Fig. 3.6).

DIEL DIFFERENCES FOR MENIDIA MENIDIA COHORTS

A single adult and two major young-of-year (YOY) cohorts of M. menidia were apparent during both 1988 and 1989 (Fig. 3.7). During each year the first and second YOY cohorts were tracked through early August when a major peak in the first cohort abundance occurred (Fig. 3.8). After early August it became difficult to distinguish the limits of the size cohorts, and all subsequent individuals were assigned to an "unknown" cohort. This cohort was most likely comprised mainly of the second YOY cohort, but also included small numbers of adult and first YOY cohort individuals, as well as a small number of new recruits which continued to enter the catches through early September (especially in the intertidal creek samples, Fig. 3.7, 3.8). Mean length of _Menidia_ _menidia_ captured during day tides was much smaller than mean length during night tides from July-September in the intertidal weir samples due to the complete lack of adults, and near absence of first cohort YOY (Fig. 3.7, 3.8). During night in intertidal weir samples large numbers of adults and older YOY (60-80 mmTL) were captured in addition to the smaller individuals (Fig. 3.7, 3.8). However, similar diel differences in length were not apparent for data pooled from both subtidal creeks (Fig. 3.7).

Day and night differences in total _M_. _menidia_ seasonal abundance patterns, appear to result from differences among cohorts (Fig. 3.8). While day subtidal weir and seine samples were dominated by the unknown size cohort, night samples were dominated by the first YOY cohort in subtidal weir samples. In the intertidal weir samples, day samples were dominated by the second and unknown cohorts, while night samples were dominated by the first cohort.

Discussion

DIEL PATTERNS

New Jersey marsh creek community structure, as measured by species relative abundance dominance hierarchies (Fig. 3.2) and canonical discrimination analyses (Fig. 3.3, 3.4), was found to exhibit strong diel differences. Total abundance also exhibited strikingly different seasonal diel patterns, with abundances typically much higher at night than day, except in the fall (Fig. 3.5). It is clear from these patterns, that sampling exclusively during day or night could lead to very different pictures of marsh creek community structure. A sampling program using only day collections would have incorrectly concluded that L. xanthurus and P. vulgaris were the dominant species in subtidal creeks, and P. vulgaris and F. heteroclitus were dominant in intertidal creeks within New Jersey marshes (Fig. 3.2). The abundance of M. menidia, as well as total fish abundance, would have been greatly underestimated (Fig. 3.5).

Many of the diel patterns observed in New Jersey marsh creeks appear to reflect diel movements among habitats, rather than gear bias due to net avoidance during the day or to diel patterns in local activity (see my comments in the introduction). Since the intertidal creeks drain completely, most species can not avoid the intertidal weirs during the day. Several species which one might suspect to be most likely to avoid the subtidal weir and seine during the day, exhibited higher day abundance (P. saltatrix) or equal day and night abundances (L. xanthurus), therefore, net avoidance obviously was not a problem for these species. Net avoidance during the day by other, smaller species, such as A. mitchilli or M. menidia, therefore, appears unlikely.

The potential for gear bias due to diel patterns in local activity to result in the observed diel abundance patterns can most confidently be rejected in the intertidal creek habitats, because the intertidal creeks drain completely with each tide, thereby forcing most species into the weir (i.e., gear effectiveness is not related to diel activity rhythms, most fish and macroinvertebrates using the habitat must leave with the tide regardless of their activity state). For example, extremely high night abundances of Menidia menidia relative to day abundances in the intertidal creeks clearly reflect nocturnal movements into the intertidal marsh. Note that night samples are defined based on the time of flood tide, and in fact the ebb tide may have occurred during the day for some samples. Higher night abundance of M. menidia, therefore, reflect movement into the intertidal creeks prior to weir deployment at high tide, not an increased likelihood of leaving the creeks during night ebb tides.

In contrast, the subtidal creeks do not drain completely on each tide, and gear biases may be more important. However, since M. menidia diel abundance patterns are similar in both intertidal and subtidal creeks, the significantly higher night catches in subtidal weirs and seines suggest a similar nocturnal movement into subtidal creeks (again higher night abundances in subtidal weir samples reflect movement into the subtidal creeks during night flood tides prior to weir deployment). While M. menidia is distributed throughout shallow bay and marsh creek habitats during the day (Conover and Ross 1982), large numbers of larger individuals (50-70 mmTL, Fig. 3.7,3.8) move into the shallow creeks during the night accounting for the high night abundance observed during this study. This conclusion is supported by my personal observations. While hauling the weir at low tides following night flood tides (night samples), very large concentrations of M. menidia were typically observed apparently trapped in the creek by the weir. In fact, on one occasion, during a subsequent study (Chapter 2), an extremely large school of literally millions of individuals (over 200,000 were captured in the weir and seine) was trapped in the creek at low tide following a night flood tide. Such large concentrations of M. menidia were not evident at low tide following day flood tides.

CAUSES OF DIEL MOVEMENTS

Diel movements into intertidal and subtidal marsh creek habitats can result from several causes including, responses to diel changes in physical conditions, foraging movements of a species exhibiting a diel activity rhythm (e.g., a diurnal predator might move into subtidal creeks during the day to feed, but remain outside of the creek during inactive periods), predator avoidance behavior, and diel reproductive behavior. Diel movements might result from two major types of predator avoidance behavior: 1) response of a prey species to diel changes in predation pressures, or 2) movement between foraging and refuge habitats in order to avoid predation during non-feeding periods by a prey species with a diel foraging behavior (e.g., a diurnal foraging species might move into marsh creeks to avoid predation during its non-feeding nocturnal period). However, it should be made clear that cyclic diel movements between habitats require both attraction and repulsion from each habitat, and, hence, many of these potential causes are inter-related. For example, movement out of the creeks due to stressful day conditions must be followed by nocturnal movements back into the creeks due to some other incentive such as predation refuge or foraging behavior, otherwise no diel pattern would be observed (in fact, the species would tend to simply avoid the creeks).

Reproductive behavior does not appear to be an important cause of the diel patterns observed during this study. Adults were present in only nine (_M_. _menidia_, _O_. _tau_, _P_. _longicarpus_, _C_. _regalis_, _G_. _bosci_, _L_. _parva_, _C_.

variegatus, M. beryllina and C. septemspinosa) of the fifteen species which exhibited significant diel abundance patterns (Table 3.4, 3.5, see Chapter 1). The remaining six species (P. saltatrix, M. curema, P. americanus, M. canis, T. onitis, and A. pseudoharengus) were present exclusively as juveniles (see Chapter 1). Although adults of M. menidia, M. beryllina and O. tau were collected, the observed diel patterns resulted primarily from YOY movements (see Fig. 2.7, 3.8 for M. menidia), hence, were not related to reproductive activities. Further, M. menidia is known to spawn exclusively on diurnal high tides in the intertidal marsh (Middaugh and Lempesis 1976, Middaugh 1981, Middaugh et al. 1981, Middaugh and Takita 1983, Conover and Kynard 1984), therefore, its high nocturnal abundance in both intertidal and subtidal marsh creeks is not due to reproductive movements. Reproductive behavior can not be completely ruled out as the cause of the diel patterns for O. tau, C. regalis, M. beryllina, or C. septemspinosa, but is considered very unlikely.

High diurnal abundances of G. bosci, L. parva, and C. variegatus in subtidal seine samples, however, probably reflects gear bias due to diel activity patterns, as these species are not expected to undergo tidal movements in the creeks (Chapter 2). Similarly, higher day abundances of the hermit crab, P. longicarpus, in the subtidal weir samples probably results from gear bias.

Environmental influences on diel movements

Diel variation in environmental conditions in marsh creeks may have influenced diel movements of fishes and decapods. Water temperature averaged 3 C warmer during day low tides than night low tides, and tidal range in water temperature was greater during the day than night (Table 3.1). In fact, day low tides ranged from 1 to 8 C warmer than day high tides, while night low tides ranged from 5 C colder to 7 C warmer than night high tides (Table 3.1). Further, salinity dropped an average of 3 ‰, and as much as 7‰, from night high to night low tide during intertidal creek sampling.

Some diel movement pattern, particularly those restricted to particular seasons, may result from a response to diel occurrences of stressful or lethal conditions. For example, the extreme day low tide water temperatures recorded in the creeks (28-29 C, Table 3.1) are near the lethal temperatures for _P_. _americanus_ (Hoff and Westman 1966, Pearce 1969). The rapid rate of change of physical conditions within the creeks may pose an additional stress to some species, and may potentially be more important than the absolute conditions at any given time. Important factors which are affected by time of day are temperature, salinity, and dissolved oxygen concentration (Hackney et al. 1976, Table 3.1). Despite indications from numerous studies of strong diel changes in environmental conditions in shallow estuarine habitats (Nicol 1936, Hoese and Jones 1963, Cameron 1969, Nixon and Oviatt 1973, Müller 1978, Vetter and Hodson 1982, Breitberg 1988, Portnoy 1991) the influence of diel environmental variability on estuarine communities has received little attention (However, see Nixon and Oviatt 1973, Hackney et al. 1976, and Müller 1978).

In addition to the direct response of animals to lethal or stressful conditions, diel and spatial movements can result from a more subtile energetic response to sublethal environmental changes in two ways: 1) behavioral regulation of homeostasis (Miller and Dunn 1980), often in the form of behavioral thermoregulation (Brett 1971, Beitinger et al. 1975, Beitinger 1976, Reynolds and Casterlin 1976, Holland et al. 1990, Clark and Green 1991), and 2) through a bioenergetic advantage (McLaren 1963, McAllister 1969, Brett 1971, Stuntz and Magnuson 1976, Mauchlin 1980, Abou-Seedo et al. 1990). In the first case, animals undergo diel or spatial movements to maintain a preferred temperature over ranges as narrow as 3 C. Both mean tidal and mean diel changes in water temperature were on this scale and ranged as high as 8 C (Table 3.1). Olla and Studholme (1978) report that *Pomatomus saltatrix* is highly sensitive to temperature changes, and exhibit thermoregulatory movements in the laboratory. The high day abundance of *P. saltatrix* in the subtidal weir samples may have resulted from thermoregulatory movements rather than from avoidance of lethal conditions. Similarly, rapid tidal and diel changes in salinity (Table 3.1) may induce movements to avoid the energetic cost of osmoregulation.

The strong spatial and diel interaction on subtidal and intertidal marsh creek community structure indicated by the CDA may have resulted from the influence of location within a creek on diel variation in environmental conditions. Discrimination between subtidal (Table 3.2, Fig. 3.3) and intertidal (Table 3.3, Fig. 3.4) creek communities were greater during the day than night. Additionally, discrimination between day and night subtidal creek communities was stronger at the smaller, shallower Foxboro Creek compared to Schooner Creek (Table 3.2, Fig. 3.3).

Hackney et al. (1976) found that diel changes in physical conditions in oligohaline tidal marsh creeks were a function of location in the creek, and that they had a strong influence on community structure. And in an earlier study (Chapter 2) I discuss the influence of creek morphology on environmental conditions within the creeks. Both tidal and diel variation in physical conditions tends to increase with decreasing water depth (Hackney et al. 1976, Chapter 2), and consequently with increasing creek size (Chapter 2). Hence the increased discrimination between Upper and Lower intertidal creek communities during the day may result from a changes in environmental conditions along a mouth-to-headwater creek gradient.

While the increased discrimination between day and night communities at Foxboro Creek relative to Schooner Creek may result from increased diel variation in conditions at the shallower Foxboro Creek.

Predator refuge

Menidia menidia is known to forage primarily during the day (Moore 1968, Morgan 1990), and while some nocturnal foraging may occur under extreme tidal conditions (Gilmurray and Daborn 1981), peak foraging activity at night is certainly not supported by previous studies. I conclude, therefore, that the nocturnal movement of *M. menidia* into subtidal and intertidal creeks occurs in response to predation pressures. If the nocturnal movements of *M. menidia* into the shallow marsh do occur in response to predation pressure, then some equally strong incentive must cause *M. menidia* to move out of these habitats during the day. *Menidia menidia* may move out of intertidal and shallow subtidal habitat during the day in order to obtain food. Although *M. menidia* is an omnivore it feeds primarily on copepods and other zooplankton (Moore 1968, Gilmurray and Daborn 1981, Werme 1981, Cadigan and Fell 1985, Morgan 1990), and probably does not depend specifically on the shallow marsh as a forage ground. This agrees with Werme's (1981) report that *M. menidia* tended to be restricted to subtidal creek areas, where it fed on small zooplankton, and avoided intertidal areas during the day. It has been similarly been suggested that adult M. menidia undergo diel vertical migrations while overwintering on the continental shelf (Conover and Murawski 1982), which may be related to diel foraging behavior (Warkentine and Rachlin 1989). It appears likely, therefore, that M. menidia moves out of the shallows during the day to forage, but takes refuge in shallow marsh habitats at night to avoid predation during non-feeding periods. This behavior is perhaps better described as a tendency to spread out among creek and shallow bay habitats during the day to forage, and a tendency to concentrate within shallow areas during the night to avoid predation during the non-feeding period.

Similar arguments can be made to suggest that A. mitchilli also utilizes marsh creeks as a nocturnal refuge. Anchoa mitchilli is known to feed primarily on zooplankton (Carr and Adams 1973, and citations therein) during the day in marsh creeks (Morgan 1990). Nocturnal movements into marsh creeks are further supported by a previous study in New Jersey, which reported higher day catches of A. mitchilli in trawl and seine catches near the mouths of marsh creeks and in the shallow (<2m) open bay (Vouglitois et al. 1987).

Comparable diel movements between foraging and refuge habitats, resulting from the need to avoid predation during inactive periods (Hobson 1975), are widespread among many freshwater and marine habitats (e.g., Hobson 1968, Ebeling and Bray 1976, Major 1977, Robblee and Zieman 1984, see review by Helfman 1978). Sometimes extensive diel migrations between foraging and refuge habitats are undertaken by fish of similar size to M. menidia (Hobson and Chess 1973).

Foraging behavior

Both C. septemspinosa (Haefner 1979) and M. canis (Casterlin and Reynolds 1979) are known to have strong nocturnal activity rhythms, and their respective nocturnal movements into the intertidal and subtidal creek habitats may result from foraging activity. Likewise, I have occasionally observed C. regalis actively feeding in the subtidal study creeks during early stages of night flood tides (gut contents of 13 individuals collected at night in the creeks primarily contained P. vulgaris, M. menidia, and F. heteroclitus, unpublished data). Cynoscion regalis (n=43, 139-521 mm Standard Length, mean=389 mmSL) and M. canis (n=127, 320-493 mm Total Length, mean 410 mmTL) were the two largest fishes collected in the creeks (Chapter 1), and are unlikely to have retreated to the creeks to avoid predation.

Three species with significantly higher day abundances in the subtidal weirs are known to be weakly (P. saltatrix) to strongly diurnal (T. onitis and P. americanus, see Olla et al. 1969, Olla and Studholme 1978) and may use the creeks during diurnal foraging. Since P. americanus has previously been shown to undergo tidal foraging movements into shallow marsh habitats (Olla et al. 1969, Tyler 1971, Wells et al. 1973), its diel abundance patterns in the marsh creeks are likely to be related to foraging activity. Similarly, higher day catches of M. curema and M. beryllina in the intertidal creeks probably result from diurnal foraging movements. As mentioned above, diel use of creeks for foraging purposes, implies diel avoidance of creeks. I suspect that diel changes in environmental conditions within the creeks, rather than in predation pressure within the creeks, cause species such as C. septemspinosa, C. regalis, M. canis, P. americanus and P. saltatrix to leave the creek foraging habitat. Interestingly, these species are ones which one might suspect to be most sensitive to diel changes in water temperature.

SPECIES WITHOUT DIEL PATTERNS

Equal day and night abundances occurred for many species which are known to have strong foraging, reproductive, or other links with the marsh, including F. heteroclitus, F. majalis, C. variegatus, F. luciae, and L. xanthurus (Dawson 1958, Harrington and Harrington 1961, Smith et al. 1974, Subrahmanyam and Drake 1975, Baker-Dittus 1978, Kneib and Stiven 1978, Hodson et al. 1981, Weisberg et al. 1981, Werme 1981, Able et al. 1983, Talbot and Able 1984, Talbot et al. 1986, Able 1990). Equal day and night collections suggest residence, or continuous tidal movements into the marsh, particularly from intertidal weir collections. This behavior is exemplified by *Fundulus heteroclitus* in intertidal creeks and by *Leiostomus xanthurus* in subtidal creeks. Both these species have been reported to exhibit tidal foraging movements in the marsh (Baker-Dittus 1978, Kneib and Stiven 1978, Hodson et al. 1981, Weisberg et al. 1981). While tidal movements of *F. heteroclitus* obviously occur in the intertidal habitat, I have also suggested that *L. xanthurus* exhibits some degree of tidal movements within the subtidal creeks (Chapter 2).

Interestingly no diel abundance differences were observed for either of these species despite previous reports indicating nocturnal (*L. xanthurus*, Hodson et al. 1981) and diurnal (*Fundulus heteroclitus*, Baker-Dittus 1978, Weisberg et al. 1981) activity patterns. These observations agree well with studies suggesting that *F. heteroclitus* has a basic diurnal activity pattern in non-tidal areas on which a tidal foraging pattern can be superimposed in tidal areas (Davis and Bardach 1965, Baker-Dittus 1978, Weisberg et al. 1981). In effect some fishes appear to be able to modify a basic circadian activity rhythm when "conditioned" by the timing of food availability (Davis and Bardach 1965). Nixon and Oviatt

(1973) estimated intertidal foraging habitat was only available 25% of the time in a New England marsh. Therefore, suppression of a basic diel activity rhythm under tidal conditions may be an adaptation to increase foraging opportunities when tidal access to food is limited (i.e., fish abandon a diel feeding periodicity and feed during limited periods of tidal access to food regardless of time of day).

ONTOGENETIC PATTERNS

Ontogenetic differences in habitat use by *M. menidia* are suggested from diel patterns in cohort abundance and size (Fig. 3.7, 3.8). *Menidia menidia* abundances were very low during the day in the intertidal creek, with those few individuals taken belonging to the smallest size classes. Larger size cohorts of YOY and adults appear at night when feeding is assumed to have stopped, based on previous feeding studies (Moore 1968, Morgan 1990, see my comments above). Similar, less extreme cohort abundance patterns were evident in the subtidal creeks, particularly in the subtidal weir samples (cohort size patterns for the smaller Foxboro Creek were also very similar to intertidal creek patterns, with smaller size classes taken in day samples).

These apparent changes in habitat use with growth may explain some of the conflicting diel patterns reported in the literature. Most previous estuarine studies have also reported higher night catches of *M. menidia* (McCleave and Fried 1975, Shenker and Dean 1979, Middleton 1986) and *A. mitchilli* (Shenker and Dean 1979, Middleton 1986, Livingston 1976). The high night catches of *M. menidia* in intertidal and subtidal creeks, and of *A. mitchilli* in the subtidal creeks were mainly due to large size classes of YOY (i.e., >50mmTL), while day samples were dominated by small size classes of *M. menidia* (<40mmTL, Fig. 3.7, 3.8, also see Chapter 1 and 5), except in the fall (see my discussion below). Contrastingly, the high day catches of these two species reported by Reis and Dean (1981) resulted from the dominance of small size classes in his samples (38 mmTL, 22 mmTL, mean length respectively, Reis 1977).

These diel patterns may be explained by ontogenetic changes in the need for refuge. *Menidia menidia* are spawned, and hatch in the intertidal and shallow subtidal marsh (Middaugh 1981, Middaugh et al. 1981). During early development, *M. menidia* is probably highly susceptible to predation. In fact, it has been suggested that the nocturnal hatching time of *M. menidia* may be a mechanism to reduce cannibalism by the diurnal adults (Middaugh 1981, Middaugh et al. 1981). As *M. menidia* grows it might undergo diurnal movements into deeper habitats to feed, in order to avoid excess crowding and competition for food. This movement would be possible if there is an ontogenetic release of predation pressures (Helfman 1978). At night however, when feeding stops, *M. menidia* retreats to shallow areas to avoid aquatic predators. The importance of direct and indirect predation effects in regulating size related habitat use patterns has been extensively studied in other systems (see discussions in Helfman 1978, Hobson 1979, Milinski 1986, Mittelbach 1986, Mittelbach and Chesson 1987). Generally, increased predation pressure (or threat of predation) from aquatic nekton can result in a restriction of small size classes to shallow water or to dense vegetation (Hobson 1968, Werner et al. 1977, Power 1987).

SEASONAL CHANGES

Seasonal changes in diel abundance patterns were apparent for total fauna abundance, and for the abundance of several species (Fig. 3.5, 3.6). These changes were most striking for _M_. _menidia_, which was most abundant at night during the summer, but most abundant during the day during the fall (Fig. 3.5). Although it is not clear what caused these diel differences in seasonal patterns, several hypotheses can be suggested: 1) seasonal changes in diel patterns in physical conditions within the creeks; 2) inter-cohort differences in diel behavior resulting from resource partitioning; and 3) seasonal changes in predation pressure and/or diel patterns of predation pressure.

Low day catches of _M_. _menidia_ during the summer may have resulted from high summer water temperatures (Chapter

1), or from extreme diel variation in other physical conditions such as dissolved oxygen concentration (pers. observ.). Later cohorts might shift diel activity patterns to avoid intraspecific competition with the extremely abundant earlier cohorts. In fact there is some evidence of slower growth of later spawned *M. menidia* cohorts (Barkman et al. 1981, see also chapter 5), which Bengston (1984) has suggested may be caused by a reduced food supply during the summer.

Alternatively, increased nocturnal movement by *M. menidia* into the marsh during July-September may result from increased predation pressures. The timing of this period corresponded with the appearance and peak abundance of several piscivorous predators (see discussion in Chapter 1), including: the adult crab *Callinectes sapidus* (Fitz and Wiegert 1991), and fishes *Paralichthys dentatus* (Chapter 2), *Strongylura marina* (Tracy 1910, Car and Adams 1973, Subrahmanyam and Drake 1975), *Pomatomus saltatrix* (Friedland et al. 1988), *Sphyraena borealis* and *Cynoscion regalis* (pers. observ.). The October-November shift to increased day abundance additionally corresponded with the strong decline and disappearance of all of these potential predators.

In general, species which exhibited seasonal changes in diel patterns tended to be small marsh residents (and potential highly vulnerable prey species), such as *P. vulgaris*, *F. heteroclitus*, and *M. menidia* (Fig. 3.5, 3.6), while larger (less vulnerable) species, such as *L. xanthurus* and *P. saltatrix*, tended to exhibited similar seasonal diel patterns (Fig. 3.6), suggesting that seasonal diel changes occur primarily in response to changing predation pressures.

Table 3.1. Comparison of mean (minimum, maximum) physical conditions between high and low tide stages, and between day and night for two subtidal creeks (July-September 1988) and two intertidal creeks (July-October 1989) in a southern New Jersey estuary. Differences between day and night were tested separately for subtidal and intertidal creeks with a multivariate analysis of variance (MANOVA) with day and night response variables and month, week (within month) and creek main effects (see text). Significant differences between day and night are indicated ($^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$).

	Subtidal creeks		Intertidal creeks	
Variable	Day	Night	Day	Night
High tide				
Air temperature	24 (17, 32)**	19 (11, 27)	21 (12, 23)	19 (6, 23)
Water temperature	20 (17, 25)	20 (16, 26)	21 (13, 24)	21 (11, 24)
Salinity	32 (30, 32)*	31 (30, 32)	27 (24, 30)	28 (22, 30)
Secchi depth (m)	0.9 (0.4, 1.4)*	0.7 (0.4, 0.9)	no data	no data
Depth (m)	1.5 (0.8, 2.0)*	1.3 (0.8, 1.7)	1.7 (1.4, 2.1)	1.9 (1.2, 2.3)
Low tide				
Air temperature	22 (15, 28)***	20 (9, 31)	22 (9, 28)	19 (9, 23)
Water temperature	24 (19, 28)***	21 (13, 26)	24 (12, 29)*	21 (10, 24)
Salinity	31 (25, 33)	31 (30, 33)	26 (21, 29)	25 (20, 28)
Secchi depth (m)	0.4 (0.2, 0.6)	0.4 (0.3, 0.8)	no data	no data
Depth (m)	0.7 (0.3, 1.0)*	0.6 (0.3, 0.9)	0.7 (0.5, 1.0)	0.8 (0.5, 1.0)
Tidal range (high - low)				
Air temperature	2.8 (2, 4)	-0.5 (-13, 8)	-1.6 (-5, 3)	0 (-6, 4)
Water temperature	-4.0 (-8, -1)**	-1.1 (-7, 5)	-2.5 (-5, 1)**	-0.2 (-4, 3)
Salinity	0.6 (-1, 7)	-0.5 (-1, 0)	0.7 (-1, 4)	3.3 (0, 7)*
Secchi depth (m)	0.5 (0.1, 0.8)	0.2 (-0.1, 0.5)	no data	no data
Depth (m)	0.8 (0.5, 1.1)	0.8 (0.5, 1.0)	1.0 (0.6, 1.4)	1.1 (0.4, 1.4)
Sample size	12	15	11	12

Table 3.2. Canonical discrimination analyses of species relative abundance variables (arcsine square-root transformed) for data grouped by subtidal creek (Schooner and Foxboro), and diel period (day and night) for weir (n=21) and seine (n=22) samples taken from July-September 1988 (see plot of canonicals in Fig. 3.2). Pearson correlations of the transformed species variables on the derived canonical variables (Can1 and Can2) are given.

Subtidal weir			Subtidal seine		
	Pearson correlation			Pearson correlation	
Species	Can1	Can2	Species	Can1	Can2
Strongylura marina	0.59^{**}	0.26	*Fundulus heteroclitus*	0.58^{**}	-0.18
Fundulus heteroclitus	0.26	0.33	*Callinectes sapidus*	0.57^{**}	-0.04
Pomatomus saltatrix	0.17	-0.21	*Gobiosoma bosci*	0.49^{*}	0.41
Anchoa mitchilli	0.11	0.10	*Palaemonetes vulgaris*	0.48^{*}	0.56^{**}
Leiostomus xanthurus	0.05	-0.21	*Anchoa mitchilli*	0.06	0.01
Callinectes sapidus	-0.03	-0.17	*Sphyraena borealis*	-0.07	0.54^{**}
Anchoa hepsetus	-0.13	-0.17	*Leiostomus xanthurus*	-0.10	0.34
Menidia menidia	-0.14	0.13	*Syngnathus fuscus*	-0.25	0.76^{***}
Sphyraena borealis	-0.31	-0.48^{*}	*Crangon septemspinosa*	-0.25	0.62^{**}
Palaemonetes vulgaris	-0.34	0.78^{***}	*Menidia menidia*	-0.58^{**}	-0.58^{**}
Squared canonical correlation	0.95^{**}	0.64		0.95^{***}	0.73
Multivariate F (difference among groups)	2.79^{**}			3.6^{***}	

$^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

Table 3.3. Canonical discrimination analysis among intertidal creek and diel collection groups for species relative abundance data (see plot of canonicals in Fig. 2.3). Pearson correlations of the original transformed (arcsine square-root) species variables on the derived canonical variables (Can1 and Can2) are given.

Species	Pearson correlation	
	Can1	Can2
Callinectes sapidus	0.61^{***}	-0.43^{*}
Fundulus majalis	0.50^{**}	-0.32
Fundulus heteroclitus	0.43^{*}	-0.26
Sphyraena borealis	0.41^{*}	-0.23
Crangon septemspinosa	0.20	0.15
Pomatomus saltatrix	0.17	-0.09
Cyprinodon variegatus	0.10	-0.16
Mugil curema	0.04	-0.08
Menidia menidia	-0.06	-0.65^{***}
Menidia beryllina	-0.49^{*}	-0.24
Palaemonetes vulgaris	-0.78^{*}	-0.51^{**}
Squared canonical corralation	0.96^{***}	0.80^{a}
Multivariate F (difference among goups)	4.9^{***}	
Sample size	26	

$^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$
$^{a}p=0.06$

Table 3.4. Diel comparison of mean (SE) species abundances for subtidal weir and seine samples collected from Foxboro and Schooner creeks (July-September 1988). Abundances of eleven dominant species, plus additional species exhibiting significant diel differences are given. Within each gear, significant diel differences are indicated ($^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

	Weir		Seine	
Species	Day	Night	Day	Night
Menidia menidia	119 (48)	5126 (3062)**	536 (249)	3087 (1146)**
Palaemonetes vulgaris	15 (9)	544 (376)	1208 (238)	883 (258)
Leiostomus xanthurus	361 (143)	433 (137)	52 (21)	30 (12)
Anchoa mitchilli	48 (34)	420 (223)	58 (36)	20 (8)
Fundulus heteroclitus	36 (33)	291 (204)	100 (49)	54 (17)
Crangon septemspinosa	0	17 (14)	99 (36)	158 (87)
Gobiosoma bosci	0	0	53 (15)*	28 (8)
Anchoa hepsetus	56 (56)	4 (4)	0.1 (0.1)	0
Pomatomus saltatrix	39 (8)**	17 (4)	2 (1)	5 (2)
Sphyraena borealis	9 (8)	1 (1)	26 (24)	0
Mugil curema	0.2 (0.2)	11 (7)*	1 (0.9)	1.7 (1)
Pseudopleuronectes americanus	2.5 (1)**	0.8 (0.4)	3.6 (1)	1.8 (1)
Mustelus canis	0	4.4 (2.4)**	0	0.9 (0.8)
Lucania parva	0	0	5.3 (2.9)***	0.1 (0.1)
Opsanus tau	0	0.5 (0.2)*	0.6 (0.2)	1.3 (0.6)
Tautoga onitis	0.5 (0.2)**	0.1 (0.1)	1.4 (1)	0.6 (0.3)
Pagurus longicarpus	0.6 (0.4)*	0	2 (1)	0
Cyprinodon variegatus	0	2.2 (1.9)	3.2 (2.1)*	0.2 (1.1)
Alosa pseudoharengus	0.2 (0.1)	1.1 (0.7)**	0	0
Cynoscion regalis	0	0.9 (0.5)**	0	0
Total invertebrates	18 (10)	672 (458)	1327 (266)	1061 (332)
Total fish	758 (272)	6413 (3114)*	878 (292)	3626 (1159)**
Total	781 (272)	7769 (3773)*	2205 (489)	4324 (1214)*
Sample size	11-13	12-15	11-12	11-13

Table 3.5. Mean (SE) density per 100 m^2 of the dominant intertidal creek species. Diel differences were tested with a multivariate analysis of variance (MANOVA) with day and night response variables and month, week (within month), and creek main effects (see text). Significant differences are indicated as $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

Species	Day	Night
<u>Menidia menidia</u>	25.4 (13)	608 (392)*
<u>Palaemonetes vulgaris</u>	115 (43)	36 (13)
<u>Fundulus heteroclitus</u>	48.8 (12)	78 (39)
<u>Callinectes sapidus</u>	6.1 (1)	3.4 (0.9)
<u>Mugil curema</u>	2.8 (1.8)*	1.2 (0.6)
<u>Fundulus majalis</u>	1.8 (0.6)	1.4 (0.6)
<u>Cyprinodon variegatus</u>	1.6 (0.7)	1.4 (0.8)
<u>Menidia beryllina</u>	1.6 (1.0)*	0.3 (0.2)
<u>Crangon septemspinosa</u>	0.4 (0.3)	0.8 (0.5)**
<u>Fundulus luciae</u>	0.3 (0.1)	0.7 (0.5)
Total invertebrates	121 (43)	41 (13)
Total fishes	83 (22)	693 (389)*
Total	204 (58)	734 (392)
Sample size	13	13

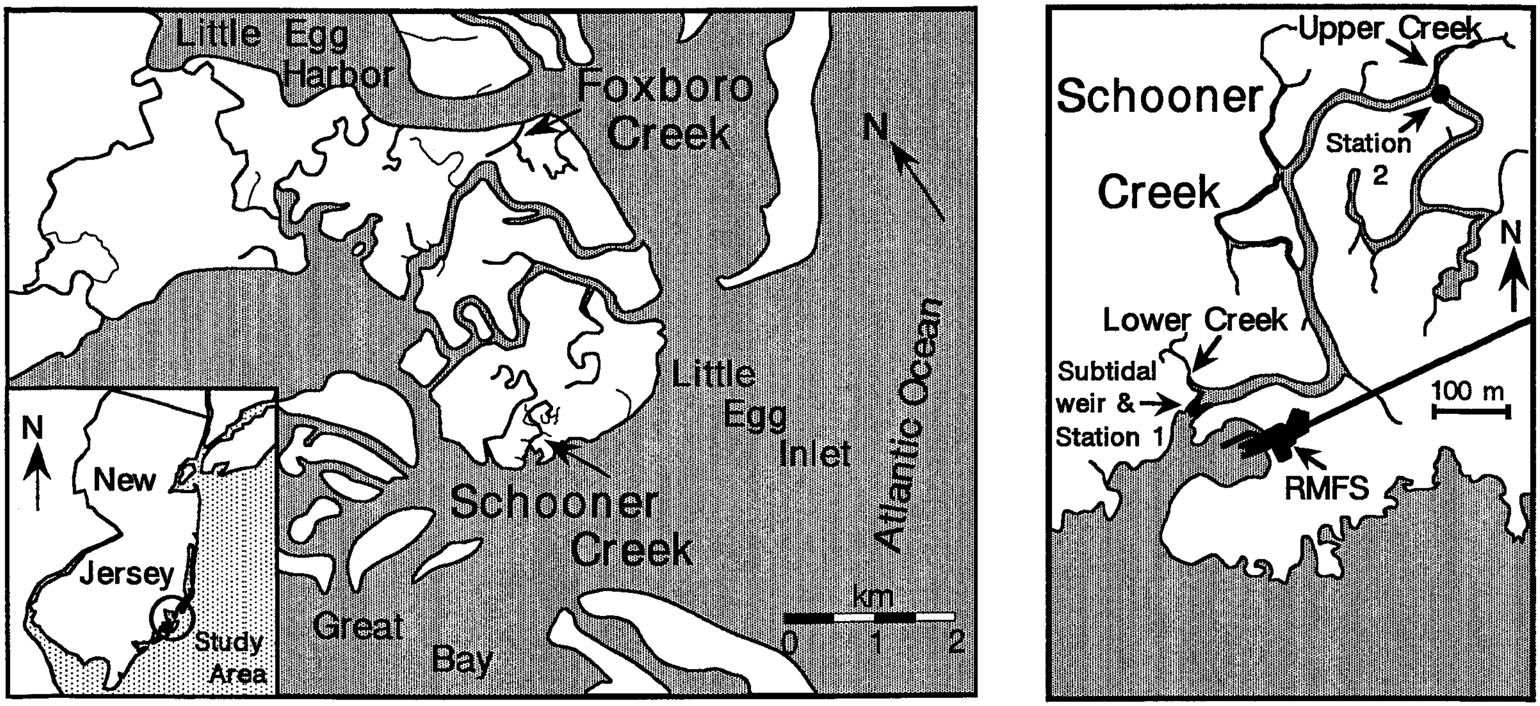


Figure 3.1. Great Bay-Little Egg Harbor estuarine complex and study creeks located in southern New Jersey. The subtidal Schooner and Foxboro creeks were sampled with weirs and seines approximately fortnightly from April-November 1988 (top), while the intertidal Lower and Upper creeks were samples with weirs fortnightly from July-October 1989 (bottom).

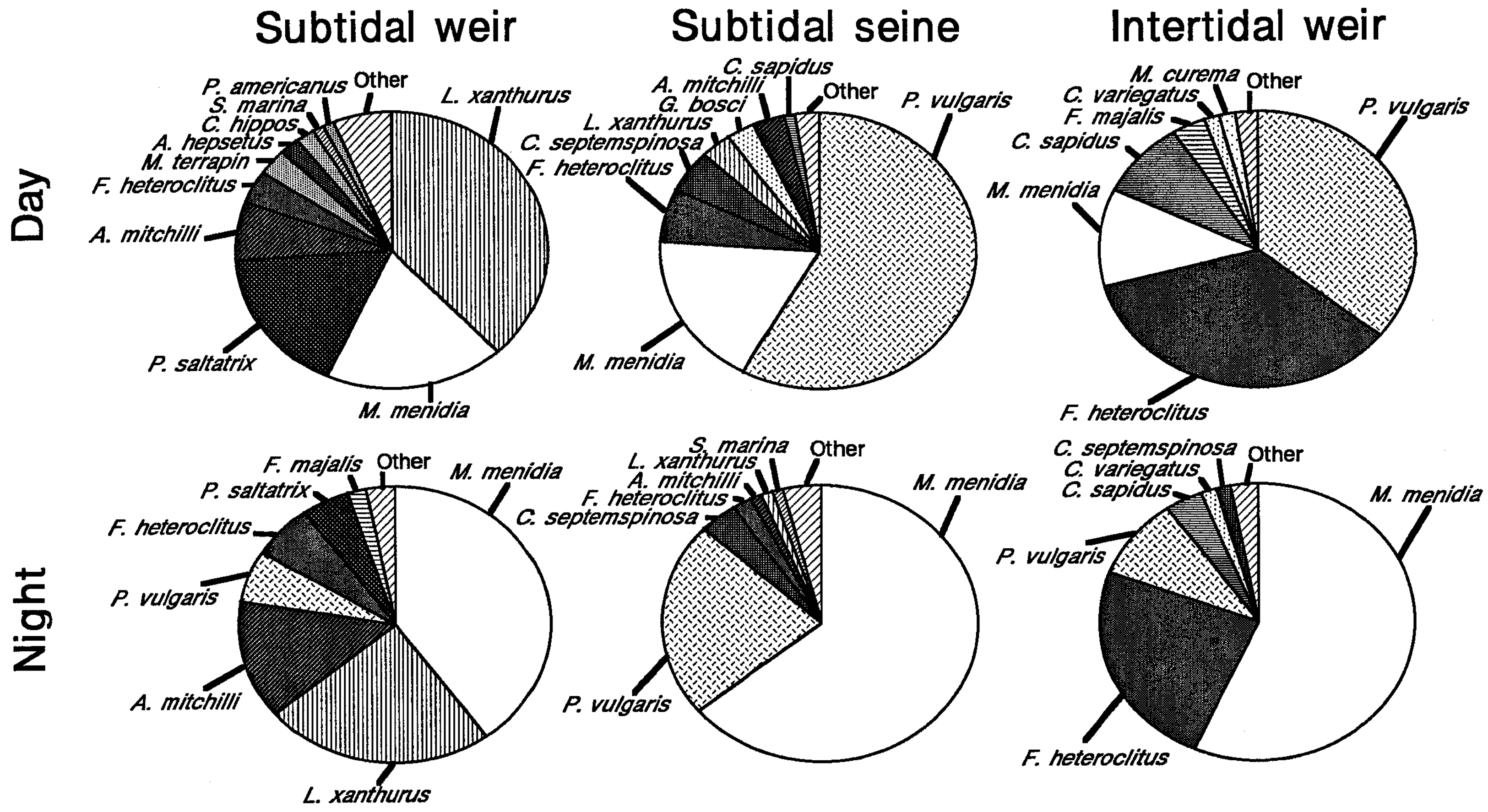


Figure 3.2. Mean percent relative abundance of all species >1% by diel period and sampling gear. Subtidal weir (n=21) and seine samples (n=22) were taken fortnightly from two creeks during July-September 1988. Intertidal weir samples (n=26) were taken fortnightly from two creeks during July-October 1989.

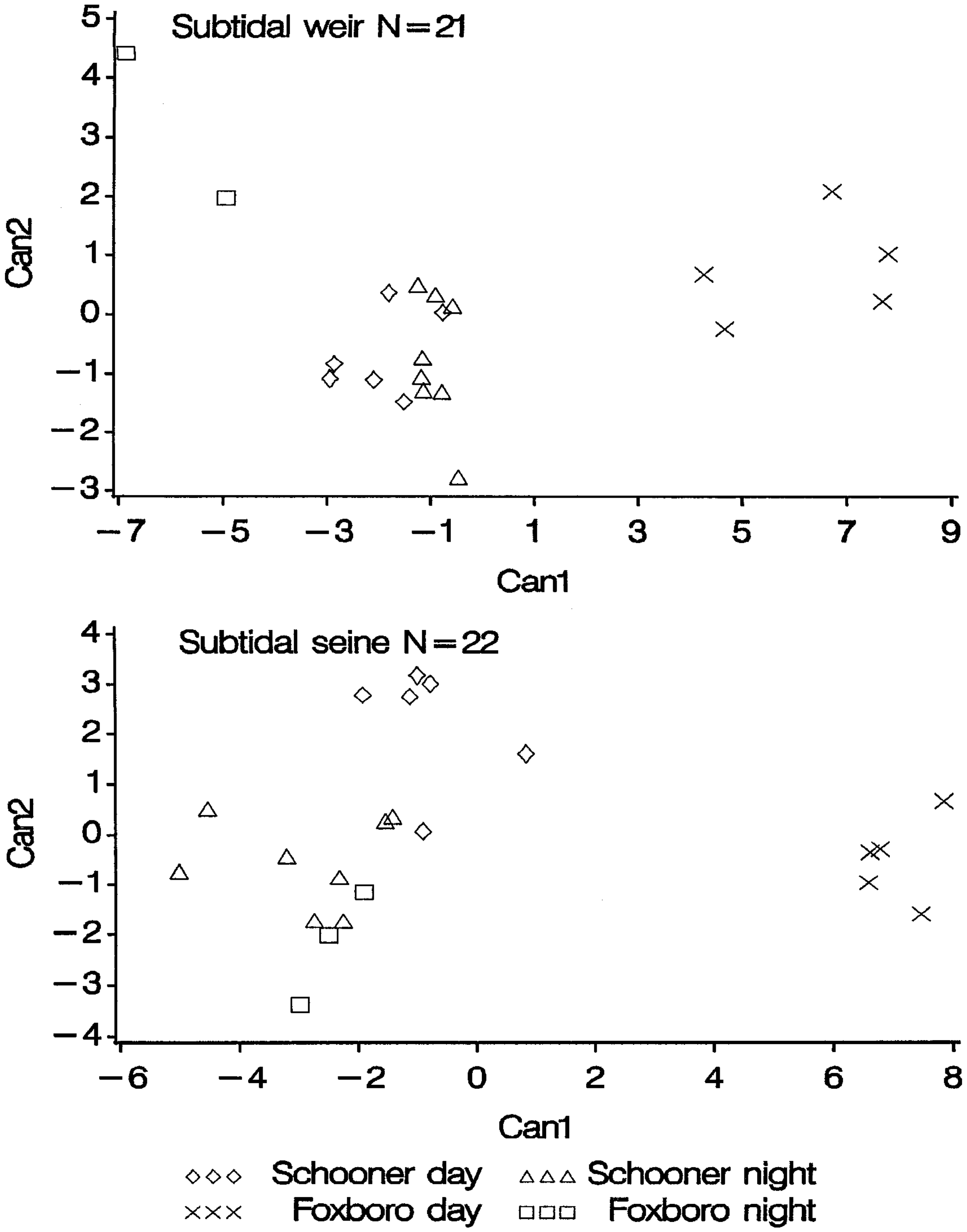


Figure 3.3. Canonical discrimination analyses of subtidal creek weir and seine species relative abundance (arcsine square-root transformed) data grouped by creek and diel period. Statistics are given in Table 3.2.

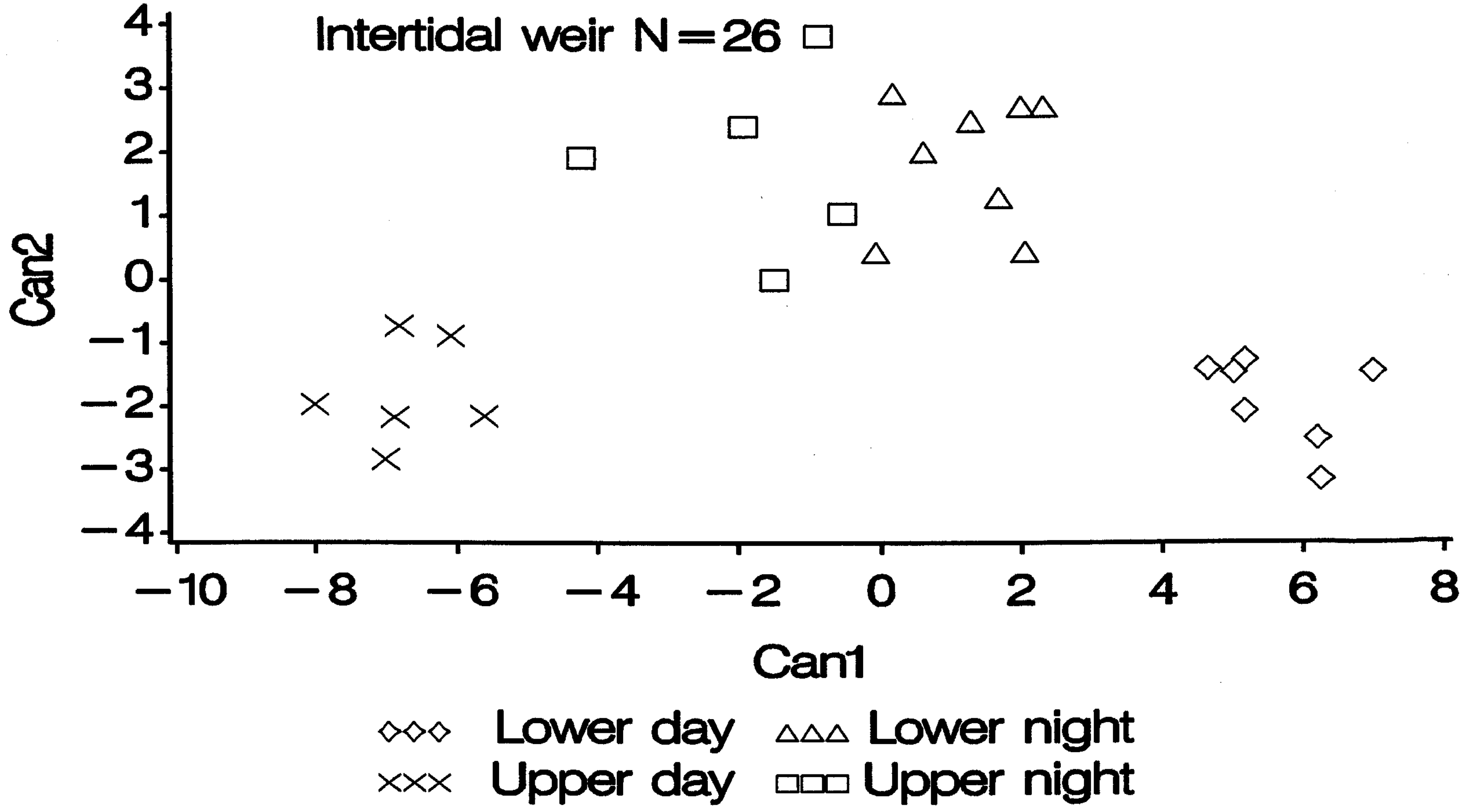


Figure 3.4. Canonical discrimination analysis of intertidal weir species relative abundance (arcsine square-root transformed) data grouped by creek and diel period. Statistics are given in Table 3.3.

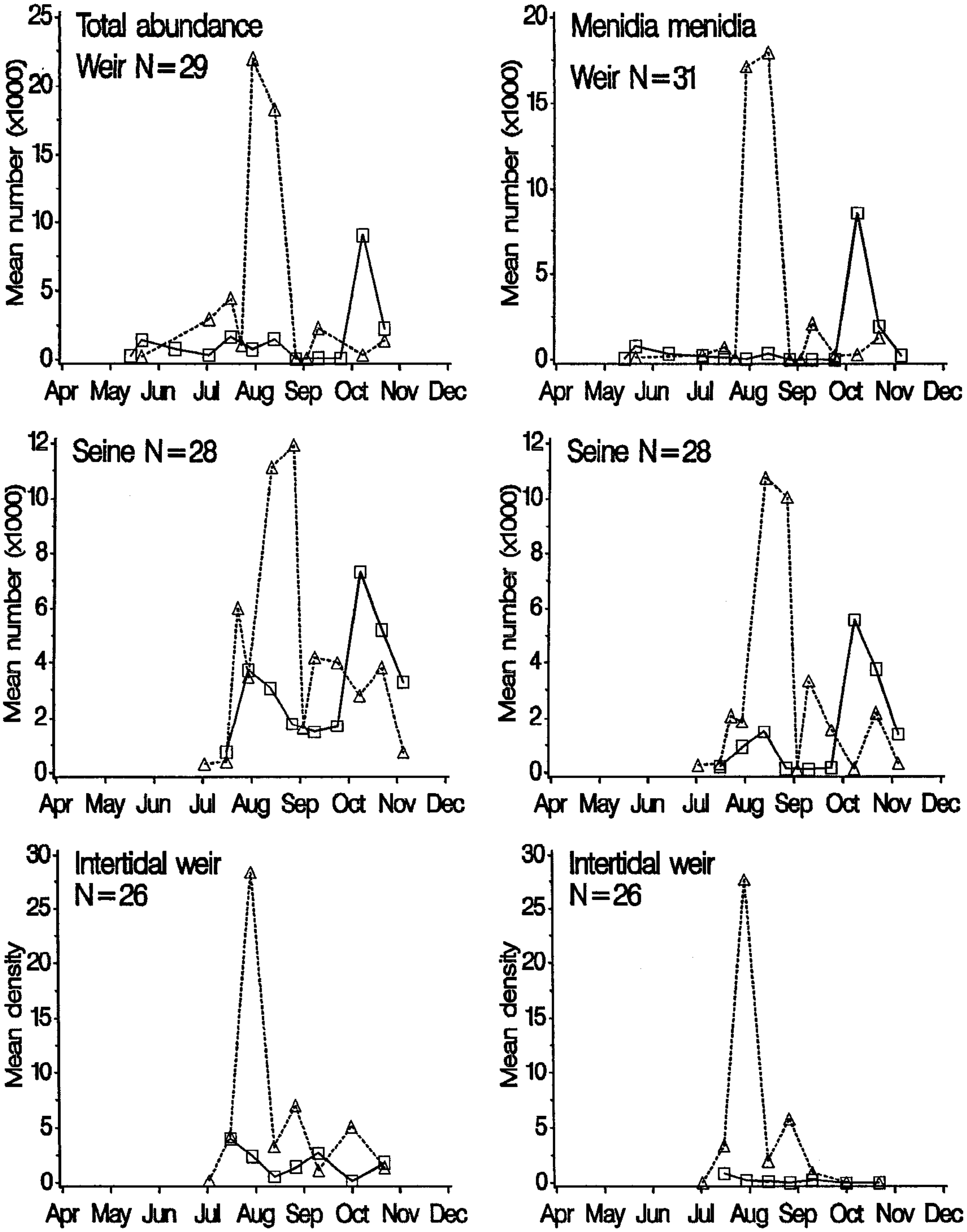


Figure 3.5. Weakly mean total fauna abundance (left column) and <u>Menidia menidia</u> abundance (right column) by gear and diel period (square=day, triangle=night). Subtidal weir and seine samples were collected from Foxboro and Schooner creeks during 1988, while intertidal weir samples were collected from Lower and Upper creeks during 1989.

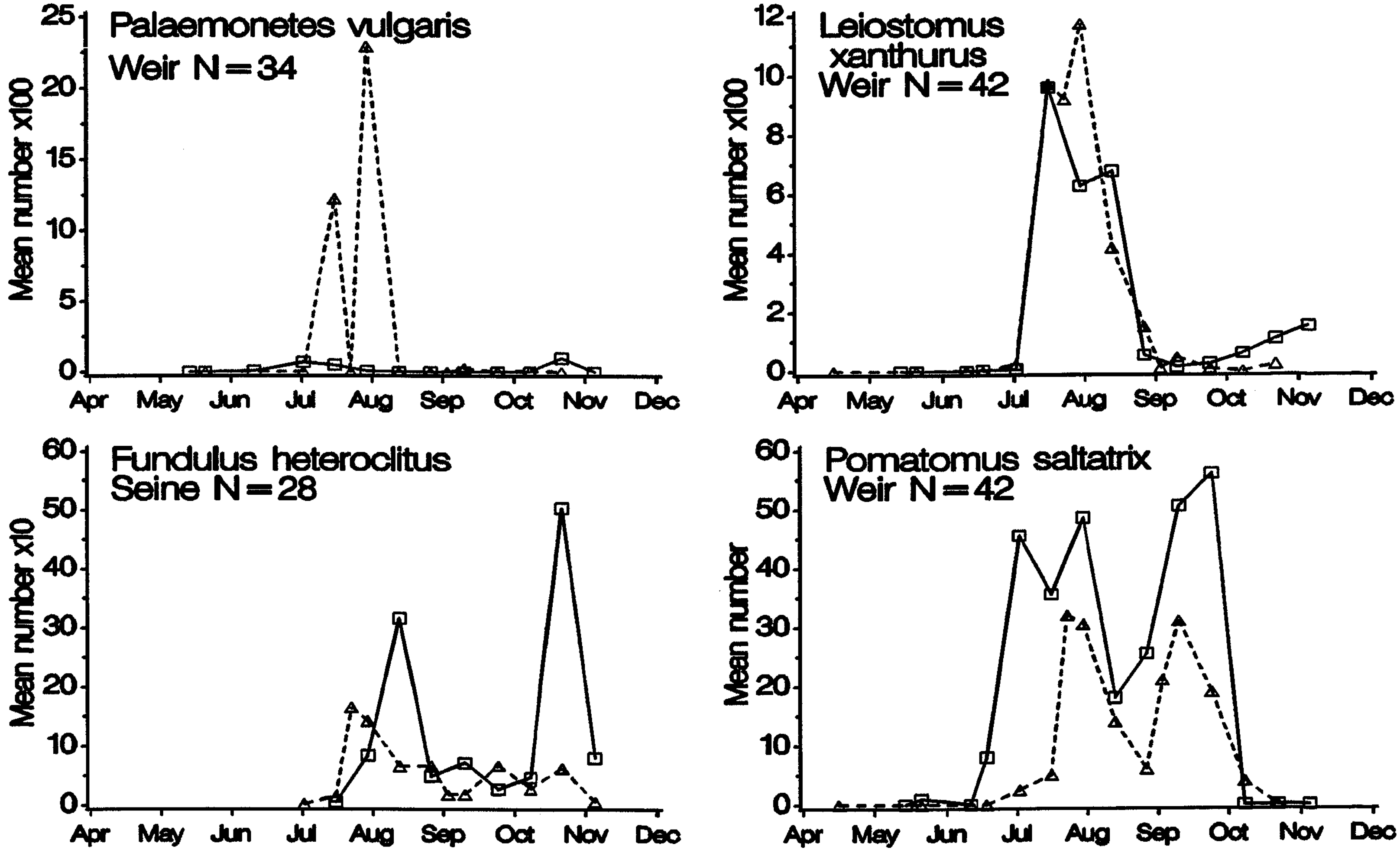


Figure 3.6. Seasonal abundance patterns of selected species and gears from subtidal creek sampling during April-November 1988 (square=day, triangle=night).

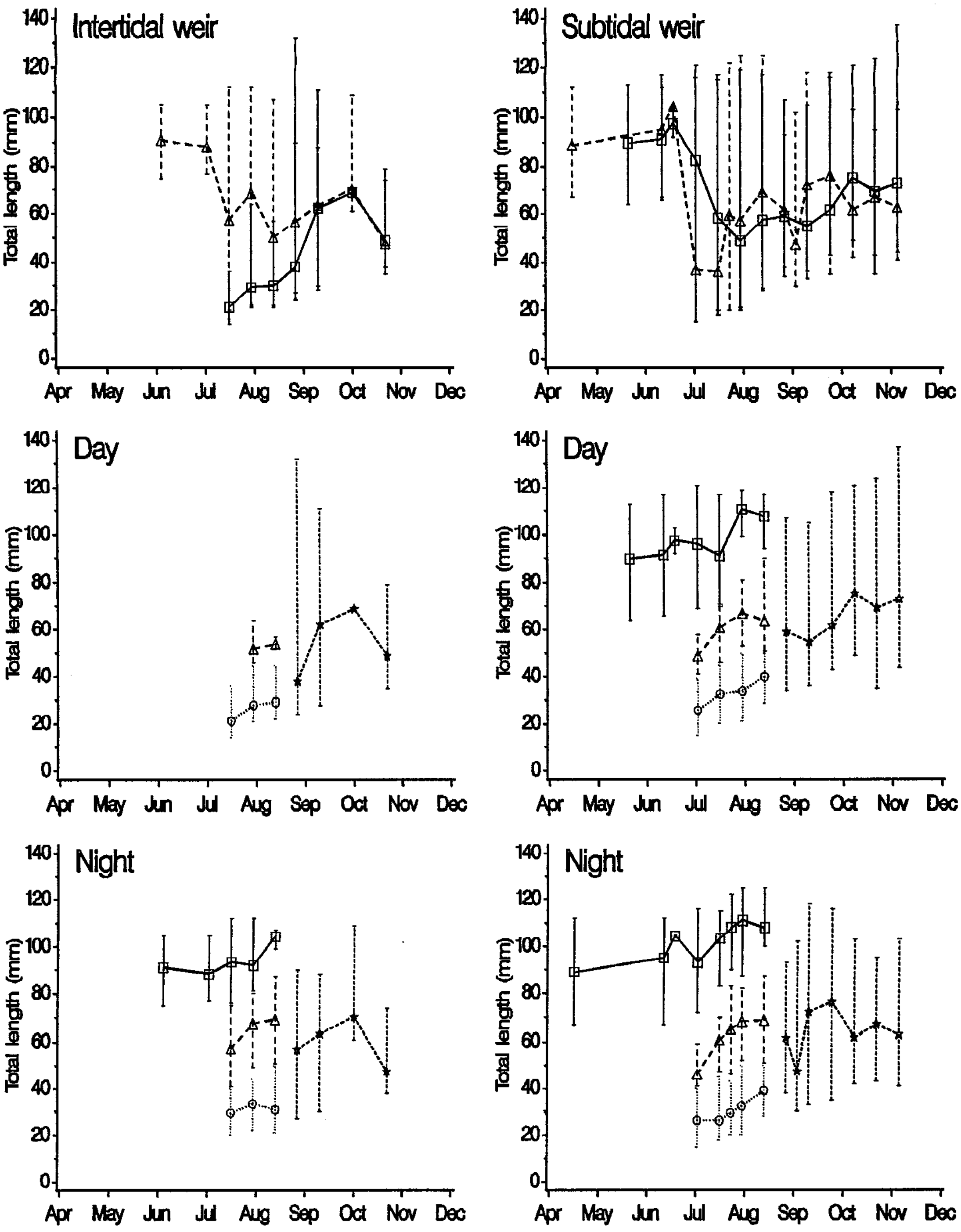


Figure 3.7. Comparison of day and night seasonal patterns in Menidia menidia mean total length (TL) from intertidal creeks during June-October 1989 (n=1743 fish, left column) and from subtidal creeks (weir and seine pooled) during April-November 1988 (n=4554 fish, right column). Overall mean length by day (squares) and night (triangles) are shown in the top graphs, while mean length by size cohort (adult = square, first YOY cohort=triangle, second YOY cohort=circle, unknown cohort=star) for day and night samples are shown in the center and bottom graphs, respectively.

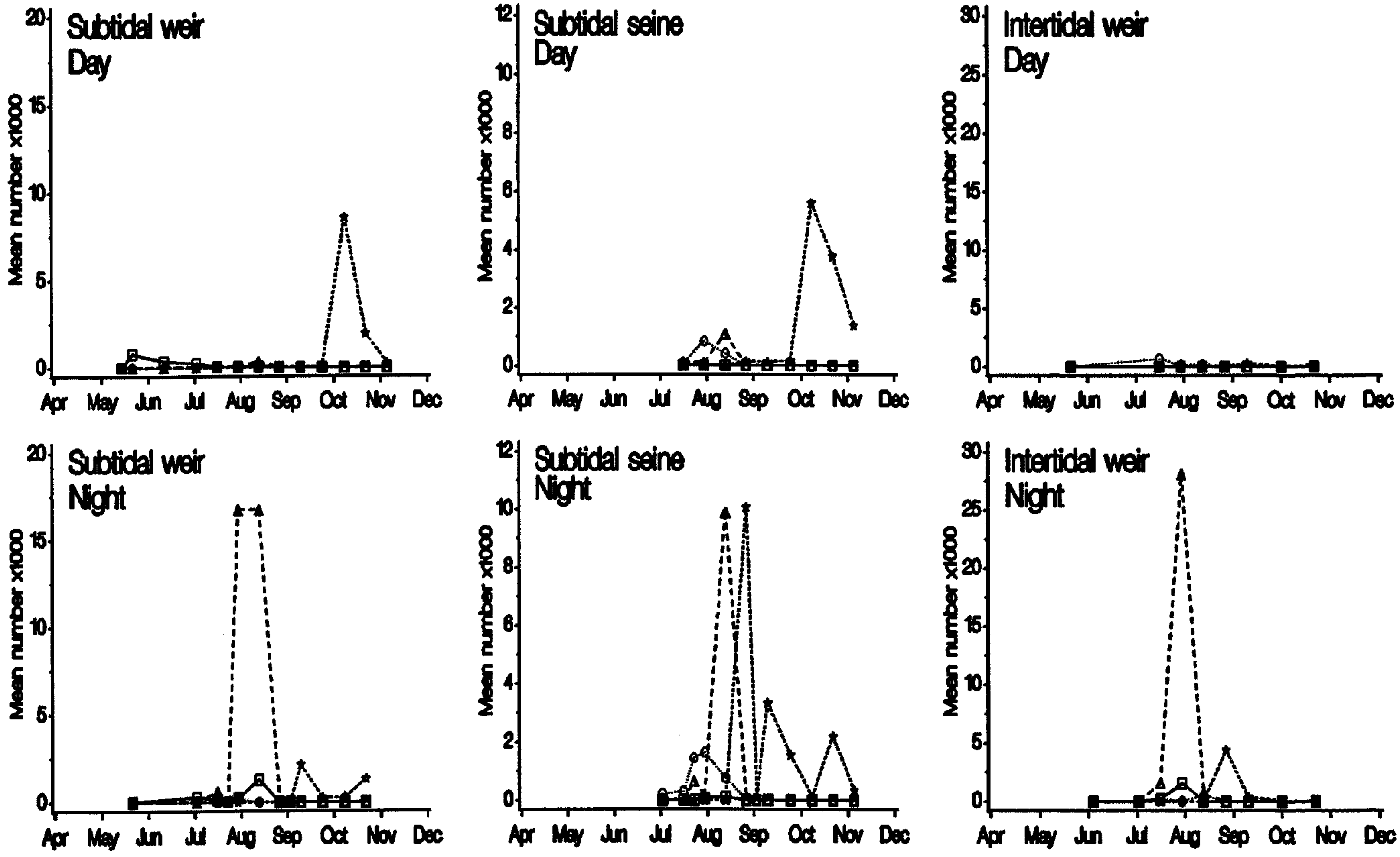


Figure 3.8. Seasonal <u>Menidia menidia</u> mean abundance for each size cohort (square=adult, triangle=first YOY cohort, circle=second YOY cohort, star=unknown cohort) by gear and day and night.

Chapter 4. Foraging habits, growth, and temporal patterns of salt marsh creek habitat use by juvenile summer flounder in New Jersey

Abstract

Summer flounder, Paralichthys dentatus, were collected from intertidal and subtidal polyhaline marsh creeks in the Great Bay-Little Egg Harbor estuarine system in southern New Jersey from 1987 through 1990 to determine seasonality, duration of creek use by individuals, emigration rate, foraging habits, and daily growth rate of young-of-year (YOY) fish utilizing marsh creeks. A total of 458 YOY individuals (mean, 238 mm total length; range, 156-312 mm TL) were collected from a combination of weir, seine, gill net, and gig sampling methods. They were available to the collecting gear from late July through October, with peak numbers in September. Sixty-three (39%) of 162 tagged YOY summer flounder were recaptured at least once during August-September. The average period of creek use was estimated at 17 d (range, 5-38 d) from release. Decline in percent recaptures suggested an emigration rate of 1.0% d^{-1} with 100% emigration within 50 days of release during August-October. Summer flounder appear to undergo tidal movements in and out of the creeks. Average growth rate predicted by length frequency analysis was 1.7 mm TL d^{-1}, whereas growth rate measured directly from tag recaptures

averaged 1.3 mm TL d^{-1}.

Summer flounder preyed on creek fauna in order of prey abundance, with the fishes Menidia menidia, Fundulus heteroclitus, and shrimps Palaemonetes vulgaris and Crangon septemspinosa contributing most significantly to their diet. Stomach fullness of fish captured leaving the creeks on ebb tide was significantly greater than that of fish captured entering the creeks on flood tide, suggesting that summer flounder undergo tidal movements to take advantage of high concentrations of prey available in the creeks. These analyses provide compelling evidence that salt marsh creeks in southern New Jersey are important nursery habitats for YOY summer flounder.

Introduction

It has recently become apparent that summer flounder, Paralichthys dentatus, use Mid-Atlantic Bight estuaries as nurseries (Able et al. 1990; Szedlmayer et al. 1992), as is well known for South Atlantic Bight estuaries (Powell and Schwartz 1977, Gilbert 1986). However, despite the great importance of summer flounder to recreational and commercial fisheries in the eastern United States (particularly in the Mid-Atlantic Bight region), little is known of the specific estuarine habitat requirements of the species (Rogers and Van den Avyle 1983; Gilbert 1986; Grimes et al. 1989). Based on high abundance of summer flounder in preliminary collections in subtidal salt marsh creeks (Szedlmayer et al. 1992, Chapter 1), I hypothesized that marsh creeks are an important habitat for summer flounder in New Jersey estuaries. The goal of this study was to determine patterns of salt marsh creek use by summer flounder. Specific objectives were to determine seasonal abundance, duration of creek use by individuals, growth, and food habits, in order to better understand the role of marsh creeks as nurseries for summer flounder.

Materials and Methods

STUDY AREA

The study was conducted in polyhaline (22-33‰) marsh creeks located within the Great Bay - Little Egg Harbor estuarine complex in southern New Jersey (Fig. 4.1). The unaltered marsh in the study area is dominated by Spartina alterniflora (short form) and Spartina patens, and is characteristic of salt marshes in the northeastern United States (Chapman 1960). The four primary study creeks (Schooner, New, Foxboro, and Story Island creeks) were approximately 1.0 km long, had a single connection with the bay, and received fresh water only through rainwater runoff (Fig. 4.1). Story Island Creek was intertidal except for a shallow (<0.5 m) subtidal cove formed at the mouth at low tide. The other three creeks were subtidal, although Foxboro Creek was generally shallower throughout its length (maximum depth 0.5 m at low tide and 1.1 m at high tide) than either Schooner or New creeks (both the latter with maximum depths of 2 m at low tide and 3 m at high tide). All creeks had a mud bottom substrate and were located 1.3 km to 2.9 km from Little Egg Inlet (for a more complete description of the study creeks see Chapter 1 and 2).

WEIR SAMPLING

A temporary weir was erected at high tide just inside of a creek mouth for each sample event (Chapter 1). The mouth of the creek was entirely blocked off by two wing nets (15.2 m x 3.0 m; 6.4-mm mesh) that ran at an angle from each creek bank to a large weir (1.2 m wide x 3.0 m long x 3.0 m high; 6.4-mm mesh) located in the center of the creek channel. Deployment of the weir and wings began about 30 min before slack high tide and was completed within 1 h. Fish moving out of the creek with the ebb tide were lead along the wings into the weir, where they were trapped by a set of internal doors. At low tide, live fish were removed from the weir through a cod-end after raising the weir above the water line. The weir was removed from the creek after each sampling event.

In an effort to capture fish that did not move into the weir during the ebb tide, seine samples were collected at low tide (immediately prior to hauling the weir) within the approximately 100-m^2 triangular area enclosed by the wings. Prior to making the haul, however, the weir was first closed off by means of a sliding panel to prevent additional fish from being driven into the weir. During 1988, a block net was stretched across the creek at the head of the wings to trap fish within the triangular wing area, and one to three hauls of a bag seine (6.2 m x 1.2 m; 3.2-mm mesh) were made in the enclosed area. During 1989, seining operations were standardized to a single haul with a larger bag seine (18.3 m x 1.2 m; 6.4-mm mesh), which was large enough to completely enclose and "purse in" the area between the wings (hence the additional block net used during 1988 was not necessary). A more complete description of the weir and seine sampling methods are provided elsewhere (Chapter 1).

Preliminary weir sampling was conducted irregularly within Schooner Creek during August-December 1987 (Table 4.1). Intensive weir and seine sampling was conducted approximately fortnightly from April-November 1988 in Schooner and Foxboro creeks, and from April-October 1989 in Schooner, Foxboro and New creeks (Table 4.1). During 1988 consecutive day and night tides were sampled within each creek, while only night tides were sampled during 1989. Day and night tides were those in which at least the last two hours of flood occurred after sunrise or sunset, respectively. During 1988 and 1989 all creeks were sampled within a three-day period during each sampling week.

GILL NET SAMPLING

Gill net sampling conducted during 1989 and 1990 (Table 4.1) had two major objectives: 1) to describe prey composition of summer flounder, and 2) to compare gut contents of fish entering creeks on flood tide with gut contents of fish leaving creeks on ebb tide in order to determine if summer flounder use creeks as a foraging habitat. Sampling was conducted once at Foxboro Creek (August) and once at Schooner Creek (September) during 1989. On each date gill nets (23 m long x 1.8 m high; 38-mm square mesh) were stretched across the width of the creek at the mouth, and at four locations at varying distances upstream, so as to completely block fish passage. A sixth net was placed in the shallow bay near the creek entrance. The upstream nets were eliminated during 1990 sampling, and sampling locations were standardized as follows. One net was set at the mouth of Foxboro Creek, and three nets were set in the bay at 10-30 m from the creek. Two additional nets were set in the mouth of Story Island Creek (Fig. 4.1). However, since the mouth of this creek was wider, the nets did not completely block off the creek entrance. Gill nets were deployed at night between 1600-2200 h at either high or low tide, and were checked repeatedly until 0900-1100 h the next day. Catches of summer flounder were standardized by net-h (number captured/h fished) for each net. Sampling effort was approximately equally divided between ebb and flood tides (298 and 252 net-h, respectively; Table 4.1). By noting which side of the gill net an individual was captured on (upstream or downstream), direction of movement (i.e., into or out of the creek) was determined for 117 summer flounder captured in the creeks.

GIG SAMPLING

On five consecutive nights during September 1990, I searched for summer flounder within marsh creeks using a spotlight. Fish could be observed along the creek banks in water depths of 10-100 cm, and were readily gigged. Data from gigged summer flounder were used to supplement gut content data obtained with gill nets.

TAG-RECAPTURE

Tagging began during August 1989 when summer flounder first appeared in large numbers in the weir samples. Live summer flounder were removed from the weir and brought back to the laboratory in live wells. Total length (TL) and wet weight (WT) were recorded for each individual. Fish were tagged with individually coded yellow t-bar anchor tags (total tag length, 40 mm; Hallprint Pty. Ltd., Holden Hill, South Australia 5088, Australia) and released at the site of capture within 6 h of the weir haul. Fish were tagged just behind the midpoint of the dorsal fin on the left side of the body.

Short-term tag retention and tag-induced mortality were estimated with 39 fish (mean, 220 mm TL; range 188-252 mm TL). These fish were held in outdoor tanks in four groups with running seawater from 6 to 30 d. No mortality or tag loss was observed.

Eight groups of tagged fish (mean, 241 mm TL; range, 188-299 mm TL; $\underline{N}$=162) were released into the creek from which they were captured (Table 4.2). It was possible to recapture tagged fish in nine subsequent weir samples. Lengths and weights of recaptured fish were measured and the fish re-released. Two estimates of the length of creek habitat use by summer flounder were made: 1) the mean length of habitat use by recaptured individuals in days was calculated as the mean number of days between release and final recapture for all recaptured individuals; and 2) a regression of percent recapture data, pooled from all release groups, on days-at-large was used to predict the maximum length of creek use.

The rate of decline in the percent recapture of individuals from each release group in subsequent samples was used as an estimate of the rate of summer flounder emigration from the study area. However, it must be recognized that this estimate assumes no mortality or tag loss, and, hence, may be somewhat inflated.

A correction was applied to percent recapture data that adjusted the data to include individuals that were known to have been missed in a given weir sample based on their recapture in subsequent samples. For example, 20 summer flounder were captured, tagged, and released in Schooner Creek on 15 August 1989 (release group-1; Table 4.2). Nine days later (24 August), five of these tagged fish were recaptured (25%). However, in subsequent samples, six other individuals from release group-1 were captured. It was therefore assumed that these six individuals were "missed" in the Schooner Creek collection taken on 24 August, and obviously had not emigrated from the study area. Hence, on 24 August, the percent recapture was adjusted from 25% to 55% (Table 4.2). Percent recaptures were adjusted for seven of the nine weir samples in which tag recaptures were possible (Table 4.2). Both adjusted and raw percent recapture data are provided.

The percent of individuals from all release groups that were known to have been missed in a given weir sample (based on subsequent recaptures) was determined and used as an estimate of the capture efficiency of the weir. Additionally, gear efficiency was estimated by releasing 10 tagged fish into Foxboro Creek just above the weir during sampling.

GROWTH RATE

Growth rate of YOY summer flounder was measured directly as the increase in TL and weight (WT) from release to recapture divided by the number of days at large. To allow comparison with a recent laboratory study of YOY summer flounder growth (Malloy and Targett 1991), size-specific daily growth rate for weight was calculated as: $G_{WT} = [(\mathrm{Ln}\ WT_{release} - \mathrm{Ln}\ WT_{recapture})/d] \times 100$. Size-specific daily growth rate was similarly calculated for length (G_{TL}). Additionally, absolute growth rates (TL, WT) estimated by regression of fish size (measured live) on date of capture, were determined and compared with actual growth rates measured from tagged fish. Temporal trends in growth rate (absolute and size-specific) were tested with an analysis of covariance (ANCOVA) with creek and week of initial capture as class variables, and with initial size (TL, WT) as a covariate (separate analyses were performed for length and weight).

FORAGING HABITS

Summer flounder collected during gill net and gig sampling were measured live, packed in ice, and transported to the laboratory for freezing. Thawed summer flounder were measured and weighed prior to stomach removal. After the wet weights of the entire gut contents, including mucus and water were recorded, prey items were identified to the nearest taxon, enumerated, and weighed (wet WT).

An index of gut fullness (%full) which incorporates body weight rather than gut capacity (Hyslop 1980) was calculated as:

%full = [(prey WT)/(total body WT - total gut WT)] x 100; where prey WT is weight of a given prey species (or sum of all prey species), total body WT is the weight of the summer flounder, and total gut WT is the weight of the entire gut contents (excluding the stomach itself). This measure allowed a direct statistical comparison of prey consumption between ebb and flood tide that was not biased by summer flounder size.

The effects of tide stage (ebb vs. flood) on frequency of dominant prey items and on gut fullness indices were tested for gill net caught fish with the log-likelihood chi-square test and analysis of variance (ANOVA), respectively (Sokal and Rohlf 1981). The ANOVA was performed on arcsine square root transformed data.

Results

TEMPORAL PATTERNS

Based on size at date of capture (Able et al. 1990; Szedlmayer et al. 1992), a total of 458 of the summer flounder collected in the creeks from 1987 through 1990 were YOY (mean, 238 mm TL; Table 4.1). Young-of-year summer flounder were abundant during 1989 and 1990, however, despite an intensive sampling effort, only one YOY was collected during 1988. They were collected from late July through October, with peak abundance occurring during September (Fig. 4.2 and 4.3). Water temperatures ranged from 15-27°C (mean, 21.7°C; Fig. 4.2) and salinity ranged from 23.5-30.0‰ (mean, 27.3‰) during that period.

The tag recapture study was highly successful with 39% of the tagged fish recaptured (Table 4.2). Eleven (17.5%) fish were recaptured twice, and one (1.6%) was recaptured three times. All but one tag recapture occurred in the same creek in which fish were released. One fish originally tagged in New Creek was later recaptured in Foxboro Creek, which was located 300 m away. The average length of creek use for recaptured individuals was 16.9 d (SE, 1.1; range, 5-38; $\underline{N}$=63) from release. The regression of adjusted percent recapture on days from release (pooled over all release groups), indicated an emigration rate of 1% d^{-1} (Table 4.2, Fig. 4.4). There was no significant difference between the emigration rate estimated from unadjusted and adjusted percent recaptures, and the latter is reported (however, the raw unadjusted and adjusted data used in the regressions is provided in Table 4.2). The X-intercepts from the regression predicts that all summer flounder emigrate from the study area within 50 d. Based on the percentage of missed summer flounder in each weir sample, the weir efficiency was estimated at 65% (SE, 13; N=7 weir samples) of the total number of tagged individuals known to be at large in the study area. With New Creek excluded, because of the low number of tagged summer flounder (N=11), the weir efficiency was estimated at 76% (SE, 9; N=6 weir samples). A similar estimate of gear efficiency was obtained in the gear efficiency trial, as eight of the 10 fish (80%) released into the creek were recaptured.

GROWTH

Summer flounder grew rapidly during the period of marsh creek use, increasing from 170-210 mm TL at first appearance in late July, to 260 mm TL by September (Fig. 4.2). Mean length remained constant at approximately 260 mm TL (190 g Wt) through September. Growth estimated from linear regression of size on date of capture (excluding data after 7 September) was 1.7 mm TL d^{-1} and 3.1 g d^{-1} (Table 4.3). Growth rates measured directly from tag recaptures were 1.3 mm TL d^{-1} and 2.4 g d^{-1} (Table 4.3).

Size-specific growth rates averaged 0.53% TL (SE, 0.02; range, 0.15-0.81) and 1.47% WT (SE, 0.09; range, 0.34-3.62). Growth rates declined significantly (TL, P=0.0197; WT, P=0.0001; ANCOVA) between August (1.5 mm TL d^{-1}; 2.5 g d^{-1}) and September (1.0 mm TL d^{-1}; 1.6 g d^{-1}; Fig. 4.2).

FORAGING HABITS

Small fishes and shrimps were the primary prey of YOY summer flounder (Table 4.4). *Crangon septemspinosa* (sevenspine bay shrimp), *Menidia menidia* (Atlantic silverside), *Palaemonetes vulgaris* (marsh grass shrimp) and *Fundulus heteroclitus* (mummichog) were the dominant prey by percent frequency, mean number, mean weight, and mean percent gut fullness per stomach (Table 4.4). Although *C. septemspinosa* was the most frequent prey item and occurred in the second highest numbers per stomach, it had the lowest mean weight per stomach and percent gut fullness of the four prey species. The average summer flounder (232 mm TL, 144 g WT) contained 1.7 g of total prey corresponding to an average gut fullness of 1.1% of body WT. *Menidia menidia* contributed the greatest prey bulk to stomach fullness averaging 0.5% of body WT and ranging up to 6.9% of body WT. *Fundulus heteroclitus* was the largest (0.8 g/prey) dominant prey species, while *C. septemspinosa* was the smallest (0.1 g/prey).

Prey composition and gut fullness exhibited a seasonal influence. Frequencies of _M_. _menidia_ declined through the study period (61, 21, and 0% in August, September and October, respectively); while those for _C_. _septemspinosa_ rose through the season (13, 51 and 78%, respectively). Gut fullness decreased from 2.7% in August to 1.9% and 1.4% in September and October (_N_=38, 43, and 9, respectively).

Summer flounder foraging habits were strongly influenced by tide stage. Catches (_N_=135) in gill nets were greatest on mid-late ebb and early flood tides, suggesting that summer flounder are most active at these times. Most individuals (_N_=117, 93%) were captured on the current side of nets stretched across the mouth of creeks (i.e., during ebb tides they were captured on the up stream side, while during flood tides they were captured on the bay side), suggesting tidal movement in and out of creeks. Summer flounder caught while apparently entering the creeks with the flood tide had significantly lower gut fullness than those captured leaving the creeks on ebb tide ($P \leq 0.5$; Table 4.5), suggesting that tidal movements result from foraging activity. Frequency and gut fullness for _M_. _menidia_ was significantly higher during ebb tide than flood tide (Table 4.5). Similar trends were observed for _P_. _vulgaris_ and _F_. _heteroclitus_. _Crangon_ _septemspinosa_ was the only common prey species occurring more frequently on flood than on ebb tides.

Discussion

PATTERNS OF MARSH CREEK USE

The abundance and high percentage of recaptures of summer flounder suggests that marsh creeks are an important habitat for YOY of this species. Tag recapture data indicated that some individuals used specific creeks for up to 38 d during the period of availability to the gear (July-October). During this period, summer flounder appear to use creeks as a tidal foraging habitat, based on tidal patterns in gill net collections. Additionally, catches in the passive weir are most easily explained as resulting from tidal movements out of the creeks. This conclusion has recently been confirmed by a telemetry study of YOY summer flounder tidal movements within Schooner Creek (Szedlmayer and Able unpubl. data). Tidal stage had a strong effect on both gut fullness and the contribution of prey species to the diet. The significantly greater gut contents on ebb tide indicated feeding in the creeks. During high water stages of night tides, YOY summer flounder were observed in shallow water along the creek banks as far as 1 km upstream. Stomach contents of individuals gigged in these areas (*N*=27) tended to show no sign of digestion, suggesting recent consumption. The importance of the creeks as a foraging habitat is further suggested by the dominance of species in their diet (i.e., *M. menidia*, *F. heteroclitus*, and *P. vulgaris*), which are characteristic of marsh creek habitat in southern New Jersey (Sogard and Able 1991; Chapter 1). Each of these species were more important in the stomachs of fish captured leaving the creeks on ebb tide than those captured entering the creeks on flood tide, further indicating that creeks are used as a foraging habitat. Similar tidal foraging behavior has been described for the YOY of several other flatfishes (Tyler 1971; Wells et al. 1973; Gibson 1980; Summers 1980; Wirjoatmodjo and Pitcher 1984; Veer and Bergman 1986; Berghahn 1987).

I hypothesize that tidal movements of summer flounder in marsh creeks may partly result from a mechanism for behavioral homeostasis (e.g., behavioral thermoregulation). All study creeks except Story Island Creek had extensive subtidal areas, thus tidal movements do not appear to result from a risk of stranding. Physical conditions in the creeks, however, can change drastically over a diel and tidal cycle (Chapter 2 and 3). During the summer, water temperature can rise as much as 8°C and decline as much as 6°C from high to low tide, while salinity can decrease as much as 7‰, and dissolved oxygen can drop from supersaturation concentrations to below 2 ppm. Although summer flounder could easily tolerate most of these conditions, these rapid environmental fluctuations could have important energetic costs (Miller and Dunn 1980). Because of the lower water volume in marsh creeks relative to the adjacent bay, tidal and diel changes in marsh creeks tend to be greater (Hackney et al. 1976; Chapter 2 and 3). By moving with the tides, summer flounder may be able to remain within the same water mass, and under nearly constant physical conditions. Thus, they would avoid the energetic cost of acclimation to tidal changes in physical conditions. Additionally, by making use of tidal transport, fish may be able to accomplish these movements with very little expenditure of energy. This hypothetical mechanism to maintain homeostasis is supported by a growing body of evidence that some fishes respond to sublethal changes in environmental conditions by moving to maintain a narrow range of preferred physiological conditions (Brett 1971; Beitinger et al. 1975; Major 1978, Olla and Studholme 1978; Clark and Green 1991).

The sudden appearance of YOY summer flounder at relatively large sizes (mean, 214 mm TL; range, 170-240 mm TL) in both weir and gill net collections during late July and early August is puzzling. Post-larval summer flounder are known to immigrate into the Great Bay-Little Egg Harbor estuary from November-May (Szedlmayer et al. 1992), and small numbers of pelagic and settling metamorphs have been collected in Schooner Creek throughout the winter (Able, unpubl. data). Further, early juveniles (< 100 mm TL) were abundant in other marsh creeks sampled during June 1989 in a concurrent trawl survey in the same estuary (Szedlmayer et al. 1992). My failure to capture YOY summer flounder in the study creeks prior to late July was not due to gear selectivity based on fish size. Much smaller bodied fishes, such as *M. menidia*, were abundant in the weir and seine samples, and the morphologically similar winter flounder was commonly collected at sizes less than 80 mm TL (Chapter 1). Similarly, the gill nets were capable of capturing summer flounder ≥ 100 mm TL. Summer flounder are known to reach 100 mm TL by mid-June (Szedlmayer et al. 1992), and therefore, should have been available to the gill nets throughout July, if they exhibit tidal movements similar to that observed during August and September.

The absence of YOY summer flounder in weir and gill net samples taken prior to late July, therefore, suggests two possibilities: 1) YOY do not use the study creeks prior to late July, or 2) YOY remain resident in marsh creeks, but are not collected by the passive sampling methodologies used because they do not undergo tidal movements, and they do not occur near the creek mouth. At the present time, I lack sufficient data to distinguish from these possibilities. However, both of these scenarios suggest a major change in YOY summer flounder behavior in late July. That is, they either begin using marsh creek habitat at this time, or they begin undergoing extensive tidal movements. In the latter case, it may be hypothesized that YOY summer flounder progress from a relatively non-motile creek resident stage as early YOY, to a tidal migratory stage as older YOY, perhaps as a prelude to seasonal emigration from the estuary in the late summer and fall. A similar pattern has been described for the European plaice (Pleuronectes platessa), which remains resident on shallow tidal flats during early YOY stages, but develops tidal migration behavior as they grow larger (Veer and Bergman 1986).

The behavioral change, and consequent increase in the susceptibility of summer flounder to the gear, may have been cued by environmental changes in the creeks during late July. Veer and Bergman (1986) noted that the onset of tidal migration in European plaice appeared to be cued by changes in low tide conditions in early summer (most importantly water temperature and dissolved oxygen concentrations). Although my data are not conclusive, a similar pattern is suggested. Mean low and high tide water temperatures peaked at 26°C in late July (Fig. 4.2). Further, low tide water temperature tended to be greater than high tide water temperature until late July, after which time low tide water temperature tended to be lower than high tide. Since high tide temperature in the marsh creeks reflects the temperature of bay water moving into the creeks with the flood tide, this pattern indicates that bay water tended to be colder than creek water prior to late July, after which time bay water tended to be warmer than creek water. This seasonal transition between high tide (i.e. bay water) and low tide (i.e. creek water) temperatures may serve as an environmental cue for seasonal migration. Deegan (1990) similarly proposed that YOY

Brevoortia patronus (gulf menhaden) emigrate from marsh creek to bay habitat in response to seasonal changes in temperature and productivity between the habitats.

The high annual variation in summer flounder abundance in the creeks (Table 4.2) may result from a high variation in recruitment success of the YOY to estuaries in the Mid-Atlantic Bight. Occurrence of post-larvae in Mid-Atlantic Bight estuaries has been reported to be highly variable among years (Able et al. 1990). It has been suggested that the variation in the timing and duration of critical winter water temperatures may be an important contributor to variable year-class success (Malloy and Targett 1991; Szedlmayer et al. 1992).

GROWTH RATE

Age and growth of summer flounder and determination of size attained during the first year of growth have been problematic (Powell 1982; Rogers and Van den Avyle 1983; Able et al 1990; Szedlmayer et al. 1992). Recently, Szedlmayer et al. (1992) reported that YOY summer flounder in New Jersey reach 200-300 mm TL, with an estimated growth rate of 1.9 mm TL d^{-1}, based on length-frequency data. Tag recapture data provided in this study indicate that summer flounder grow an average of 1.3 mm TL d^{-1}, with growth for some individuals measured as high as 1.8 mm TL $d^{-1.}$ This confirms previously reported high growth rates (based on length frequency analysis) in the Mid-Atlantic Bight (Poole 1962; Able et al. 1990; Szedlmayer et al. 1992).

A unique aspect of this study was that I was able to compare estimates of YOY summer flounder growth based on two methods: 1) linear regression of size (TL or WT) on date of capture, and 2) direct measurement of individual growth from tag recaptures. The growth rate of 1.2 mm d^{-1} estimate through linear regression agreed remarkably well with the 1.3 mm TL d^{-1} growth rate measured from tag recaptures. However, growth rate measured from tag recaptures (1.3 mm TL d^{-1}) was lower than growth rate estimated from linear regression when data after 7 September 1989 was excluded (because the constant mean size after this time suggested emigration of larger individuals) from the analysis (1.7 mm TL d^{-1}). Malloy and Targett (1991) obtained much greater size-specific growth rates (G_{WT}=3.8%) in their laboratory study than I obtained with tag recaptures (G_{WT}=1.5%). This also suggests my tag recapture data may underestimate YOY growth. The lower growth estimate based on tag recaptures may reflect a detrimental effect of the tags, or a tendency for slower-growing fish to migrate later than fast-growing fish. The temporal decline in growth of recaptured fish supports the suggestion that slower-growing individuals remain in the creeks longer (and are thus more likely to be recaptured). However, since the growth of non-recaptured fish is not known, I can not reject the possibility that the decline in growth represents a real seasonal effect on growth rather than differential susceptibility of slow- and fast-growing individuals to recapture.

DIET COMPOSITION

Differences in diet composition between this study and others (Poole 1964; Powell and Schwartz 1979; Smith et al. 1984) may reflect differences in summer flounder size, and differences in prey availability in the specific habitats. Summer flounder fed on creek fauna in order of prey abundance in the creeks, with seasonal shifts in diet reflecting seasonal changes in creek faunal composition. The four dominant prey species in summer flounder stomachs were the four most abundant species reported for the study creeks (Chapter 1). Smith et al. (1984) examined YOY summer flounder from marsh creeks and bay shoals in Virginia that were much smaller (81-160 mm standard length, *N*=28) than those I examined. They reported fish, mysids and *Palaemonetes* spp. as dominant food items. Poole (1964) examined food habits of larger summer flounder (250-650 mm TL, *N*=1210) from Great South Bay, New York and reported *C. septemspinosa* and *Pseudopleuronectes americanus* (winter flounder) as dominant prey species. Powell and Schwartz (1979) examined fish of a size similar to those in my study (92% were under 300 mm TL, *N*=564) from Pamlico Sound, North Carolina. Unfortunately they itemize only major taxonomic prey categories (e.g., Pisces), but indicated that mysids and fish were the most frequent prey.

The abundance and high growth rate of summer flounder observed during this study suggest that marsh creeks are an important habitat for YOY in southern New Jersey from late July through October. In fact, summer flounder are one of the dominant species utilizing the creeks (Chapter 1). Juvenile summer flounder have been collected from marsh creeks over much of the species range including Georgia (Reichert and Veer 1991), South Carolina (Cain and Dean 1976; Shenker and Dean 1979; Bozeman and Dean 1980; C.A. Wenner, South Carolina Marine Resources Research Institute, pers. comm.), North Carolina (Weinstein 1979; Hettler 1989), Virginia (Weinstein and Brooks 1983; Smith et al. 1984; Wyanski 1988), and New Jersey (Able et al. 1990; Szedlmayer et al. 1992). It is clear from these observations, and from the findings made during this study, that salt marsh creeks are an important habitat for YOY summer flounder.

Table 4.1. Sampling effort and total catch of summer flounder collected in selected New Jersey marsh creeks during 1987-1990 (YOY=young-of-year, TL=total length). See Figure 4.1 for location study creeks.

				Number of summer flounder collected		
Year	Gear	Sampling period	Sampling effort	YOY (mm TL range)	Non-YOY (mm TL range)	Total
1987	Weir	Aug, Oct-Dec (irregular day and night)	8 samples	0	51 (267-371)	51
1988	Weir	Apr-Nov Fortnightly (day and night)	42 samples	1 (287)	12 (330-455)	13
	Seine	Jul-Nov Fortnightly (day and night)	32 samples	0	0	0
1989	Weir	Apr-Oct Fortnightly (night)	27 samples	301 (156-310)	0	301
	Seine	Apr-Oct Fortnightly (night)	25 samples	2 (203-244)	0	2

Table 4.1. Continued.

Year	Gear	Sampling period	Sampling effort	Number of summer flounder collected		
				YOY (mm TL range)	Non-YOY (mm TL range)	Total
	Gill net[1]	Aug-Sep (night)	138 net hrs	50 (198-260)	0	50
1990	Gill net	May, Jul-Nov	550 net hrs	78 (169-311)	4 (320-390)	82
		Fortnightly (night)				
	Gig[1]	25-30 Sep.	30 hrs	26 (234-312)	1 (400)	27
		5 consecutive nights				
Total				458 (156-311)	68 (267-455)	526

[1] used in food habits analysis only

Table 4.2. Tag and recapture data for young-of-year summer flounder captured in 12 weir samples from three southern New Jersey subtidal marsh creeks during 1989. Recaptures were possible in nine weir samples taken from 23 August through 17 October. Separate recapture statistics for each release group within the nine weir samples are given (e.g., on 17 October it was possible to recapture individuals from all four Schooner Creek release groups). Data include: days from release to recapture (d free), percent of release group recaptured (% recaptured), and adjusted percent recaptured (adjusted %). The adjusted percent recaptured includes a correction for tagged individuals known to have been missed in a given weir sample based on their recapture in subsequent weir samples. See Figure 4.1 for creek locations.

				Recapture period				
				Statistic: d free, % recaptured, adjusted %				
Creek	Release group	Release date	Original number released	23-25 Aug	5-7 Sep	20-22 Sep	17 Oct	Overall % (number) recaptured
				Weir sample 1	Weir sample 4	Weir sample 7	Weir sample 9	
Schooner	1	15 Aug	20	9,25,55	21,26,32	38,16,16	63,0,0	55 (11)
	2	24 Aug	45	------	12,42,51	29,18,18	54,0,0	53 (24)
	3	5 Sep	27	------	------	17,19,19	42,0,0	19 (5)
	4	22 Sep	15	------	------	------	25,0,0	0 (0)
				Weir sample 2	Weir sample 5	Weir sample 8		
Foxboro	5	18 Aug	14	6,29,50	21,30,30	34,0,0	------	50 (7)
	6	23 Aug	10	------	15,29,43	28,14,14	------	60 (6)
	7	6 Sep	20	------	------	13,35,35	------	35 (7)
				Weir sample 3	Weir sample 6			
New	9	18 Aug	11	8,0,27	22,27,27	------	------	27 (3)
Total tagged			162					39 (63)

Table 4.3. Growth rate of young-of-year summer flounder captured in selected New Jersey salt marsh creeks from July-October 1989, based on linear regression of total length (TL) and body weight (g) on date of capture, and on direct measurement of growth from tag recaptures. Two estimates based on linear regression are given: 1) with all data included, and 2) with data after 7 September 1989 excluded. The latter estimate is provided because mean summer flounder size remains constant after 7 September (see Fig. 4.2), suggesting emigration of larger individuals.

	Linear regression			Tag recapture		
Measurement	Slope (SE)	r^2	N	Mean (SE) mm TL	Minimum, Maximum	N
mm TL d^{-1}	1.2 (0.1)	0.47^{***}	306	1.3 (0.04)	0.3, 1.8	58
(with 7 Sep cut off date)	1.7 (0.1)	0.57^{***}				
g d^{-1}	2.0 (0.2)	0.37^{***}	306	2.4 (0.13)	-0.5, 3.8	58
(with 7 Sep cut off date)	3.1 (0.2)	0.51^{***}	256			

$^{***}P \leq 0.001$

Table 4.4. Food habits of YOY summer flounder (range, 167-305 mm total length; mean, 232 mm TL, *N*=137) collected from August-October 1989 and 1990 with gill nets and gigs in marsh creeks located in southern New Jersey. Percent frequency, mean number, mean weight, and mean gut fullness index are given for all prey species occurring in at least 1% of the stomachs. Empty stomachs (23%, *N*=31) are included in all calculations.

Prey species	Percent frequency	Mean number (SE)	Mean weight (SE)	Mean fullness (SE)
Crangon septemspinosa	38	1.06 (0.16)	0.13 (0.02)	0.13 (0.02)
Menidia menidia	32	1.18 (0.22)	0.72 (0.13)	0.43 (0.09)
Palaemonetes vulgaris	24	0.57 (0.16)	0.15 (0.05)	0.16 (0.06)
Fundulus heteroclitus	16	0.69 (0.24)	0.56 (0.18)	0.30 (0.08)
Unidentified fish	10	0.10 (0.03)	0.02 (0.01)	0.02 (0.01)
Detritus	8	0.08 (0.02)	<0.01	<0.01
Callinectes sapidus	4	0.06 (0.03)	0.01 (0.01)	0.01 (0.01)
Ovalipes ocellatus	3	0.03 (0.01)	0.01 (0.01)	0.01 (0.01)
Isopoda	3	0.03 (0.01)	<0.01	<0.01
Unidentified	1	0.02 (0.01)	<0.01	<0.01
Unidentified crab	1	0.01 (0.01)	<0.01	<0.01
Cyprinodon variegatus	1	0.02 (0.02)	0.02 (0.02)	0.01 (0.01)
Fundulus majalis	1	0.01 (0.01)	0.03 (0.02)	0.01 (0.01)
Gobiosoma bosc	1	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
Total prey	---	3.94 (0.39)	1.68 (0.25)	1.14 (0.13)

Table 4.5. Comparison of prey percent frequency (log-likelihood chi-square test) and mean gut fullness indices (analysis of variance) by tide stage of dominant species consumed by YOY summer flounder (range, 167-305 mm total length, 44-384 g body weight). Summer flounder were captured in selected marsh creeks located in southern New Jersey from August-October 1989 and 1990.

	Ebb tide		Flood tide	
Diet composition	Percent frequency	Mean (SE) fullness	Percent frequency	Mean (SE) fullness
Total contents		2.2 (0.2)*		1.1 (0.3)
Sum of prey		1.4 (0.2)*		0.6 (0.2)
Menidia menidia	36**	0.6 (0.1)*	4	0.2 (0.2)
Paleomonetes vulgaris	26	0.2 (0.1)	17	0.1 (0.1)
Fundulus heteroclitus	17	0.4 (0.1)	4	0.1 (0.1)
Crangon septemspinosa	39	0.1 (0.03)	43	0.2 (0.1)
Empty	23		30	
Number of stomachs	88		23	

*$P \leq 0.05$, **$P \leq 0.01$

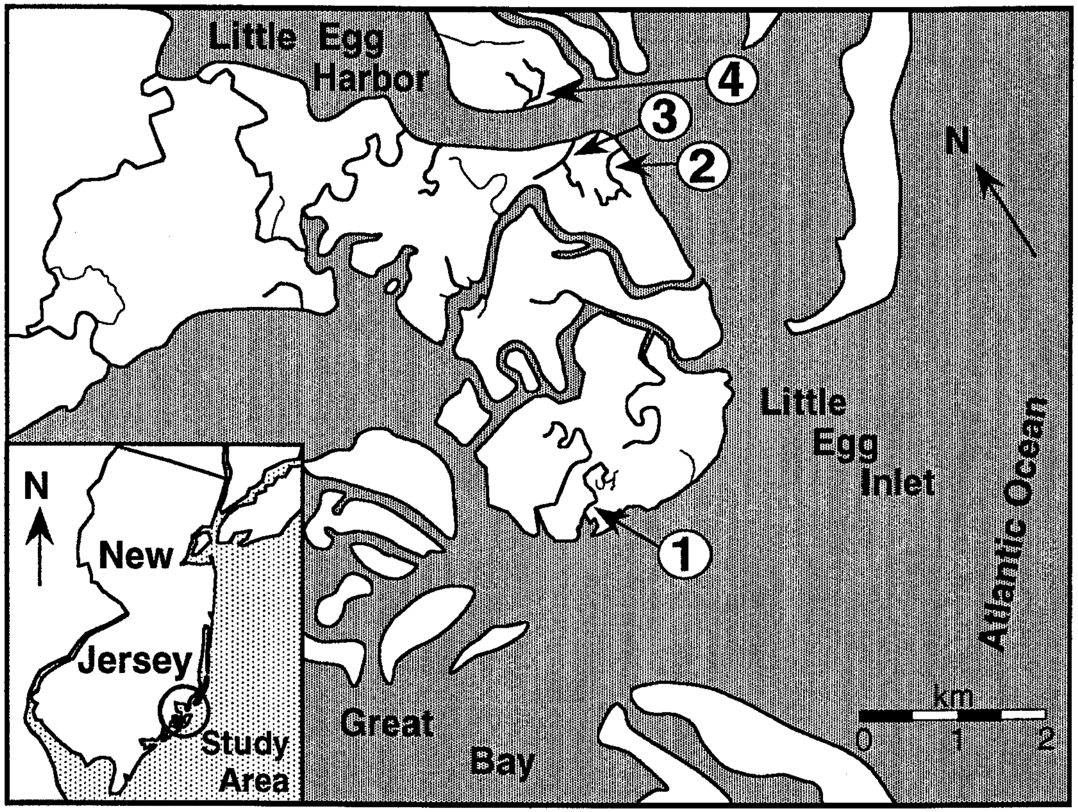


Figure 4.1. Little Egg Harbor-Great Bay estuarine complex and location of study creeks in southern New Jersey. Schooner (1), New (2) and Foxboro (3) creeks were the primary weir sampling sites during 1988-1989. Foxboro and Story Island (4) creeks were regularly sampled with gill nets during 1990.

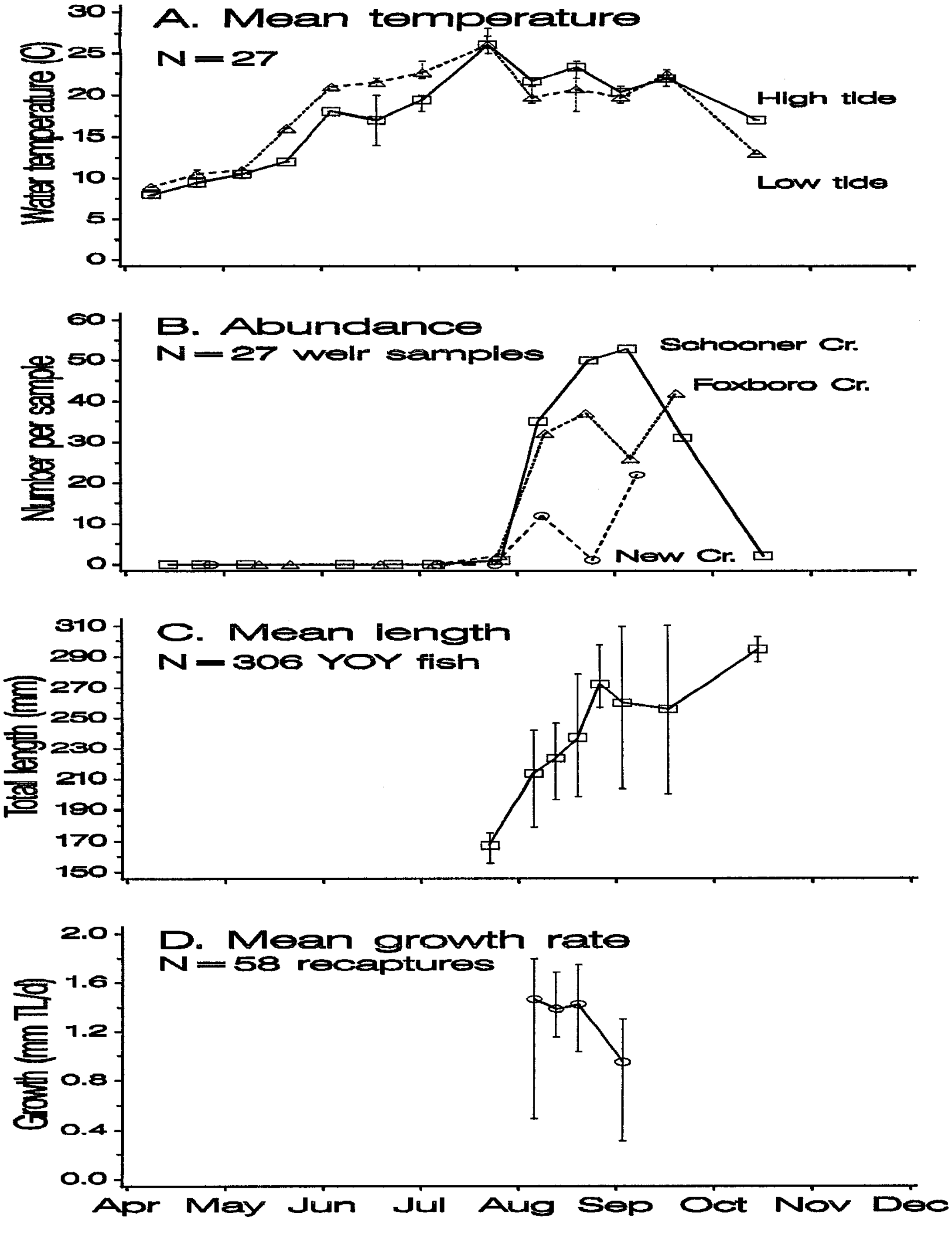


Figure 4.2. Seasonal change in mean water temperature, YOY summer flounder abundance, mean total length, and mean daily growth, based on weir collections (N=27) in Schooner, Foxboro and New creeks during 1989. Abundance is expressed as number per weir sample. Mean water temperatures, total lengths, and growth rates were calculated by pooling all samples made during a collection week; and are graphed by the date of the first day of the week. Vertical bars are ranges.

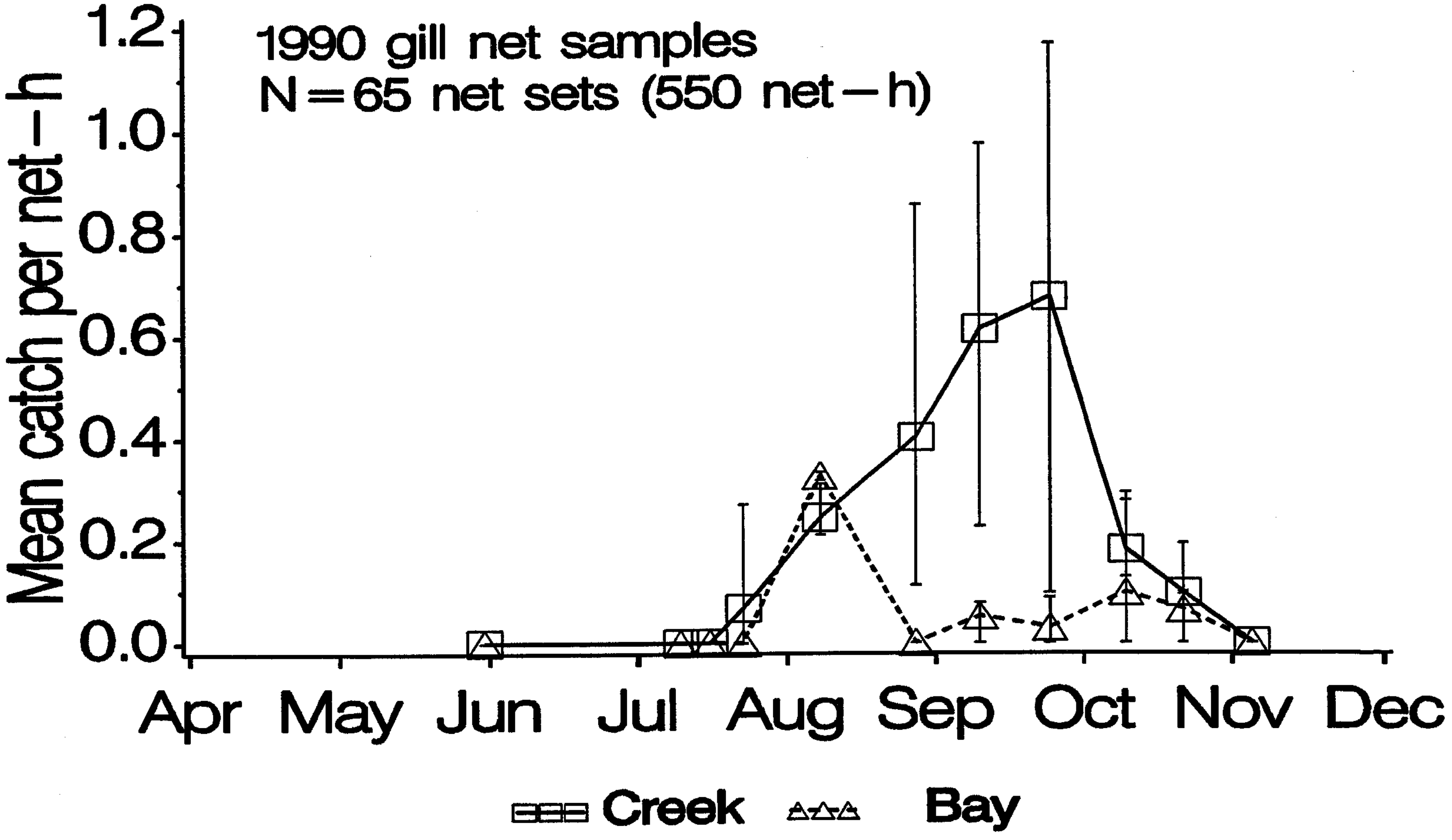


Figure 4.3. Seasonal variation in catch per unit effort, expressed as mean number per net-h, of YOY summer flounder collected with gill nets in marsh creeks and in the shallow bay during 1990. On each sample date, gill nets were placed at Foxboro (N=1) and Story Island (N=2) creek mouths, and in the shallow bay 10-30 m from the mouth of Foxboro Creek (N=3). Vertical bars are ranges.

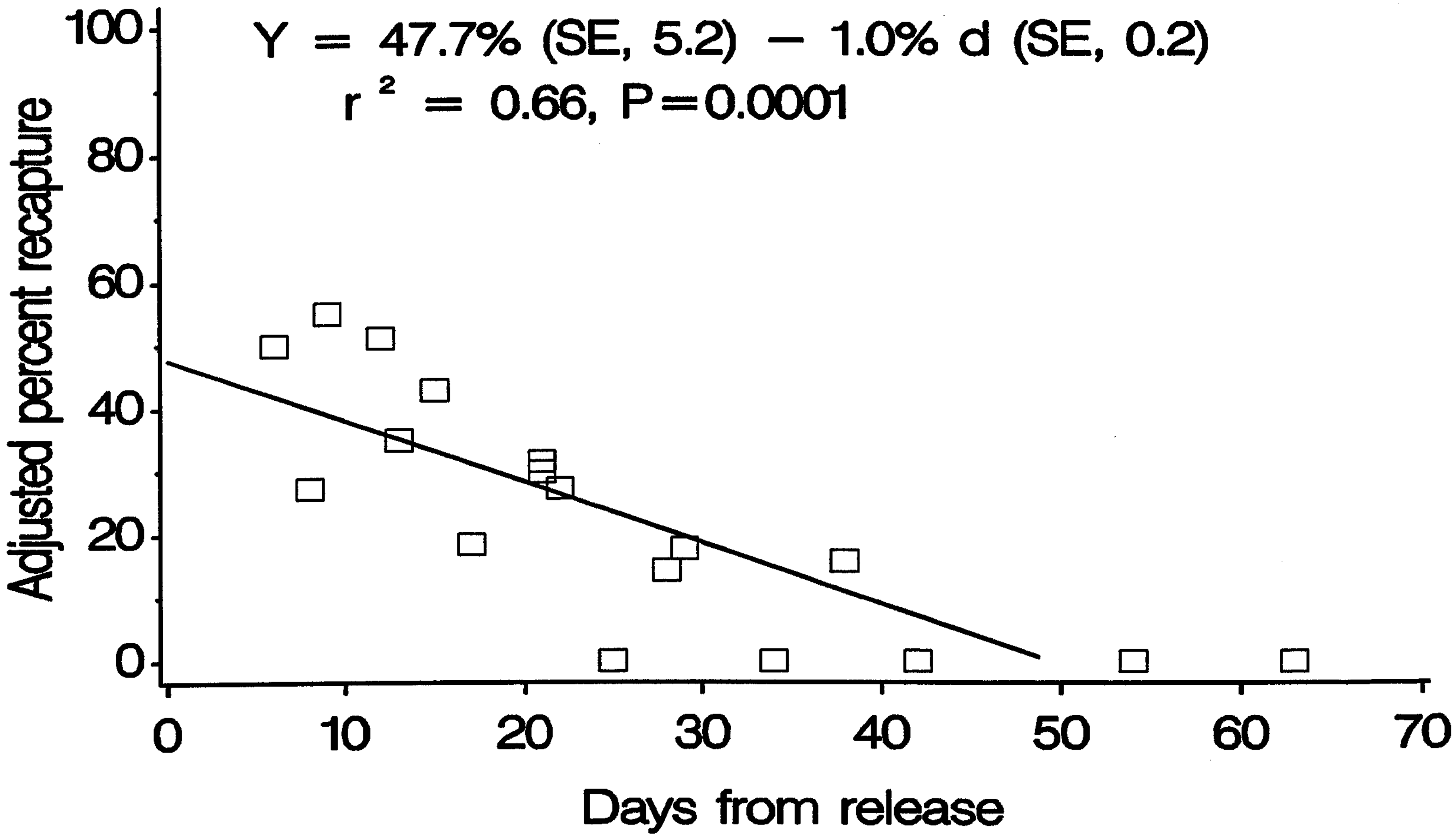


Figure 4.4. Decline in percent recapture with increasing number of days from release of tagged YOY summer flounder (raw data are presented in Table 4.2). Emigration of summer flounder from the study area was estimated by linear regression of adjusted percent recapture on days from release based on data pooled from all eight release groups (N=18). Adjusted percent recapture data are corrected for tagged individuals known to have been missed in a given weir sample based on their subsequent recaptures.

Chapter 5. Patterns in growth and seasonal emigration of fishes utilizing polyhaline subtidal creeks in a New Jersey estuary: role in energy export from the salt marsh.

Abstract

Abundance and size data for 15 fishes which use subtidal marsh creeks in southern New Jersey were examined to determine fish growth rates and seasonal patterns of peak emigration and immigration in marsh habitats. Fishes were collected with weirs and seines from three subtidal marsh creeks located in the Great Bay-Little Egg Harbor estuarine complex from April-November 1988 and April-October 1989. A total of 69 weir and 57 seine samples were collected during fortnightly sampling. Length frequency data were used to classify individuals of fifteen species into size cohorts for which temporal abundance and growth patterns were determined. Temporal patterns of mean abundance and mean size (length and weight) for each cohort were compared to determine periods of emigration and immigration, and size at emigration. Linear regression of length and weight on date of capture was used to determine growth rates of each cohort. In general, young-of-year (YOY) fish grew very fast during a one to three month period of creek use. Growth rates ranged from 0.2-1.8 mm/day (0.1-3.4 g/day). Greatest length growth rates were exhibited by Strongylura marina (1.7-2.1 mmBL/day),

Mustelus canis (1.8 mmTL/day) and Paralichthys dentatus (1.5 mmSL/day), while greatest weight growth rates were exhibited by M. canis (3.4 g/day), P. dentatus (3.1 g/day) and Pomatomus saltatrix (1.1 g/day).

Major pulses of YOY emigration from the creeks occurred from July through mid-September. Two types of emigration patterns were evident: 1) emigration at a specific size (size dependent emigration), and 2) seasonal emigration independent of size. Size dependent emigration appeared particularly important for Menidia menidia, Leiostomus xanthurus, P. saltatrix, and Mugil curema, but may also be important for P. dentatus, Gobiosoma bosci and Pseudopleuronectes americanus. Season dependent emigration appeared most important for S. marina, Clupea harengus, Pollachius virens, and Sphyraena borealis. The most important vectors of energy export from the creeks through emigration are M. menidia, L. xanthurus, Clupea harengus, P. saltatrix, P. dentatus and Mugil curema. Substantial return of biomass to the creek habitat may result from immigration of adults of species such as M. menidia and Anchoa mitchilli in the spring and early summer. Patterns in abundance and growth of YOY fishes utilizing marsh creek habitat in New Jersey estuaries, suggest that seasonal migrations of fishes constitutes a major pathway by which energy is exported from the marsh into coastal waters.

Introduction

Because tidal marsh creeks are a primary interface between the salt marsh and open estuarine waters, and because they provide fish access to the marsh, numerous researchers have pointed to the need for research into the role of marsh creeks as fish habitat and in energy exportation from the marsh (Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Bozeman and Dean 1980, Weinstein et al. 1980, Currin et al. 1984, Weinstein 1984, Weinstein et al. 1984). Tidal marsh creeks have been reported as important nursery grounds within the estuary (Cain and Dean 1976, Shenker and Dean 1979, Weinstein 1979, Bozeman and Dean 1980, Weinstein et al. 1980, Hodson et al. 1981, Weinstein and Brooks 1983, Rozas and Hackney 1984, Rozas and Odum 1987, Chapter 1), and some researchers have suggested that the abundant fishes utilizing the creeks as nursery grounds would effectively transfer large amounts of energy when they undergo seasonal migrations out of the creeks (Currin et al. 1984, Weinstein 1984, Rozas and Odum 1987). However, direct studies quantifying the exchange of energy through immigration/emigration of fishes have been limited (Conover and Ross 1982, Weinstein et al. 1984, Zimmerman and Minello 1984).

The goal of this study was to examine abundance and size data for 15 dominant species which utilize subtidal marsh creeks in a southern New Jersey estuary (Chapter 1) in order to elucidate seasonal patterns of peak energy exchange from marsh creeks through fish movements. Although quantification of the amount of energy exported from marsh creeks through the seasonal movements of fishes is beyond the scope of this study, it was possible to: 1) describe the timing of peak movements in and out of marsh creeks; 2) identify species which contribute most to this type of exchange; and 3) to estimate growth rates of fishes during their period of creek use, and to estimate the size at which some species migrate from the creek (or cease use of the habitat). Growth while utilizing marsh creek habitat, and size at emigration, together with information on temporal abundance patterns, are used to provide an indication of the magnitude of energy export from the creeks which results from fish emigration. Since I have previously suggested that many fishes appear to undergo tidal and/or diel movements in the creeks, and thus may not always be true residents of creek habitat (Chapter 2, 3 and 4), it must be made clear that I am interested in growth during a period of habitat use, rather than strictly during a period of habitat residency.

Materials and Methods

STUDY SITES

The study was conducted within the Great Bay - Little Egg Harbor estuarine complex in southern New Jersey (Fig.

5.1). Fishes were collected from three polyhaline (22-33‰) subtidal marsh creeks with a weir system (Chapter 1). Schooner, Foxboro, and New creeks were chosen because of their similar size and location (Fig. 5.1). All creeks were located 1.3 to 2.3 km from Little Egg Inlet, and were of similar length (930 - 1390 m), and aerial extent (23 - 26 ha subtidal areas).

SAMPLING GEAR AND TECHNIQUES

Sampling was conducted within the creeks over a 3 - 5 day sample week approximately fortnightly from April-November 1988 and April-October 1989 (see Table 1.1, Chapter 1 for monthly sample sizes). During 1988 consecutive day and night tides were sampled from Schooner and Foxboro creeks, while night tides were sampled from all three creeks during 1989. Day and night tides were those in which at least the last two hours of flood occurred after sunrise and sunset, respectively.

A weir (1.2 m wide by 3.0 m long by 3.0 m high, with 6.4 mm mesh) was set to block off the mouth of a creek at high tide and captured fishes leaving the creek with the ebb tide (see Chapter 1 for a more complete description). Two wing nets (15.2 m long by 3.0 m high, with 6.4 mm mesh) were used to block off the mouth of the creek and to lead fishes into the weir. Deployment of the weir was begun about 30 minutes before slack high tide and was completed within on hour. At low tide fish were removed from the weir through a cod-end.

Because the weir is a passive gear which primarily captures animals moving with the tide, seine sampling was also conducted within the creeks to capture less mobile forms and species/individuals which actively avoid the weir and remain within the creeks. Seine samples were collected in the creek above the weir after the weir was closed off at low tide. Regular seine sampling was not initiated until July 1988. During 1988 a block net was stretched across the creek at the head of the wings to contain fishes within the approximately 100 m^2 area enclosed by the wings. Then one haul with a bag seine (6.1 m long by 1.2 m high, with 3.2 mm mesh) was made inside of the wing area. Additional seine hauls were made on an irregular basis to collect additional length-frequency data on species of special interest. During 1989, seining operations were standardized to a single haul of a larger bag seine without the use of a block net. The seine was large enough (18.3 m long by 1.2 m high with 6.4 mm mesh) to allow the entire area enclosed by the wings to be swept with a single "purse" of the seine.

SAMPLE ANALYSIS

A total of 69 weir and 57 seine samples were collected during the study. However abundances of some species were not quantified in some of the early samples (see Chapter 1). Catches from weir and seine samples were put on ice and transported back to the laboratory for sorting and identification. Total abundance and biomass for each species was determined from a 10%-50% (by weight) subsample of the catch. Standard lengths (SL) measured to the nearest millimeter (or in some cases total lengths - TL) of a subsample of up to one hundred individuals of each fish species were measured. Because of frequent damage to the jaw, body length (BL) was measured for Strongylura marina. Individual wet weights (g) were recorded for all species except Anchoa mitchilli, Fundulus heteroclitus, Fundulus majalis, Menidia menidia, and Gobiosoma bosci. However, average wet weight per individual was calculated from the total wet weight of the measured subsample for these species.

Cohort identification

Length frequency histograms of fifteen species for each sample week were examined to identify size cohorts. Raw length data and the length frequency histograms of each of these species is available as an Institute of Marine and Coastal Sciences Technical Report (Rutgers University, in prep.). Cohorts were identified by the presence of distinct length modes. After visual examination of the length frequency histograms, each fish length was assigned a cohort designation based on its length at date of capture.

Cohort abundance

Abundance of each cohort within each sample was estimated by multiplying the cohort's percent frequency in a sample (determined from the measured subsample) by the species total abundance in the sample. Cohort abundances within each paired weir and seine sample were then summed together to obtain a "combined gear" abundance which was used to determine an average pooled over all creeks for each sample week. To examine temporal abundance patterns, mean cohort abundances were graphed by assigning a date to each sample week which corresponded to the date of the first day of week (standardized to the year 1988). Because regular seine sampling did not begin until July 1988, plots of cohort abundances based on combined gear samples exclude data prior to this time. However, abundance data from weir samples taken prior to July 1988 were taken into consideration for several species (e.g., *Pollachius virens*, *Clupea harengus*, *Anchoa mitchilli* and *M. menidia*).

Cohort biomass at peak abundance

Cohort biomass at peak abundance was estimated by multiplying mean individual wet weight by peak mean abundance. This cohort biomass estimate was used to indicate the temporal timing of major pulses of energy export from the creeks, and to compare the relative contributions of each species and cohort to energy export from the marsh.

Cohort growth

Mean size for each cohort and sampling week was determined and plotted against the first day of the week for comparison with cohort abundance data. As similar analyses to compare seasonal diel patterns for Menidia menidia during 1988 was presented elsewhere (Chapter 3), cohort abundance and size data for 1988 will not be repeated here. Growth of fishes utilizing marsh creeks is expressed both as the size attained while utilizing the habitat and as daily growth rate. A comparison of length and abundance data was made to determine the approximate size of fish at emigration from the creeks. Two basic patterns were considered: 1) mean size steadily increased throughout the period of occurrence; 2) mean size increased to a point and then leveled off, or declined, often coincident with either a peak, or a sharp decline in abundance. The tendency for mean fish size to remain constant after a period of rapid increase can result from the completion of growth, size selectivity of gear, selective mortality of large individuals, or from emigration of larger size classes. While the sampling gear and methodology may have been biased against some small size classes (i.e., sizes able to pass through 6.4 mm mesh), gear bias against larger size classes (due to active avoidance of the gear) is unlikely. Therefore, emigration size was considered as the size at peak abundance for species exhibiting the first pattern, while it was considered the size when mean length leveled off (which I refer to as the emigration size threshold) for species exhibiting the second pattern.

Length, and weight by date regression analyses were used to determine growth rates of each cohort. For species exhibiting an apparent emigration size threshold, regression analyses exclude data beyond the date at which size levels off. Annual and inter-cohort variation in growth rates were compared with an Analysis of Covariance (ANCOVA) with year and cohort class variables and date covariate.

Results

CREEK USE PATTERNS

The fifteen species are categorized into two major groups: 1) species for which both YOY and older year classes occur, and 2) species for which only YOY were collected (Table 5.1). In the first category adult size classes were abundant for Menidia menidia, Fundulus heteroclitus, Fundulus majalis and Anchoa mitchilli, but were rare for Strongylura marina (n=14, 240-400 mmBL), Pseudopleuronectes americanus (n=10, 91-186), and Gobiosoma bosci (n=4, 34-55 mmSL). In the second category Mugil curema and Pomatomus saltatrix exhibited two strong YOY cohorts during 1988, while Sphyraena borealis and Clupea harengus exhibited some minor indications of additional YOY cohorts. All other species in the second category, Mustelus canis, Leiostomus xanthurus, Pollachius virens, and Paralichthys dentatus, exhibited a single major YOY cohort.

Size at peak cohort abundance was considered the size at emigration for most species/cohorts (Table 5.1). However, several cohorts exhibited a sharp leveling off of mean size, suggesting a size threshold at which large individuals emigrate from the creeks (Table 5.1, see my comments under individual species below). Species which exhibited an emigration size threshold include: M. menidia (at about 70 mmTL), G. bosci (20 mmSL), P. americanus (80-90 mmSL, 10-20 g), L. xanthurus (75 mmSL, 10 g), M. curema (100 mmSL, 25 g), P. dentatus (210 mmSL, 170 g), and Cohort A of Pomatomus saltatrix (140 mmSL, 70g).

BIOMASS PATTERNS

Most YOY cohorts exhibited peak biomass during July and August, while adult cohorts peaked in May and June.

Menidia menidia was the most important species, with peak adult biomass occurring during May, and peak YOY biomass occurring during early August (Fig. 5.2). Only M. menidia, F. heteroclitus, A. mitchilli and F. majalis were important as adults. The first M. menidia YOY cohorts (A) were the most important single cohorts during both years. Clupea harengus was the most important spring YOY cohort. During 1988, L. xanthurus was the second most important species after M. menidia (cohorts A and unknown), followed by M. canis, S. borealis, and Mugil curema. Clupea harengus was second only to M. menidia during 1989, followed by P. dentatus and the second peak of P. saltatrix cohort A. The second cohort (B) of both M. menidia and P. saltatrix were considerably less important than the first cohort (A).

INDIVIDUAL SPECIES ACCOUNTS

Fundulus spp.

Determination of size cohorts for Fundulus heteroclitus and F. majalis were very difficult. Although at least two adult year classes were present in early spring, there was insufficient data to follow both cohorts through the year. Consequently they have been grouped into a single "adult" cohort for each species. Due to the lack of seine samples prior to July 1988, analysis was performed only on 1989 data. Abundance of the adult cohort peaked in May and June for F. heteroclitus and F. majalis, respectively (Table 5.1, Fig. 5.3). Young-of-year of both species were clearly distinguished from older cohorts and first appeared in mid-June at about 33 mmTL for *F. heteroclitus*, and in early July at about 37 mmTL for *F. majalis*. Peak YOY abundance occurred in July for both species at a size of 37 mmTL and 46 mmTL, respectively, followed by rapid declines to near zero abundances. Growth estimates could not be made for the adult *F. majalis* cohort, but means sizes increased steadily for adult *F. heteroclitus* and YOY of both species. Mean sizes for YOY cohorts did appear to level off by late summer for both species, but abundances were very low at this time. Daily growth rates were similar between adult and YOY *F. heteroclitus* (0.21 and 0.26 mmTL/day), and were lowest for YOY *F. majalis* (0.16 mmTL/day; Table 5.2).

Menidia menidia

A single adult cohort and two major YOY cohorts were apparent during both years. During each year, YOY cohorts A and B were tracked through early August when a major peak in the abundance of cohort A occurred (Table 5.1; Fig. 5.4). At this time cohort A had reached a mean length of 66-67 mmTL (during 1989 and 1988, respectively) and it was not possible to distinguish the few remaining adults from the fastest growing members of cohort A, or the fastest growing members of cohort B from the slowest growing members of cohort A. All subsequent individuals were, therefore, designated as an "unknown" cohort. This cohort was probably mainly an extension of cohort B, but did include a small number of new recruits which continued to enter the catch at least through August. Cohort A was by far the most abundant cohort during 1989. During 1988, cohort A exhibited the greatest abundance peak, but a late fall peak in the unknown cohort was also important (Table 5.1). The extreme peak in cohort A, as well as a second adult cohort peak, which occurred in early August 1989, was due to a single collection of over 230,000 individuals in Schooner Creek. This collection represented only a fraction of what appeared to be a large migrating school which was trapped in the creek by the weir.

Coincident with the strong peak in cohort A abundance was a leveling off of the mean length at about 70 mmTL, strongly suggesting that fish migrate out of the creeks at this size. Cohort A grew significantly faster than cohort B during both years (0.44-0.58 mmTL/day and 0.22-0.33 mmTL/day, during 1989 and 1988, respectively, $p<0.0001$; Table 5.2).

Anchoa mitchilli

Anchoa mitchilli was dominated by adults during each year (Table 5.1; Fig. 5.4). Young-of-year were important only during October 1989 when high catches of older (approximately 60 mmTL) individuals were taken. However, a small number of early YOY (cohort 1988 A) were collected from mid-July (37 mmTL) through September 1988 (47 mmTL). Although adults cohorts exhibited little or no growth, the 1988 YOY cohort grew about 0.25 mmTL/day (Table 5.2).

Gobiosoma bosci

Except for four adults taken in the spring, G. bosci was not collected until mid-July when YOY first appeared. During 1988, YOY first appeared at about 12 mmSL, and peaked in late August at about 20 mmSL (Table 5.1, Fig. 5.7a). Young-of-year appeared to be much larger and less abundant during 1989, but this trend probably resulted from the change in seine net mesh size from 3.2 to 6.4 mm, and therefore growth was not estimated during 1989. During 1988 growth was estimated at 0.22 mmSL/day (Table 5.2).

Pseudopleuronectes americanus

All but ten individuals were considered part of single well defined YOY cohort which appeared in June during each year (most of the larger individuals were collected earlier in the spring). Abundances of the YOY cohorts were similar between years and peaked in mid-July 1988 and mid-August 1989 at 62 mmSL (5 g) and 72 mmSL (11 g), respectively (Table 5.1, Fig. 5.7b, 5.8a). Mean size increased steadily though mid-August when they leveled off during 1989 at about 75-80 mmSL (9-12 g). Mean size did not level off until mid-September 1988 (90 mmSL, 17-18 g). Growth rates were slightly higher during 1988 (0.57 mmSL/day, 0.22 g/day) than 1989 (0.51 mmSL/day, 0.15 g/day; Table 5.2).

Strongylura marina

A single major YOY cohort was observed during both years (Table 5.1, Fig. 5.5), however 14 adults (240-400 mmBL) were collected in August and September of both years (excluded from analysis). Mean size increased steadily through the sampling period. Growth was significantly slower during 1988 (1.7 mmBL/day, 0.5 g/day) than during 1989 (2.1 mmBL/day, 0.7 g/day; ANCOVA $p<0.0001$; Table 5.2). Strongylura marina had the fastest growth in length of any species examined.

Clupea harengus

Peak abundance of C. harengus occurred in May of both years at 60-62 mmSL (Table 5.1). A single collection in May 1989 contained over 8000 individuals, which was only a small portion of a large school trapped in Foxboro Creek by the weir. Growth was estimated at approximately 0.6 mmSL/day during 1989 (Table 5.2), although there was a wide variation in size range (Fig. 5.7c, 5.8b).

Leiostomus xanthurus

Leiostomus xanthurus was one of the most abundant species during 1988, but was present in low numbers during 1989 (Fig. 5.6). A single well defined YOY cohort was observed during each year, first appearing in mid-June at 27-30 mmSL (0.2-0.5 g; Table 5.1). Peak abundance occurred in July of both years at 46-50 mmSL (2.1-3.5 g). Mean length and weight rose rapidly until early August when they leveled off during 1988 at about 75 mmSL (10 g). However, during 1989 length and weight did not level off, but climbed steadily throughout the period. Growth rate was significantly slower during 1988 (0.92 mmSL/day, 0.32 g/day) than during 1989 (1.39 mmSL/day, 1.07 g/day; ANCOVA $p<0.0001$; Table 5.2).

Mugil curema

Abundance of Mugil curema was strongly bimodal during 1989 when the species was most abundant. Abundances were lower during 1988, but two cohorts were present (Table 5.1, Fig. 5.6). Mugil curema first appeared in early June (cohort 1989 A) and July (cohort 1988 A) at about 27 mmSL (0.5 g). Cohort B appeared in early September 1988 at about 70 mmSL and was captured into November (Fig. 5.6). Mean length and weight of cohort A increased rapidly until late August when size leveled off, particularly during

1989. Although growth in length was not significantly different between years (0.9 mmSL/day; Table 5.2), growth in body weight was significantly slower during 1989 than 1988 (0.33 and 0.42 g/day, respectively). Growth could not be estimated for cohort B because of the low sample size.

Mustelus canis

Small numbers of early YOY M. canis were collected in the creeks during both years, however, peak catches occurred a month earlier in 1989 than 1988 (Table 5.1, Fig. 5.7d, 5.8c). Few individuals were collected after mid-July. Mean length and weight increased through the capture period, with no indication of leveling off. Mustelus canis exhibited the fastest biomass growth rate (3.4 g/day) and second fastest length growth rate (1.8 mmTL/day) of the species examined (Table 5.2).

Paralichthys dentatus

Young-of-year P. dentatus were only collected during 1989. They appeared suddenly in late July at 177 mmSL (101 g), grew very rapidly to 213 mmSL (167 g) at peak abundance in mid-September (Table 5.1, Fig. 5.7e, 5.8d). Mean size leveled off at about 210-220 mmSL (160-190 g) in September. Summer flounder had the second highest biomass growth rate (3.0 g/day) and third highest length growth rate (1.5

mmSL/day, Table 5.2).

Pollachius virens

Small numbers of P. virens were collected during the spring of 1988 and 1989 beginning in April at about 50 mmSL (Table 5.1, Fig. 5.7f, 5.8e). Peak abundance occurred in May 1988 at 70 mmSL. Mean size rose steadily throughout the period of occurrence, with growth estimated at 0.9 mmSL/day pooled over both years (Table 5.2).

Pomatomus saltatrix

Abundance of P. saltatrix was strongly bimodal during 1989 when a single YOY cohort was present (Table 5.1, Fig. 5.6). Two equally abundant cohorts were present during 1988. Cohort A appeared in early June during 1989 at 71 mmSL (5.7 g), and in mid-June during 1988 at 50 mmSL (1.1 g). During 1988 cohort A peaked in late July at 74 mmSL (6.7 g), but declined when cohort B appeared. The 1989 cohort had a slightly earlier first peak at a size of 66 mmSL (4.7 g), declined in early August, but then climbed to a major peak in late September at 143 mmSL (58 g). Mean length and weight of cohort A increased steadily to a peak in early September after which time it declined. Mean length and weight of cohort B exhibited much less increase. There were significant (ANCOVA $p<0.0001$) differences in growth among all three cohorts (1989 > 1988 A > 1988 B; Table 5.2).

Sphyraena borealis

Sphyraena borealis appeared in July during 1988 and June during 1989 at about 70 mmSL (2 g) and grew rapidly to 100-134 mmSL (7-16 g) during August abundance peaks in 1988 and 1989, respectively (Table 5.1, Fig. 5.7g, 5.8f). Growth rate was not significantly different between years and was estimated at 1.2 mmSL/day, or 0.3 g/day (pooled over both years, Table 5.2).

Discussion

Categorization of marsh fauna into resident and seasonal species is somewhat difficult and misleading. For example, although M. menidia is often considered a marsh resident in southern marshes, it is a seasonal resident in northern estuaries (Conover and Ross 1982) including New Jersey (herein, Chapter 1). In contrast, Paralichthys dentatus is generally considered a seasonal component of Mid-Atlantic Bight estuaries, yet individuals at different life history stages (post-larvae through late YOY) can be collected in New Jersey marsh creeks throughout the year (Able et al. 1989, Szedlmayer et al. 1992, Chapter 4). Similar problems occur when one attempts to categorize fauna into resident and nursery species. Often a species is considered to use estuarine habitats as a nursery, despite the fact that adults are also common in the habitats (e.g. the blue crab *Callinectes sapidus*, and fishes *Cynoscion regalis* and *Leiostomus xanthurus*).

I have attempted to avoid some of these problems by identifying species which occur only as YOY in the creeks (Table 5.1). These species (*M. curema*, *P. saltatrix*, *S. borealis*, *C. harengus*, *M. canis*, *L. xanthurus*, *P. virens*, and *P. dentatus*) clearly use marsh creeks in New Jersey as nursery habitat. The rarity of adult *S. marina*, *P. americanus*, and *G. bosci* suggests that these species also use marsh creeks primarily as nursery habitat (Table 5.1), though the latter species may simply be an annual species with high winter mortality. The high abundance of both adult and YOY cohorts for *M. menidia*, *F. heteroclitus*, *F. majalis* and *A. mitchilli* in marsh creeks suggests these species may be true seasonal or permanent marsh residents (as opposed to nursery species). However, failure to consider individual cohorts for each species can lead to further confusion. For example, although *M. menidia* is abundant in New Jersey marsh creeks from April through November (Chapter 1), spring populations consist of spawning adults, while multiple YOY cohorts appear to undergo successive waves of migration out of the creek habitats as they reach 60 mmTL throughout the summer and fall (see discussion below). In many ways, then marsh creeks might be considered a seasonal nursery habitat for *M. menidia*. This pattern is masked by the continuous high abundance of the species from spring through fall.

In order to describe patterns of energy exchange between marsh creek and other habitats resulting from seasonal fish movements, it is necessary to consider movement patterns of both adult and YOY fishes, as well as of individual YOY cohorts.

SEASONAL ABUNDANCE PATTERNS

In general, few fishes appear to be year round residents in New Jersey marsh creek habitat (Chapter 1). I have, however, collected *F. heteroclitus*, *F. majalis*, *Cyprinodon variegatus*, *Menidia beryllina* and *M. menidia* during the winter (unpublished data), though only *F. heteroclitus* was abundant. Because of the highly seasonal nature of the fish fauna, seasonal export of energy from the marsh through fish migrations may be particularly important in northern marshes.

The growing season for most species/cohorts of fishes using New Jersey marsh creeks is relatively short; with most cohorts emigrating by late August or September (Fig. 5.2). Species which spawn within the estuary had the longest growing seasons, though specific cohorts of even these species exhibited restricted periods of peak abundance in the creeks. For example, *F. heteroclitus* was present throughout the sampling period, but YOY were abundant only during July. Young-of-year of many species exhibited sharp peaks in abundances, with high catches occurring over periods of one or two months (*F. heteroclitus*, *F. majalis*, *M. menidia* cohorts A & B, *C. harengus*, *M. canis*, *P. dentatus*, *P. virens*, *L. xanthurus* and *S. borealis*). The period of peak abundance for most of these species appears to represent the period of maximum emigration from the creeks, particularly for those captured primarily by the weir (e.g., *M. canis*, *P. dentatus*, *P. virens* and *L. xanthurus*, see Chapters 1 & 2). Catches of YOY *F. heteroclitus* and *F. majalis*, however, were primarily in the seine and probably represent peak movement into subtidal areas of the creeks from intertidal areas, and from the marsh surface.

Menidia menidia, *F. heteroclitus*, *F. majalis* and *A. mitchilli* were the only species abundant as adults, most of which had peaks during May and June (Table 5.1, Fig. 5.2). Peak adult abundance probably reflects the period of peak spawning. Peaks in adult abundance of the seasonal species *M. menidia* and *A. mitchilli*, may represent a peak of biomass importation into marsh creek habitat.

GROWTH PATTERNS

In general YOY fish grew very fast over a short time period with cohort growth rates ranging from 0.16-1.79

mm/day (Table 5.2). Of the ten species for which weight data was obtained, cohort growth rates of 0.1-3.4 g/day were found. Except for Mustelus canis (1.8 mmTL/day) and Strongylura marina (1.7-2.1 mmBL/day), YOY of estuarine spawners typically had slower growth rates (ranging from 0.16-0.58 mm/day, averaging 0.35 mm/day for 6 species/10 cohorts) than species which spawn on the continental shelf (0.6-1.5 mm/day, averaging 1.0 mm/day for 8 species/11 cohorts; Table 5.2). Werme (Werme 1981, Teal 1985) suggested that fishes which are resident within the marsh grow more slowly than those which use the marsh on a seasonal basis. She suggested that seasonal species use the marsh as an intensive foraging habitat during a period of rapid growth during highly vulnerable early juvenile stages, prior to migration to offshore habitats. Resident species, alternatively maintain a slower, but more constant growth throughout the year.

However, differences in growth between marsh species and offshore spawners, may result from biases related to fish size. Greatest growth rates determined during this study tended to occur in the largest species (i.e., M. canis, P. dentatus, S. marina and P. saltatrix). Therefore, the more extensive data provided, herein, suggests that Werme's findings may have resulted from a correlation of growth rate with fish size, rather than with habitat use patterns. A comparison between resident and seasonal, or between estuarine spawners and marine spawners, of growth standardized by average adult body size, would probably reveal similar growth rates between these fish groups.

Growth rates varied between years and cohorts, generally growth tended to be highest during 1989 and for early cohorts relative to late cohorts within a species (Table 5.2). Length and weight growth rates were significantly higher during 1989 for P. saltatrix, L. xanthurus and S. marina. Growth in weight was significantly higher during 1988 for M. curema, and tended to be higher during 1988 for M. menidia and P. americanus. At the same time Cohort A was the fastest growing cohort for M. menidia during both 1988 and 1989, and for P. saltatrix during 1988. If these differences are real, two possible causes can be hypothesized. First, lower water temperatures may account for slower growth rates of several species during 1988. Anomalous upwelling activity off the New Jersey coast resulted in record low water temperatures throughout August 1988 (J. Eberwine, National Weather Service, Atlantic City, NJ, Pers. comm.). In fact, temperatures as low as 9 C were recorded in the Great Bay-Little Egg harbor estuary, on several occasions during this period (pers. observ.). Interestingly, during 1988 mean P. americanus size steadily increased until mid-September, while during 1989 mean size leveled off sharply in early August (Fig. 5.7b, 5.8a). This pattern could have been caused either by a decline in growth during the late summer in 1989 due to high water temperatures, or by the delay of emigration during 1988 due to the cooler summer temperatures.

Alternatively, density effects may have influenced growth rates, particularly for M. menidia, L. xanthurus and P. saltatrix. Growth rates of the second cohorts of M. menidia and P. saltatrix were much slower than their first cohorts (cohort A), perhaps because of increased crowding and resource competition. Additionally, both cohorts of M. menidia grew more slowly during 1989, when overall M. menidia abundance was higher, than during 1988 (Table 5.2). Other studies have noted slower growth of later M. menidia cohorts (Barkman et al. 1981), which Bengston (1984) has suggested may be caused by a reduced food supply.

Similarly, during 1989, L. xanthurus reached a much larger size, grew more rapidly, and mean size increased steadily throughout the season. However, during 1988 when abundances were much greater, L. xanthurus reached a much smaller size, grew more slowly, and mean size leveled off sharply by mid-August. Although Weinstein and Walters (1981) did not observe a strong emigration size threshold, they did report strong differences in L. xanthurus growth in North Carolina marsh creeks during 1977 and 1978, but attributed these differences to water temperature effects. However, they also reported strong monthly differences in YOY growth rates and a depression in growth during July of 1977, which they attributed to high water temperatures.

They concede however, that this depression may have resulted from size related migrations. Dawson (1958) summarized data on L. xanthurus and found that estimates of size at age 1 ranged from 60-80 mmSL in New Jersey (Welsh and Breder 1923) to 160 mmSL in Virginia (Pacheco 1957). Much of this variation may result from annual and intercohort growth differences.

EMIGRATION PATTERNS

Most of the major pulses of migrations from the creeks, inferred from periods of peak abundance, occur from July through mid-September (Fig. 5.2). Therefore, emigrations from marsh creek habitat do not necessarily occur at the same time of emigration from the estuary itself. In fact, large numbers of fishes emigrate from the creeks long before fall offshore migrations are thought to occur (see citations below). For example, although substantial emigrations of M. menidia from New Jersey marsh creeks clearly occur in mid-summer (August, this study), offshore migrations do not occur until late fall (November-December) in the Mid-Atlantic Bight (Richards and Castagna 1970, Conover and Murawski 1982, Conover and Ross 1982, Warkentine and Rachlin 1989). Once they leave the creeks many other species also ultimately migrate out of the estuary to over-winter offshore, including C. harengus (Bigelow and Schroeder 1953), P. dentatus (Grosslein and

Azarovitz 1982, Szedlmayer et al. 1991), S. marina (see discussion in Hardy 1978), P. virens (Clay et al. 1989), and S. borealis (Smith 1898, Houde 1972). Other species may additionally continue to migrate down the coast to more southern latitudes, including A. mitchilli (Vouglitois et al. 1987), L. xanthurus (Chao and Musick 1977), M. curema (Anderson 1957, Collins and Stender 1989), P. saltatrix (Kendall and Walford 1979) and M. canis (Azarovitz et al. 1985). These migrations result in the exchange of energy in the form of fish biomass between the estuary and coastal waters, and even between widely separate coastal regions (such as between the Mid- and South Atlantic Bights).

Some estuarine species may exhibit seasonal migrations within the estuary, either between upper and lower regions, or between shallow and deep water habitats, including F. heteroclitus (Fritz et al. 1975, also see discussion in Hardy 1978), F. majalis (Tracy 1910, Hardy 1978), and G. bosci (Dahlberg and Conyers 1973), thereby accomplishing energy exchanges among estuarine habitats.

Growth and abundance patterns observed during this study reflect two basic emigration patterns: 1) size dependent, and 2) season dependent (size independent). Species may exhibit one or both of these patterns.

Size dependent emigration

The sharp leveling off of mean size exhibited by many species/cohorts during this study is best explained as resulting from size dependent migration. In New Jersey, size dependent emigration appears particularly important for *M. menidia*, *L. xanthurus*, *P. saltatrix*, and *M. curema*, but may also be important for *P. dentatus*, *G. bosci* and *P. americanus* (Table 5.1). In size dependent emigration, fish leave the creeks upon reaching a critical size threshold regardless of the time of year. This tendency for larger individuals to emigrate or "bleed off" out of marsh creeks has been reported for *Brevoortia patronus* (Deegan 1990), *L. xanthurus* (Weinstein et al. 1980, Weinstein and Walters 1981, Weinstein 1983, Weinstein and Brooks 1983, Weinstein et al. 1984), and *M. menidia* (Conover and Ross 1982). Similar size related migrations have also been reported for other estuarine fishes, including *Girella nigricans* (Norris 1963), *Micropogonias undulatus* (Yakupzack et al. 1977), and *Mugil cephalus* (Major 1978). In New England, *M. menidia* were reported to begin dispersing from marsh creeks to open bay areas in late July-early August at a size of 60-70 mmTL (Conover and Ross 1982), agreeing well with observations made during this study.

Despite the apparent great importance of size dependent migrations to estuarine fishes, little is known of its importance in energy exportation from the marsh. Deegan (1990) hypothesized that seasonal changes in productivity and temperature, combined with increased metabolic demands of larger fish, accounts for size related migrations of estuarine fish. Alternatively, Major (1978) in his study of _Mugil_ _cephalus_ suggested that size stratification among habitats functions to reduce intraspecific competition for food and space in the shallow intertidal zone. More importantly, he presented evidence that the stratification is cued by ontogenetic changes in environmental stress tolerances. Pre-juveniles enter the estuary and select the shallowest intertidal habitats with near lethal environmental conditions. As it grows _M._ _cephalus_ becomes increasing sensitive to environmental stress and begins to move into deeper, less stressful water. Miller and Dunn (1980) expanded on these ideas to suggest that ontogenetic changes in response to environmental cues may be important governors of migration and foraging movements of estuarine fishes. In other words sequential migrations among habitats, and ultimately emigration from the estuary, may be governed by changes in environmental tolerances/preferences with growth. This mechanism would insure intraspecific resource partitioning and movement into suitable habitats with growth.

Season dependent emigration

Seasonal dependent migrations, where seasonal environmental cues trigger migration for all individuals regardless of size, are better known than size dependent migrations. Species which exhibit a steady increase in size until disappearing from collections probably best fit this pattern (e.g., S. marina, C. harengus, P. virens, and S. borealis). Seasonal dependent emigration, however, is probably important to some degree in all species. For example, even small individuals of M. menidia migrate from the creeks during the late fall to avoid winter temperatures (Conover and Ross 1982). Similarly, declines in means size at the end of the season for P. saltatrix and P. dentatus may result from a final emigration pulse of smaller individuals. Emigration at a smaller size by later cohorts of P. saltatrix and M. curema (cohort B) during 1988 relative to the earlier cohorts (A) may be examples of season dependent migration over-riding size dependent migration behavior.

PATTERNS OF ENERGY FLUX THROUGH FISH MOVEMENTS

Immigration

Energy exchange between the marsh and adjacent estuarine waters can go both ways. Energy can be imported into the creeks through immigration of early life history stages (chiefly the larvae and early juvenile stages), or through the return of spawning adults. Those that die or are consumed by creek residents would be incorporated into the creek food web, while survivors would ultimately migrate from the creeks after a period of some growth. Movement into marsh creeks by adults fishes would constitute a pathway by which carbon is returned, or by which new carbon is brought in to the system. Potential importation of energy in the form of adult fish biomass appears to be most important during the spring and early summer (Fig. 5.2). *Menidia menidia* appears to be the most important species in this regard, followed by *F. heteroclitus*, *F. majalis* and *A. mitchilli*. *F. heteroclitus* is unique because it appears to overwinter on the marsh surface in the study area (K.J. Smith and K.W. Able, pers. comm.), and thus, may accomplish a transfer of energy from the marsh surface to the subtidal creeks, rather than from the bay and continental shelf as for the other species (see comments below).

The return of large numbers of adult *M. menidia* to marsh creek habitat, for example, might constitute a return of some of the energy exported the previous year. In fact, adult biomass during the May 1989 peak was 18% of the August peak for YOY (Fig. 5.2). Conover and Ross (1982) estimated that less than 1% of the YOY population of *M. menidia* in Massachusetts marshes survived the winter to spawn the following spring, and suggested a large one-way export of biomass to the continental shelf. The fate of the adult fish after spawning is unclear, but Conover and Ross (1982) indicate that few fish survive to a second spawning season. Because of their relatively large size, mortality of adult *M. menidia* within marsh creek habitat may represent a significant return of energy to the marsh.

Menidia menidia apparently exhibits only limited growth while over-wintering offshore (Conover and Murawski 1982, Conover and Ross 1982, Warkentine and Rachlin 1989), therefore they probably do not import much energy into the creeks, but rather simply return energy which originated from growth in marsh creek habitat during the previous year. Since adults continue to grow in the creeks through the spring and summer, migration out of the creeks by surviving adults would represent a further export of energy (as indicated by the second adult cohort peak in August 1989, Fig. 5.4).

Emigration

It is clear that M. menidia plays by far the most important role of any fish in energy exportation through seasonal emigration from polyhaline marsh creeks in New Jersey estuaries (Fig. 5.2). Additionally, YOY M. menidia is the most important prey of P. dentatus in the creeks (Chapter 4), and is also probably important prey of P. saltatrix, S. borealis, and S. marina. Much of the growth of these predators, therefore, is likely derived from predation on M. menidia, suggesting the role of M. menidia in energy exportation from the marsh is greater than is represented by its movements alone.

To determine net growth, and hence, net energy export, information on size at immigration into the marsh is needed. For many species which enter the estuary as larvae or postlarvae, the biomass at entrance can be considered negligible compared to biomass at emigration (e.g. P. dentatus weighs <<1 g upon immigration versus approx. 167 g at emigration). However, for species such as P. saltatrix and M. curema which enter the estuary as relatively large juveniles (Kendall and Walford 1979, Anderson 1957, McBride and Conover in press), size at immigration should not be considered negligible. For example, if the first peak in P. saltatrix cohort A abundance reflects the actual time and size at peak immigration into the estuary, then the average weight of fish entering the estuary is approximately 8% of those leaving the estuary (4.7 g versus 58 g per fish, respectively; Table 5.1) and as much as 53 g per fish is exported from the estuary. This suggests that a net exportation of biomass probably occurs even for species which recruit into the estuary at relatively large sizes.

Because growth in weight tends to increase with size, the length of the marsh creek use period has a strong influence on the amount of energy exported. For example, between a size of 80 and 160 mmSL, change in weight of P. saltatrix increased rapidly in Cohort A (Fig. 5.6). However, cohort B emigrates from the creek before this period of rapid weight increase. Therefore, even small variations in the timing of emigrations can have a great effect on energy exportation.

Energy in the form of fish biomass can be exported either in pulses when large numbers of individuals migrate simultaneously, or over a short time period, or it can be exported continuously over longer periods as large individuals of creek populations gradually bleed out of the creeks. While seasonal dependent migrations obviously result in pulsed export, size dependent emigration can result in both pulsed and continuous export. Menidia menidia for example exhibits a major export pulse because large numbers of individuals from the first cohort reach approximately 60 mmTL by early August and migrate from the creeks. However, smaller numbers of individuals are continuously moving out of the creeks as they reach 60 mmTL throughout August and September, until a secondary pulse of migrates occurs in the late fall. Although the relative importance of pulsed and continuous migrations to energy export could not be determined in this study, the continuous migration might well contribute as much to energy export as the pulsed migrations. Future studies of energy coupling between the marsh and coastal water through fish movements must examine both types of migration in order to fully quantify total energy export from the marsh.

Table 5.1. Date and size (length and weight) at peak abundance and size at emigration for individual size cohorts of 15 species of marsh creek fishes collected from 16 April-5 November 1988 and 9 April-15 October 1989. Lengths are given as Body, Standard or Total Lengths (BL, SL, or TL, respectively). Size at emigration is an estimate of the approximate size at which a individuals from each cohort migrates from the creek habitat (see text for further explanation). In cases where a cohort exhibited two abundance peaks, size at both peaks (labeled 1 and 2 for first and last peak) are given. Sample size is the number of measured individuals from each cohort.

		Size at Peak abundance				Sample size	
			Length	Weight			
Creek use life stages:	Species Cohort	Date	Mean (min-max)	Mean (min-max)	Emigration size threshold	Length	Weight
YOY and adults abundant	*Fundulus heteroclitus* (TL)						
	1989 Adult	7 May	52 (33-97)	no data		974	
	YOY	2 Jul	37 (24-50)	no data		659	
YOY and adults adbundant	*Fundulus majalis* (TL)						
	1989 Adult	4 Jun	122 (105-136)	no data		242	
	YOY	23 Jul	46 (27-56)	no data		207	
YOY and adults abundant	*Menidia menidia* (TL)						
	1988 Adult	21 May	90 (64-112)	no data		446	
	YOY A	30 Jul-13 Aug	67 (51-90)	no data	70 mm	1022	
	YOY B	30 Jul	33 (20-50)	no data		942	
	Unknown	27 Aug^1 8 Oct^2	60 (34-107) 69 (42-121)	no data	70 mm 70 mm	 2252	
	1989 Adult	21 May-4 Jun^1 6 Aug^2	94 (70-126) 89 (81-119)	no data		 1697	
	YOY A	6 Aug	66 (46-80)	no data	70 mm	2090	
	YOY B	20 Aug	43 (22-50)	do data		124	
	Unknown	3 Sep	71 (27-127)	no data	70 mm	1047	
YOY and adults abundant	*Anchoa mitchilli* (TL)						
	1988 Adult	2 Jul	70 (60-84)	no data		442	
	YOY	3-10 Sep	43 (33-57)	no data		200	
	1989 Adult	4 Jun-2 Jul	71 (53-95)	no data		566	
	YOY	15 Oct	60 (48-70)	no data		233	
YOY, and some adults	*Gobiosoma bosci* (SL)						
	1988 YOY	27 Aug	20 (12-28)	no data	20 mm	476	476
YOY, and some juveniles and adults	*Pseudoleuronectes americanus* (SL)						
	1988 YOY	16-23 Jul	62 (50-79)	5.0 (2.4-10.5)	90 mm, 20 g	147	147
	1989 YOY	6-13 Aug	78 (58-96)	11.1 (3.7-22)	80 mm, 10 g	204	204
YOY, and some adults	*Strongylura marina* (BL)						
	1988 YOY	16 Jul-13 Aug	99 (62-204)	4.3 (1.1-29.6)		226	200
	1989 YOY	23 Jul	98 (65-142)	6.7 (1.3-12.8)		305	260

Table 5.1. Continued.

Creek use life stages:	Species Cohort	Size at Peak abundance			Emigration size threshold	Sample size	
		Date	Length	Weight		Length	Weight
			Mean (min-max)	Mean (min-max)			
YOY only	*Clupea harengus* (SL)						
	1988 YOY	14 May	60 (49-71)	2.2 (1.2-3.9)		97	97
	1989 YOY	21 May	62 (45-75)	2.6 (0.9-4.4)		232	177
YOY only	*Leiostomus xanthurus* (SL)						
	1988 YOY	16 Jul	50 (32-93)	3.5 (0.6-23)	75 mm, 10 g	2769	2372
	1989 YOY	2 Jul	46 (31-56)	2.1 (0.6-3.8)		120	120
YOY only	*Mugil curema* (SL)						
	1988 YOY	10 Sep	100 (89-130)	27 (18-53)	100 mm, 25 g	218	212
	1989 YOY	2 Jul[1]	42 (23-78)	2.4 (0.2-11.1)			
		3 Sep[2]	96 (81-125)	23 (13-42)	100 mm, 25 g	758	620
YOY only	*Mustelus canis* (TL)						
	1988 YOY	16 Jul	420 (318-467)	264 (90-412)		93	93
	1989 YOY	18 Jun	360 (299-415)	150 (75-229)		44	42
YOY only	*Paralichthys dentatus* (SL)						
	1989 YOY	17 Sep	213 (165-263)	167 (76-295)	210 mm, 170 g	306	306
YOY only	*Pollachius virens* (SL)						
	1988 YOY	14 May	70 (44-84)	no data		122	90
YOY only	*Pomatomus saltatrix* (SL)						
	1988 YOY A	23 Jul	74 (48-113)	6.7 (1.2-28)		425	411
	YOY B	10 Sep	71 (47-109)	4.9 (1.1-19.5)	140 mm, 70 g	494	455
	1989 YOY A	2 Jul[1]	66 (47-122)	4.7 (1.5-29.5)			
		17 Sep[2]	143 (110-215)	58 (23-189)	140 mm, 70g	778	739
YOY only	*Sphyraena borealis* (SL)						
	1988 YOY	13 Aug	101 (69-132)	6.9 (2.2-13.9		184	155
	1989 YOY	20 Aug	134 (109-151)	16 (9-22)		107	77

Table 5.2. Growth rates of 15 species of fishes by intra-specific size cohort estimated from length (mm), and weight (g), regression on date of capture. Length (N1) and weight (N2) sample sizes indicate the number of measured individuals in a cohort. Lengths were measured as total length (TL), standard length (SL) or body length (BL).

	Length			Weight		
Species Cohort	Slope (SE)	R^2	N1	Slope (SE)	R^2	N2
Fundulus heteroclitus (TL)						
1989 Adult	0.21 (0.01)	0.25	974	No data		
YOY	0.26 (0.02)	0.26	490	No data		
Fundulus majalis (TL)						
1989 YOY	0.16 (0.02)	0.35	207	No data		
Menidia menidia (TL)						
1988 Adult	0.21 (0.02)	0.15	446	No data		
YOY A	0.58 (0.03)	0.39	623	No data		
YOY B	0.33 (0.02)	0.31	942	No data		
1989 Adult	0.11 (0.01)	0.11	1697	No data		
YOY A	0.44 (0.01)	0.43	1558	No data		
YOY B	0.22 (0.03)	0.35	124	No data		
Anchoa mitchilli (TL)						
1988 Adult	0.12 (0.01)	0.28	442	No data		
YOY	0.25 (0.02)	0.43	200	No data		
Gobiosoma bosci (SL)						
1988 YOY	0.22 (0.02)	0.44	216	No data		
Pseudoleuronectes americanus (SL)						
1988 YOY	0.57 (0.03)	0.74	116	0.22 (0.01)	0.69	116
1989 YOY	0.51 (0.03)	0.65	158	0.15 (0.01)	0.46	158
Strongylura marina (BL)						
1988 YOY	1.65 (0.06)	0.79	226	0.48 (0.02)	0.67	200
1989 YOY	2.07 (0.07)	0.76	305	0.71 (0.03)	0.68	260
Clupea harengus (SL)						
1989 YOY	0.59 (0.04)	0.48	232	0.10 (0.01)	0.55	177
Leiostomus xanthurus (SL)						
1988 YOY	0.92 (0.02)	0.42	1936	0.32 (0.01)	0.31	1598
1989 YOY	1.39 (0.02)	0.97	120	1.07 (0.03)	0.92	109
Mugil curema (SL)						
1988 YOY A	0.92 (0.03)	0.85	213	0.42 (0.02)	0.68	206
1989 YOY A	0.91 (0.02)	0.83	758	0.33 (0.01)	0.66	620
Mustelus canis (SL)						
1988-1989 YOY	1.79 (0.13)	0.60	137	3.40 (0.27)	0.55	136
Paralichthys dentatus (SL)						
1989 YOY	1.49 (0.09)	0.54	256	3.06 (0.19)	0.50	256
Pollachius virens (SL)						
1988-1989 YOY	0.92 (0.06)	0.65	122	0.14 (0.01)	0.72	101
Pomatomus saltatrix (SL)						
1988 YOY A	0.97 (0.03)	0.67	406	0.57 (0.03)	0.53	392
YOY B	0.65 (0.02)	0.68	494	0.14 (0.01)	0.43	455
1989 YOY A	1.34 (0.03)	0.78	557	1.09 (0.04)	0.53	518
Sphyraena borealis (SL)						
1988-1989 YOY	1.22 (0.06)	0.58	291	0.26 (0.02)	0.46	231

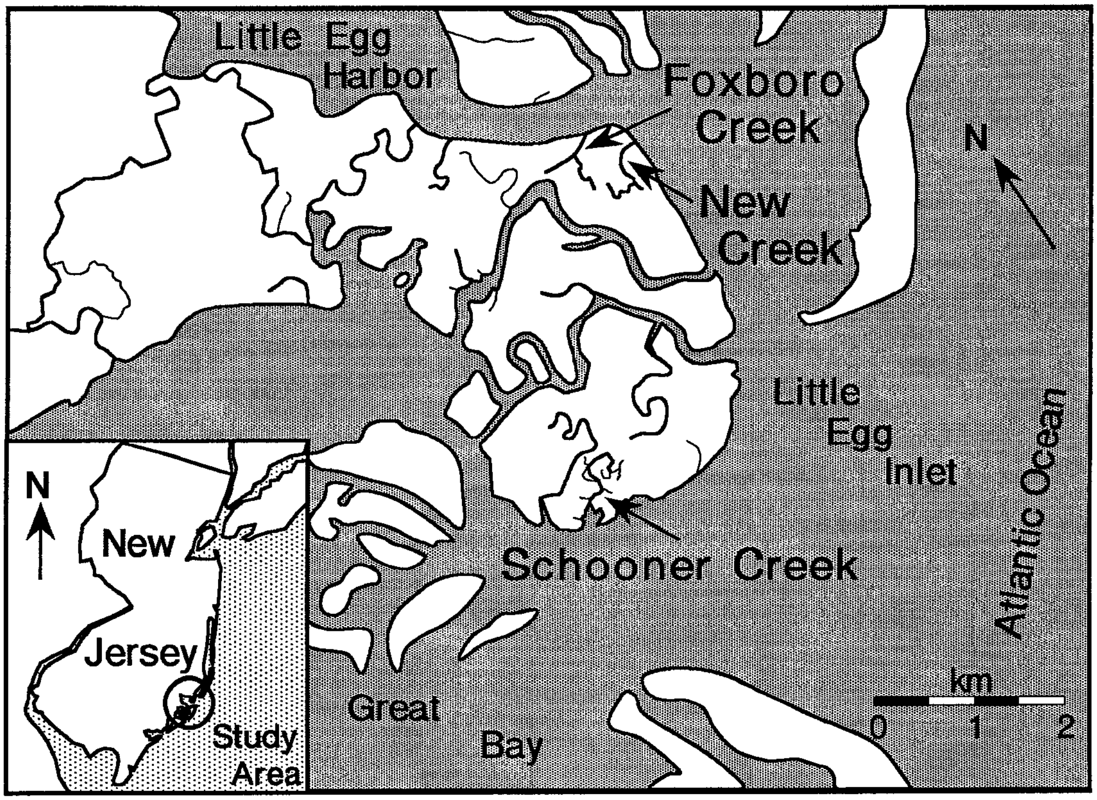


Figure 5.1. Great Bay-Little Egg Harbor estuarine complex and location of study creeks in southern New Jersey.

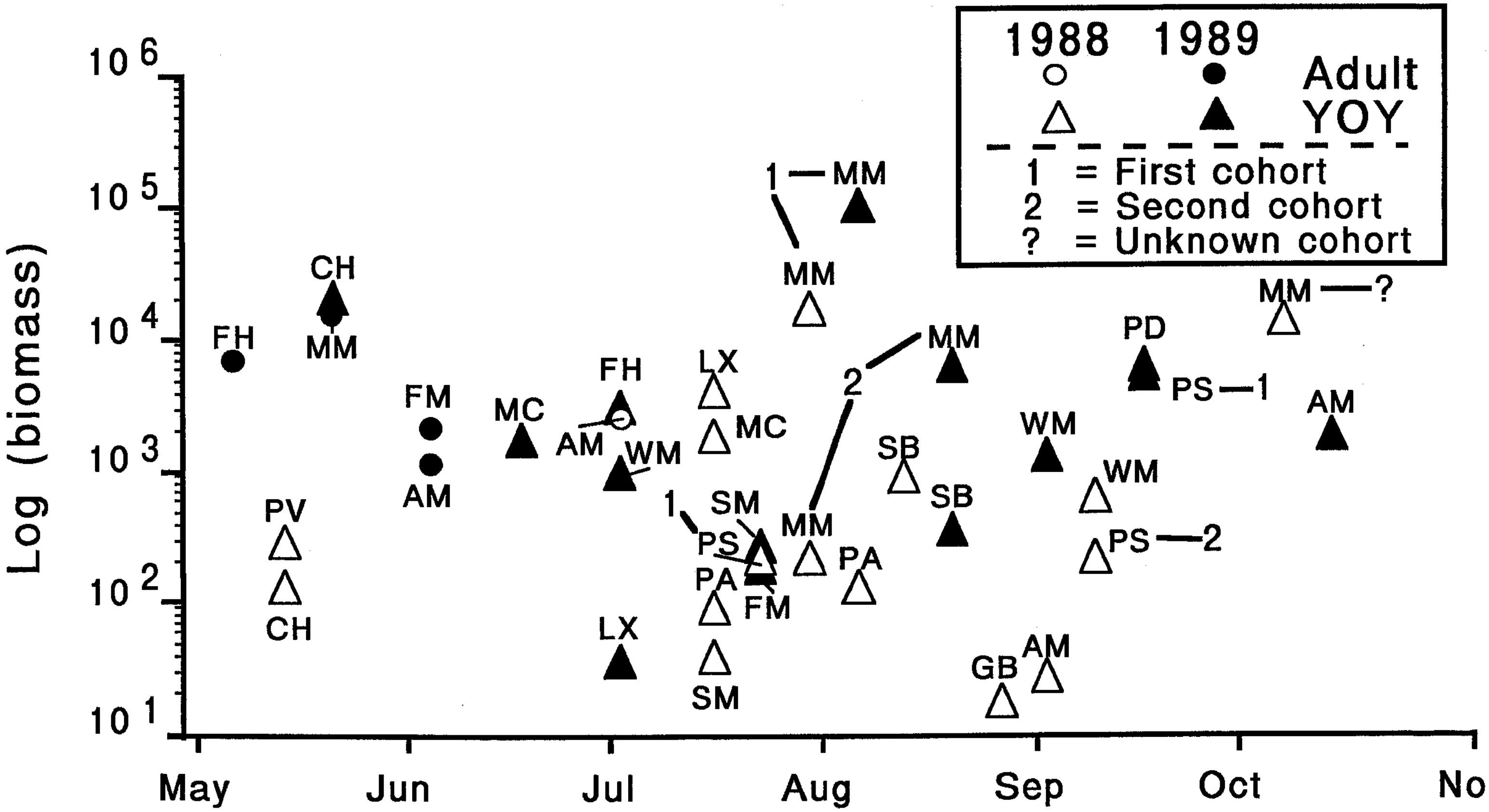


Figure 5.2. Seasonal distribution of biomass at peak abundance by species and cohort based on combined weir and seine samples taken fortnightly from April-November 1988 and April-October 1989. Peak biomass of two cohorts of *Menidia menidia* and *Pomatomus saltatrix* are shown. A possible third cohort (=unknown) was also important for *M. menidia* (see text). Several cohorts exhibited two major peaks during the year including, *Pomatomus saltatrix* (1989), and *Mugil curema* (1989). AM = *Anchoa mitchilli*, CH = *Clupea harengus*, FH = *Fundulus heteroclitus*, FM = *Fundulus majalis*, GB = *Gobiosoma bosci*, LX = *Leiostomus xanthurus*, MC = *Mustelus canis*, MM = *Menidia menidia*, PA = *Pseudopleuronectes americanus*, PD = *Paralichthys dentatus*, PS = *Pomatomus saltatrix*, PV = *Pollachius virens*, SB = *Sphyraena borealis*, SM = *Strongylura marina*, and WM = *Mugil curema*.

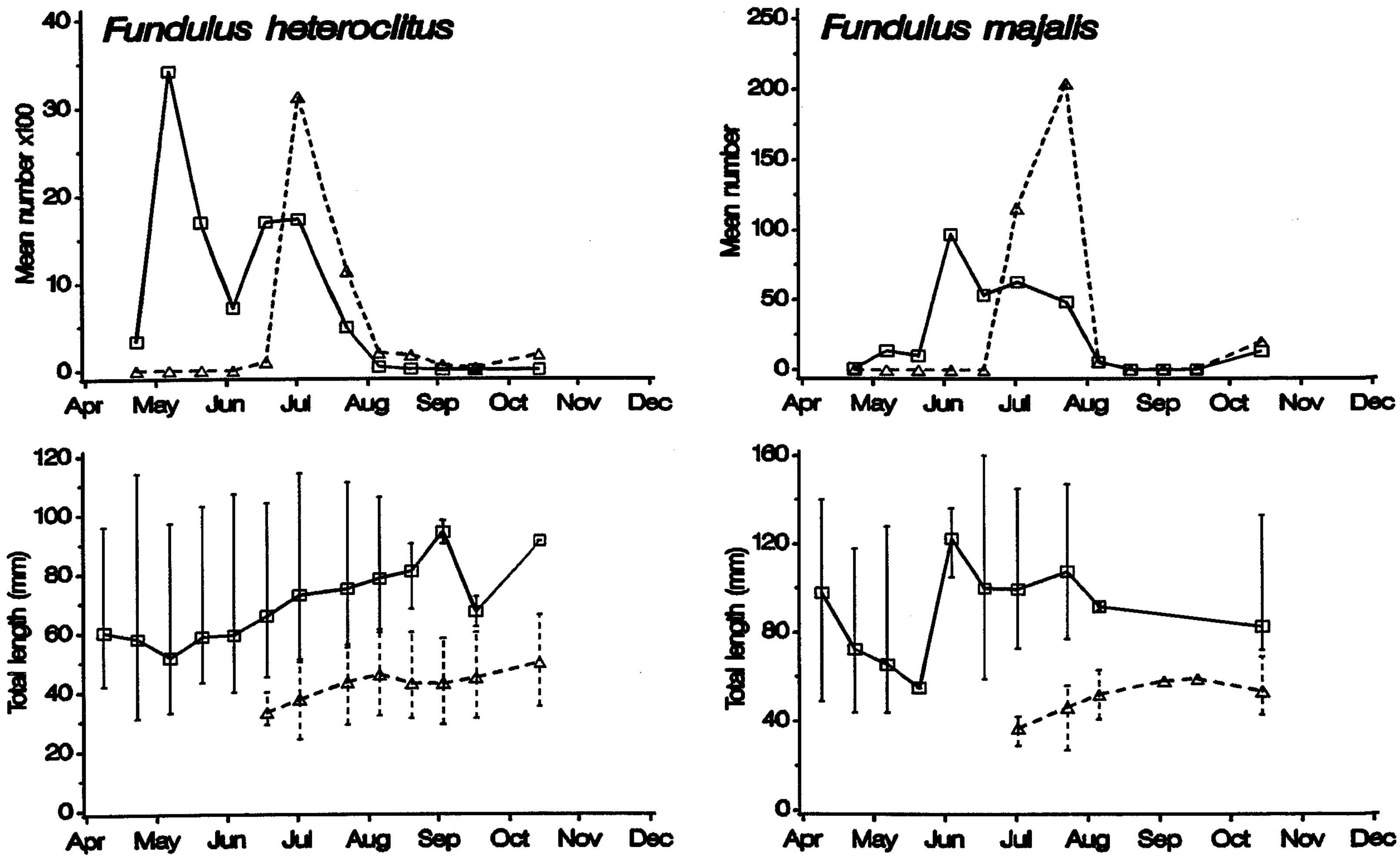


Figure 5.3. Mean weekly abundance (top) and length (bottom) by size cohort (adult=squares, YOY=triangles) of _Fundulus heteroclitus_ and _Fundulus majalis_ from combined weir and seine samples collected from April-October 1989. Vertical bars are length ranges.

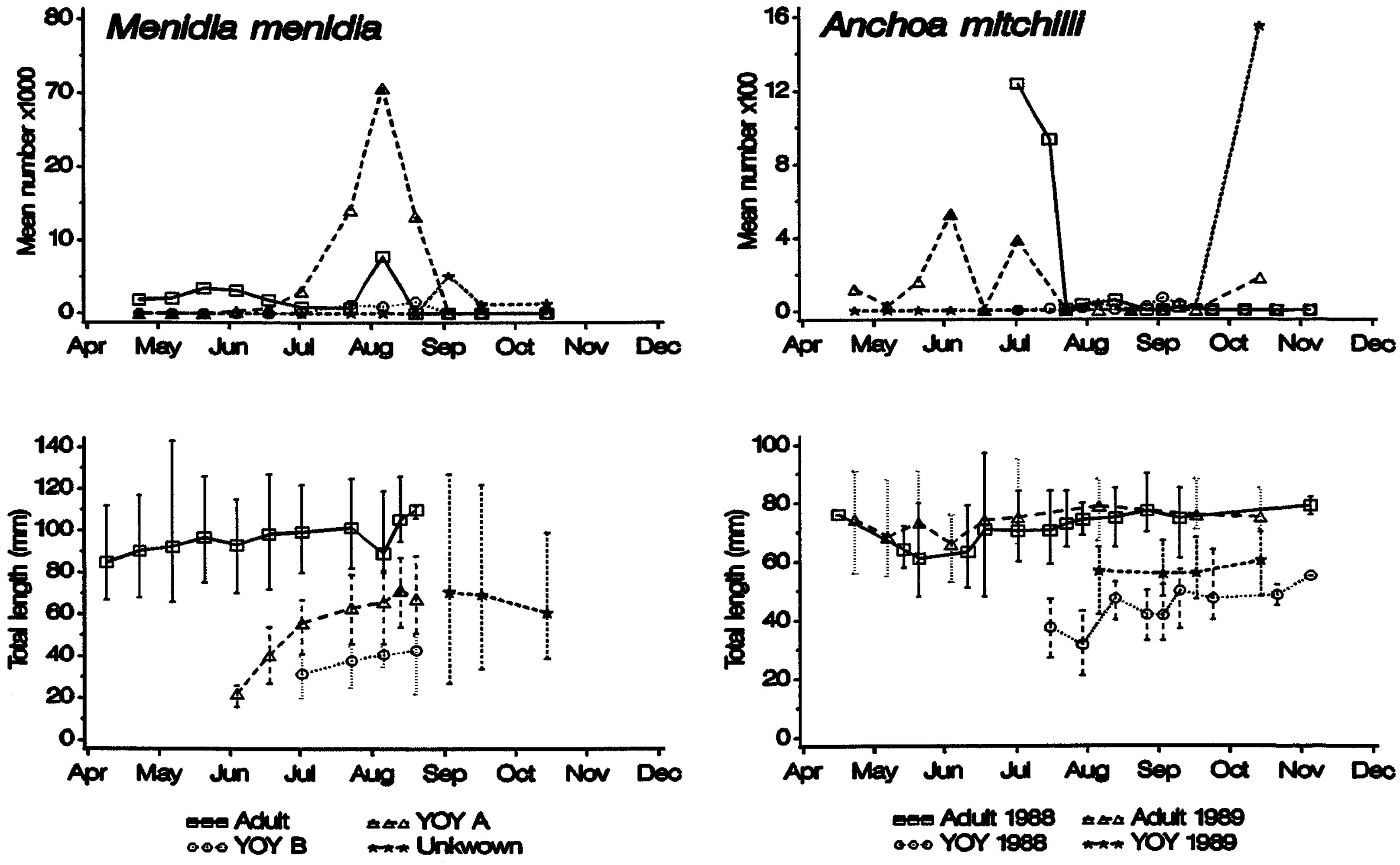


Figure 5.4. Mean weekly combined weir and seine abundance (top) and length (bottom) by cohort of Menidia menidia during 1989, and Anchoa mitchilli during 1988 and 1989. Vertical bars are length ranges.

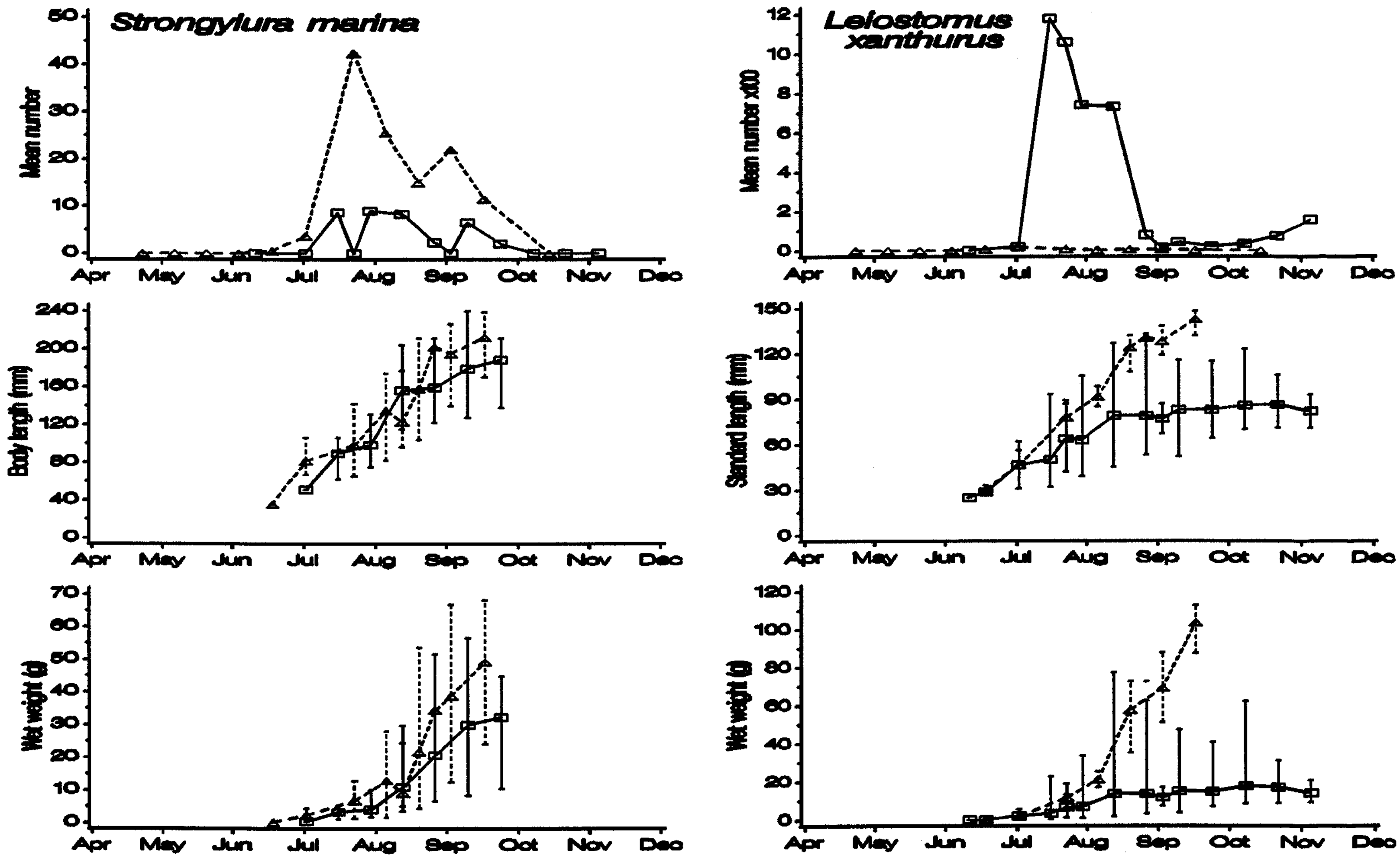


Figure 5.5. Mean weekly combined weir and seine abundance (top), length (center), and weight (bottom), of young-of-year *Strongylura marina* and *Leiostomus xanthurus* by year (1988=squares, 1989=triangles). Vertical bars are length and weight ranges.

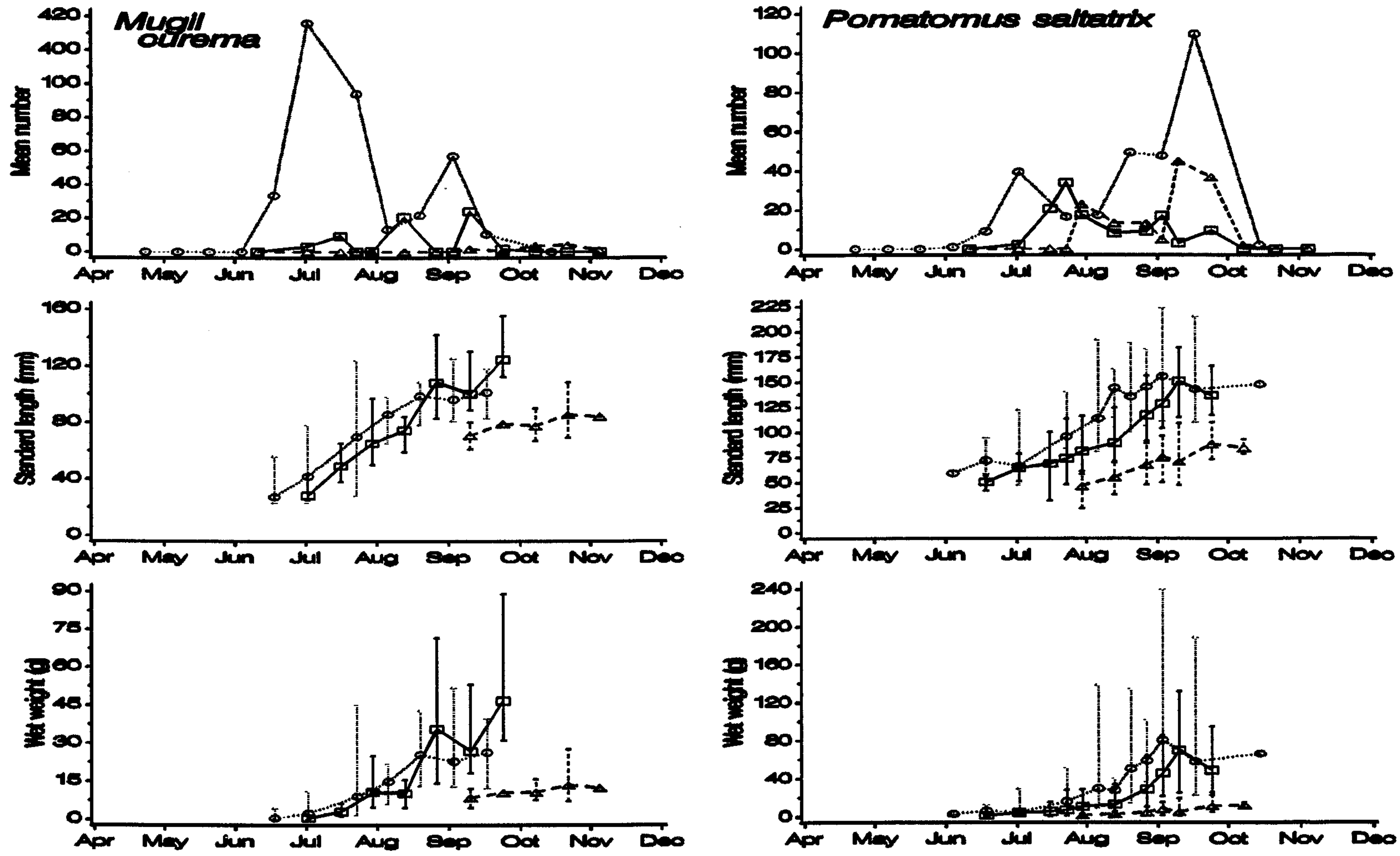


Figure 5.6. Mean weekly combined weir and seine abundance (top), length (center), ans weight (bottom) of young-od-year *Mugil curema* and *Pomatomus saltatrix* by size cohort and year (1988 cohort a = squares, 1988 cohort B = triangles, 1989 cohort A = circles). Vertical bars are length and weight ranges.

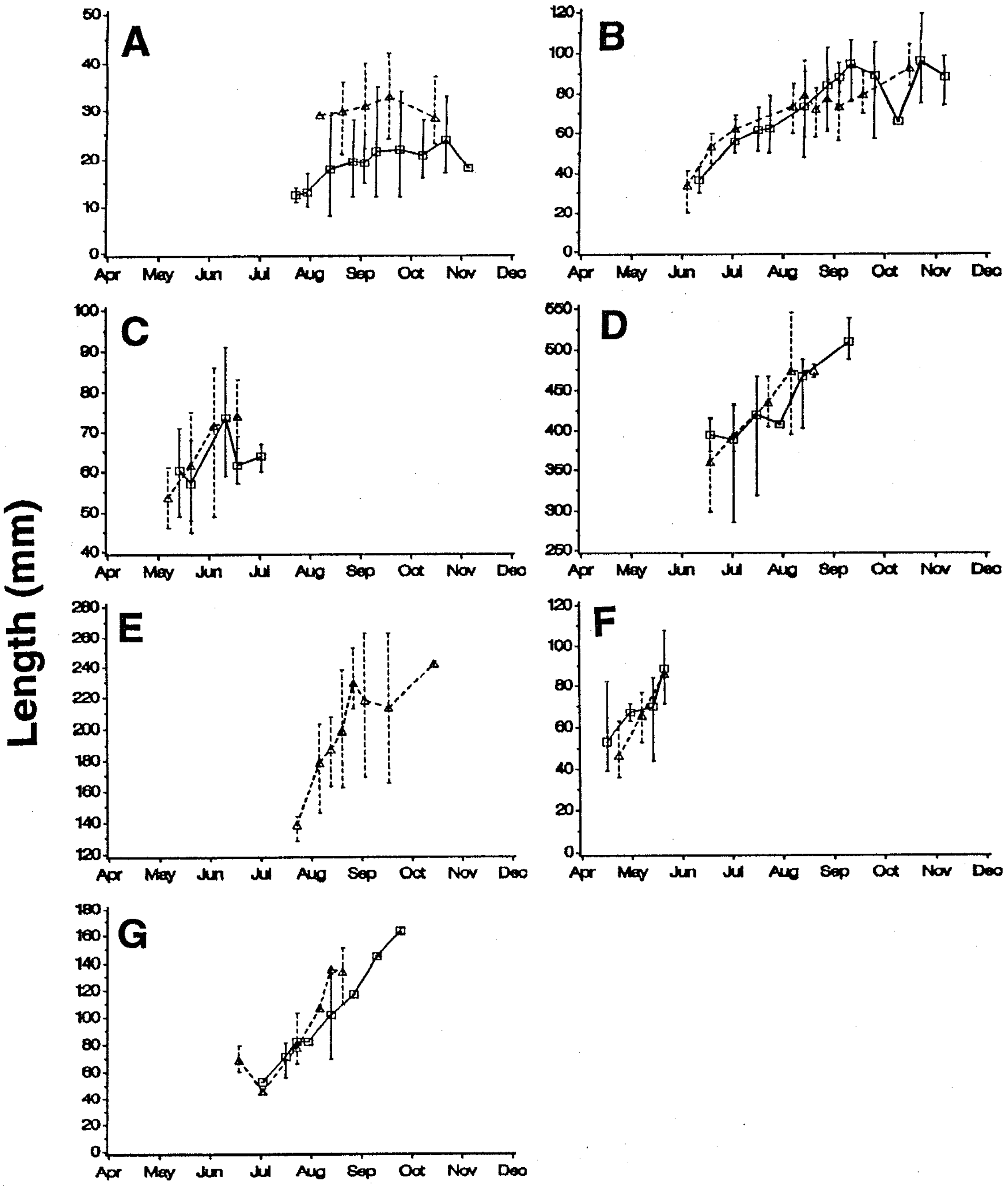


Figure 5.7. Mean weekly length by year (1988=squares, 1989=triangles) of A) <u>Gobiosoma bosci</u>, B) <u>Pseudopleuronectes americanus</u>, C) <u>Clupea harengus</u>, D) <u>Mustelus canis</u>, E) <u>Paralichthys dentatus</u>, F) <u>Pollachius virens</u>, and G) <u>Sphyraena borealis</u>. All lengths are Standard Length (mmSL) except for <u>M</u>. <u>canis</u> which is Total Length (mmTL). Vertical bars are length ranges.

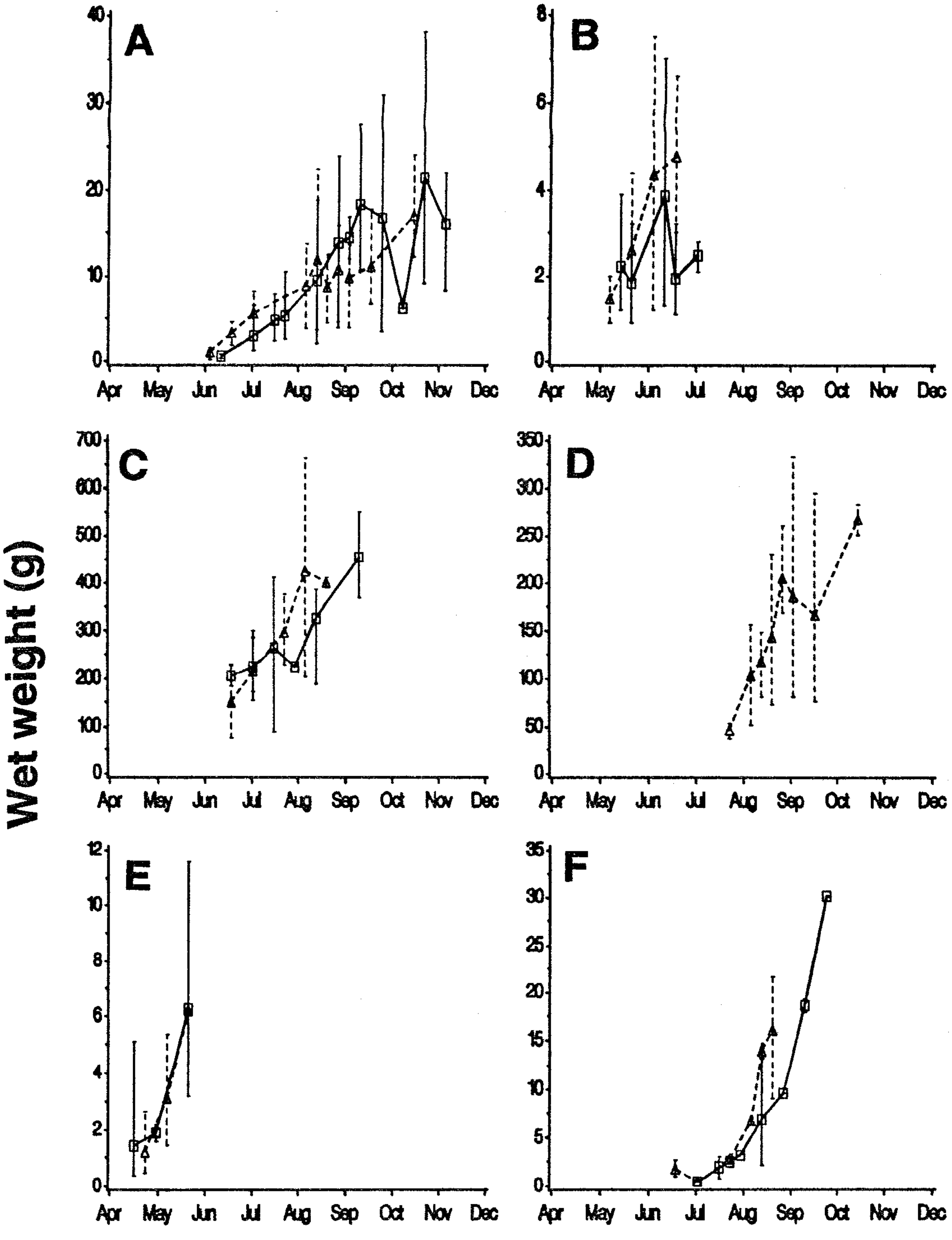


Figure 5.8. Mean weekly wet weight (g) by year (1988 = squares, 1989 = triangles) of A) Pseudopleuronectes americanus, B) Clupea harengus, C) Mustelus canis, D) Paralichthys dentatus, E) Pollachius virens, and F) Sphyraena borealis. Vertical bars are weight ranges.

Chapter 6. Synthesis of patterns of marsh creek community structure, and mechanisms of energy exchange between the marsh and marine waters.

Abstract

This paper reviews an extensive amount of research generated over the past two decades on processes which regulate salt marsh community structure and habitat use, and on processes of energy exchange between the marsh and coastal waters. Recent research efforts in salt marsh creeks located within a southern New Jersey salt marsh are summarized and discussed in context of this review.

Salt marsh creeks are one of the most important nurseries within the estuary, and support a diverse assemblage of species which utilize the habitat primarily as young-of-year or early juveniles. Marsh creek communities exhibit strong tidal and diel variations with appear to result from tidal and diel movements. These movements are influenced by diel and tidal changes in abiotic factors, such as water temperature and water volume, and by biotic factors, such as predation pressures and crowding. Spatial variation in species assemblages and abundances appear to be influenced by creek morphology in two major ways, 1) through the direct mediation of tidal dynamics such as tidal drainage, and 2) through the indirect mediation of tidal and diel changes in physical

conditions along a mouth-to-headwater creek gradient. Distributions of species within marsh creek habitats are controlled by balances between physiological tolerances, predation pressures, and competitive interactions as are other types of communities. However, the highly mobile marsh creek fauna can additionally respond to tidal and diel changes in conditions along the creek gradient by undergoing cyclic (tidal and diel) migrations along the creek gradient in order to maintain suitable conditions.

Although the mechanisms of energy exchange between the salt marsh and coastal waters are poorly understood, exchange can occur either by passive transport of suspended and dissolved organic matter and nutrients through water exchange, or by a trophic transfer of organic matter through animal movements. Major types of animal movements which result in energy exchange between the marsh and adjacent habitats include: 1) ontogenetic migrations, such as size dependent and seasonal migrations, and 2) cyclic migrations, such as diel and tidal foraging movements. All of these mechanisms allow for both import and export of materials, although relatively few studies have explored potentials for energy importation into the marsh. Patterns of community structure and energy exchange among communities exhibit striking parallels between estuarine and deep ocean systems, which may result from two underlying similarities between the systems: 1) most primary production occurs in a narrow band at shallow depths (i.e., coastal and photic zones), and 2) similar mechanisms operate to transport energy along a depth gradient (e.g., estuarine outwelling, and deep sea vertical sinking of detritus).

Introduction

Estuarine ecologists and conservationists have long believed that salt marshes are critically important habitats for economically important fishes and that they serve as important nutrient and energy sources for coastal marine waters (e.g., Nixon and Oviatt 1973, Odum and Heald 1975, Meredith and Lotrich 1979, Nixon 1980, Pomeroy and Wiegert 1981, Daiber 1982, Boesch and Turner 1984, Currin et al. 1984, Kneib 1984, Teal 1985). This view is based on the premise that fish production is coupled with salt marsh primary production through trophic interactions; however, quantitative data supporting such a coupling is conspicuously lacking (Nixon 1980, Boesch and Turner 1984, Currin et al. 1984, Weinstein 1984). Many estuarine areas are known to support large stocks of resident and transient fishes, but whether this is due to a trophic dependence on salt marsh primary production, or to other factors (e.g., shallow water predator refuge for juvenile fishes) has not been clearly determined (Nixon 1980, Boesch and Turner 1984, Currin et al. 1984, Zimmerman and Minello 1984).

Because tidal marsh creeks are a primary interface between the salt marsh and open estuarine waters, and because they provide fish access to the marsh, numerous researchers have pointed out the need for research into the role of marsh creeks as fish habitat and in energy export from the marsh (Nixon and Oviatt 1973, Subrahmanyam and

Drake 1975, Bozeman and Dean 1980, Weinstein et al. 1980, Currin et al. 1984, Weinstein 1984, Weinstein et al. 1984).

In the past decade more research has been focused on processes which regulate community structure and habitat use in the marsh, and on processes of energy export from the marsh to coastal waters. In this paper I summarize recent research conducted in New Jersey marsh creek habitats and attempt to synthesize published information on patterns of fish and macroinvertebrate community structure, habitat use, and energy exchange in the marsh.

Marsh community structure

A growing body of evidence suggests that salt marsh creeks are one of the most important nurseries within the estuary (see review in Chapter 1). In New Jersey marsh creeks support a very diverse fauna made up both of typical estuarine species (such as the fish *Fundulus heteroclitus* and shrimp *Palaemonetes vulgaris*), and species which spawn over the continental shelf (such as the fishes *Pomatomus saltatrix*, *Paralichthys dentatus* and *Mugil curema*). Many of the dominant marsh creek species exhibit wide geographic distributions, including *F. heteroclitus*, *F. majalis*, *Menidia menidia*, and *M. curema*, despite important differences in dominant marsh vegetation and other estuarine characteristics. While creek fauna tends to be numerically dominated by highly abundant estuarine species, including the fishes Menidia menidia, F. heteroclitus, the shrimp P. vulgaris, and the crab Callinectes sapidus), a diverse assemblage of highly seasonal transients species, including the fishes P. saltatrix, M. curema, P. dentatus, and C. harengus utilize the creeks exclusively as young-of-year (e.g., Richards and Castagna 1970, Nixon and Oviatt 1973, Subrahmanyam and Coultas 1980, Weinstein et al. 1980, Smith et al. 1984, Chapter 1, 5). Growth rates of fishes which use the creeks exclusively as YOY are very high, ranging from 0.6-1.5 mm/day, while species also using the creek during adult stages exhibit slower growth rates ranging from 0.2-0.6 mm/day (Chapter 5).

DIEL PATTERNS

Strong diel patterns in species abundances have been reported in the marsh (Shenker and Dean 1979, Reis and Dean 1981, Rozas and Hackney 1984, McIvor and Odum 1986, Middleton 1986, Rozas and Odum 1987, Chapter 3). As discussed in Chapter 3, diel movements appear to result from balances between food availability and predation pressures similar to those described for coral reef and seagrass communities (Hobson 1968, Helfman 1978, Robblee and Zieman 1984). Fish which feed on zooplankton, or other food sources located in open subtidal areas retreat to shallow subtidal or intertidal areas during non-feeding periods. Hence, high night abundance of Menidia menidia are suggested to result from nocturnal movement into shallow water to escape predation during non-feeding hours (Chapter 3). Contrastingly, fishes which depend directly on the intertidal or subtidal marsh as a food source tend to occur equally during both day and night, or occur most abundantly during the period of maximum feeding activity. For example, Leiostomus xanthurus, occurred in similar abundance in subtidal creek weir samples during both day and night, while the highly nocturnal M. canis occurred exclusively at night. Diel changes in physical conditions can also lead to diel movement behavior (Chapter 3). Strong diel changes in physical conditions have been noted in marsh creeks and other shallow subtidal estuarine habitats (Nixon and Oviatt 1973, Hackney et al. 1976, Breitburg 1988, Portnoy 1991, Chapter 3). Some diel movements may occur in response to diel occurrences of stressful or even lethal conditions (Chapter 3). However, animals may respond to sublethal conditions by moving to maintain preferred physiological conditions (Brett 1971, Breitinger et al. 1975, Breitinger 1976, Reynolds and Casterlin 1976, Major 1978, Clark and Green 1991), or to gain a metabolic advantage (McLaren 1963, McAllister 1969, Brett 1971, Stuntz and Magnuson 1976, Biette and Green 1980, Mauchline 1980, Wurtsbaugh and Neverman 1989, Abou-Seedo et al. 1990, Clark and Green 1991, see discussion in Chapter 3). A metabolic advantage may be gained by foraging within an environmentally variable habitat, and then moving into a more stable (often colder) habitat to digest food.

TIDAL PATTERNS

Although the importance of tidal movement is well known in the intertidal salt marsh (see Kneib 1984), little is known of tidal movements in the subtidal marsh (Subrahmanyam and Drake 1975, Blaber 1986, Chapter 2). In Chapter 2 evidence is presented which suggests that many species utilizing subtidal marsh creeks in New Jersey undergo some form of tidal movement. In fact, many species generally considered to use estuaries as a nursery appear to exhibit tidal migrations in the subtidal creeks, including *P. dentatus*, *P. saltatrix*, and *Leiostomus xanthurus* (Chapter 2).

Tidal migrations probably result from causes similar to those influencing diel movements, however physical changes brought about by the tides probably have more influence on tidal movements than physical conditions have on diel movements. In the extreme case, most natant animals are forced to abandon intertidal areas at low tide to avoid desiccation, but return on flood tides to obtain food or escape predation. In subtidal areas, tidal changes in physical conditions can also lead to similar movements (Chapter 2).

Recent research in intertidal and subtidal marsh creeks located in a southern New Jersey estuary, suggest that creek size strongly influences the prevalence of tidal movements in marsh communities (Chapter 2). In intertidal creeks virtually all species/individuals undergo tidal migrations, while progressively fewer species/individuals migrate as creek size and tidal drainage decreases. Additionally, fauna composition of weir catches were found to be influenced by tidal changes in physical conditions such as water temperature and salinity. It is suggested, therefore, that tidal movements may result from a behavioral response to tidal changes in physiological conditions in a process analogous to that proposed for diel movements (see discussion above).

Studies of the marsh creek habitat use by the summer flounder, Paralichthys dentatus, confirm that it undergoes tidal foraging movements into marsh creeks in New Jersey (Chapter 2, Chapter 4, Szedlmayer and Able in prep.). While P. dentatus appears to move into marsh creeks during flood tide to forage on marsh creek species such as M. menidia, F. heteroclitus and P. vulgaris, it is not clear what causes P. dentatus to leave its foraging habitat at low tide (Chapter 4, Szedlmayer and Able in prep.). Nine individuals tracked with ultrasonic telemetry where found to usually migrate to the bay at the creek mouth during low tide stages, where they tended to remain in a relatively lethargic state (Szedlmayer and Able in prep.). However, individuals frequently remained relatively sedentary at the creek mouth over several tidal cycles, and sometime remained within the creek through low tide. Additionally, most individuals traveled farther up creek on night flood tides than on day flood tides.

These patterns suggest the possibility that _P. dentatus_ movements result from the metabolic advantage of moving between a environmentally variable foraging habitat (creeks) and an relatively stable (bay) resting habitat (see discussion above). The magnitude of the tidal range in temperature was on the order of temperature changes known to induce behavioral thermoregulatory movements of some other fishes in laboratory studies (Brett 1971, Breitinger et al. 1975, Breitinger 1976, Reynolds and Casterlin 1976, Major 1978, Clark and Green 1991), and were greatest during the day (see discussions in Chapter 2 and 3). If _P. dentatus_ movements result from this type of metabolic advantage, then daily variation in movement behaviors may result from variation in foraging success. Gut fullness data on _P. dentatus_ captured leaving marsh creeks suggests that foraging success was highly variable (Chapter 4), therefore, individuals which have had poor foraging success may not leave the creeks during low tide, while those which were very successful may remain at the creek mouth through the next flood tide to complete digestion.

SPATIAL PATTERNS

Species assemblages in marsh creeks appear to exhibit variation both within, and among creeks (Chapter 2). Several studies have shown spatial variation in intertidal and subtidal marsh assemblages and abundances between upper and lower reaches of marsh creeks (Hackney et al. 1976, Weinstein and Brooks 1983, Smith et al. 1984, Rozas and Odum 1987, Hettler 1989, Chapter 2,3). Hackney found that the magnitude and direction of tidal and diel changes in physical conditions varied along a mouth-to-headwater creek gradient (Hackney et al. 1976). He proposed that changes in species assemblages and abundances occurred in response to this creek gradient. In Chapter 2, I develop this concept more fully, and present a model of how creek morphology influences physical conditions, and how both spatial variation among, and within creeks may be influenced by similar processes (Fig. 6.1). I suggest that creek morphology influences community structure in two major ways, 1) directly through the mediation of tidal dynamics such as tidal drainage (i.e. extent to which a creek empties, or ratio of subtidal to intertidal creek volume), and 2) indirectly through the mediation of tidal and diel changes in physical conditions along the creek gradient.

Creek morphology directly mediates tidal dynamics such as tidal drainage. The degree of tidal drainage increases moving up creek (i.e. ratio of subtidal to intertidal creek volume decreases) along the creek gradient until the entire creek becomes intertidal at its headwaters. Similarly, the extent of tidal drainage decrease from small creeks which may be entirely intertidal, to large creeks which have increasingly large subtidal water volumes. Comparison of faunal composition and abundances from weir and seine samples within creeks of different sizes suggests that community structure changes between upper and lower regions of creeks, and that among creek differences appear to be more strongly related to creek size that to creek location. Further, virtually all species undergo tidal movements within intertidal creeks, while progressively fewer species appear to undergo tidal movements as creek size increased (Chapter 2).

Creek size indirectly influences community structure through mediation of tidal and diel changes in physical conditions. Basically, land and atmospheric conditions have an increasing influence on creek conditions moving up the creek gradient towards the headwater, while bay conditions increasingly influence creek conditions moving down the creek gradient towards the creek mouth. Diel and tidal cycles in atmosphere and bay physical conditions interact such that, conditions are more variable and exhibit greater extremes towards creek headwaters, and are more stable moving towards the creek mouth. A creek gradient in overall physical conditions, therefore, is strongly influenced by creek morphology (depth, length, tidal flushing, etc.). Comparisons of creeks of different sizes, therefore, is analogous to comparisons of different locations along a single creek gradient. Spatial differences in species assemblages and abundances along a creek gradient may result from a response to differences in physical conditions.

Biological interactions also influence changes in species assemblages and abundances within creeks. Predation pressure from aquatic sources tend to increase moving down the creek gradient (Chapter 2,3). Both physical factors and biological factors combine to result in a tendency for upper creek and intertidal habitats to be dominated by small forms such as F. heteroclitus, F. majalis, P. vulgaris and Menidia beryllina, which are highly tolerant of rapid environmental changes. Some larger fishes, such as Sphyraena borealis, P. saltatrix and S. marina, which are less tolerant of rapid environmental changes may also move into these intertidal areas on night flood tides (Chapter 3). Similarly, P. dentatus appears to move into the shallow upper creek areas of subtidal creeks primarily during night flood tides (Szedlmayer and Able in prep).

Depth may serve as a master variable which integrates diel and tidal changes in many physical conditions (water temperature, salinity, turbidity, light intensity, etc.) and biological factors (crowding, competition, predation pressures) and thus is an good predictor of species assemblages, abundances and life history stage.

ONTOGENETIC CHANGE OF HABITAT

One important characteristic of many intertidal communities is the tendency for intraspecific size stratification to occur along a tidal gradient usually in the form of increasing size with depth (Gibson 1973, 1986, Helfman 1978, Kneib 1984). Intraspecific size stratification of fishes with depth, often involving occupation of different habitats, is a very widespread phenomenon occurring in freshwater lakes and streams, seagrass beds, mangroves, coral reefs, sandy beaches, and even in the deep ocean deep-scattering-layer (see reviews by Gibson 1973, 1986, Helfman 1978, Mauchline 1980, Kneib 1984, 1987, Macpherson and Duarte 1991).

Four main hypothetical causes of this size stratification have been suggested: 1) ontogenetic changes in predation pressures; 2) ontogenetic changes in food requirements/ availability; 3) intraspecific competition for food and other resources; 4) ontogenetic changes in environmental tolerances (see reviews by Gibson 1973, Helfman 1978, Mauchline 1980, Kneib 1987, Macpherson and Duarte 1991).

Kneib (1987) experimentally examined the role of predation risk on habitat selection and size stratification in the salt marsh intertidal zone and found that predation pressures on small juveniles and larvae were intense. However, unlike freshwater systems where larvae and juveniles can apparently assess the relative predation risk among habitats (Werner et al. 1983), the relative risk of predation in subtidal and intertidal habitats at low tide cannot be assessed before the fish are concentrated at low tide (Kneib 1987). Kneib (1987) concludes that the tendency to remain in shallow intertidal habitats may not be a direct response to the presence of predators in other habitats, but may be inherited through natural selection.

If intraspecific competition for some resource is great then natural selection pressure will favor some type of partitioning of the resource, but how can resource partitioning occur within a species? One widespread mechanism is thought to be the partitioning of juveniles and adults into day or night activity patterns (Helfman 1978). So the key to intraspecific resource partitioning is the presence of some type of biologically detectable environmental gradient or cycle. One of the most widespread gradients is water depth. Size stratification along the depth gradient by a species would be an effective mechanism to reduce intraspecific competition.

All of the four hypotheses listed above, except the last, require some mechanism for appropriate habitat, or depth, selection at a given size. Gibson (1973) discusses possible physical cues for depth selection in plaice, Pleuronectes platessa, including light, pressure, turbidity, wave action, salinity and temperature, but finds no convincing single cue. The last hypothesis suggests both a functional cause, and a mechanism for size stratification among habitats. In his study of the use of the intertidal zone by Mugil cephalus, Major (1978) suggests that its stratification among habitats with size functions to reduce intraspecific competition for food and space in the shallow intertidal zone. More importantly, he presents evidence that the stratification is cued by ontogenetic changes in environmental stress tolerances. Pre-juveniles enter the estuary and select the shallowest intertidal habitats with near lethal environmental conditions. As it grows M. cephalus becomes increasing sensitive to environmental stress and moves into deeper, less stressful water.

A number of fishes are thought to undergo ontogenetic changes in tolerances to environmental stress. Estuarine species, in particular, are thought to become less tolerant of stress as they grow (Norris 1963, Wohlschlag and Cech 1970, Helfman 1978, Major 1978, Brett 1979, Miller and Dunn 1980). Stratification by size of such species along the creek gradient would be expected in response to physical gradients. Miller and Dunn (1980) discuss the importance of this type of environmental cue to inducing migrations and foraging movements of fishes in the estuary, but predicts that a range of environmental factors, rather than a single factor such as water temperature operate as the cue. My observations in New Jersey marsh creeks (Chapter 2, 3) suggest to me that a gradient in overall environmental variability may function as the cue to habitat selection along the creek gradient.

ECOLOGICAL IMPLICATIONS

The community structure patterns discussed, herein, suggest that each species has a basic distribution along a creek gradient resulting both from a response to gradients in physical conditions, and from the effects of the tidal dynamics of the creek. However, species interactions such as competition, risk of predation, etc., may also influence species distributions (Kneib 1984, 1987, McIvor and Odum 1988, Chapter 2, 3). Mechanisms regulating the distributions of animals in tidal creeks, therefore, parallel those regulating other intertidal habitats, being controlled by balances between physiological tolerances/preferences, predation pressures, and competitive interactions (Connell 1961, Kneib 1984).

These ideas have important implications for theories of community structure and biodiversity. Hypothetical species distributions among three habitats connected along a gradient in physical conditions (i.e., the creek gradient) are illustrated in Figure 6.2. Species can respond to tidal (or diel) changes in conditions in two ways: 1) they can establish permanent distributions within a habitat by adapting to tolerate tidal fluxes in conditions (as for species 1-6), or 2) they can migrate along the creek gradient in response to tidal fluxes in order to stay within suitable conditions (species 8-12). Both types of distributions are ultimately regulated by tolerances to physical conditions, and by biological interactions, as in classically studied rocky intertidal communities (Connell 1961). Species 1-6 are restricted to one of each of the habitats, while species 7 occurs in each of the habitats at separate life history stages. In response to tidal changes in conditions along the creek gradient, species 8-9 move between subtidal and intertidal creek habitats; species 12 moves between bay and subtidal creek habitats; and species 11 moves directly between intertidal creek and bay habitats. Species 10 moves between intertidal and subtidal creek habitats at one life history stage, and between bay and subtidal creek habitats at another stage.

One important implication of this model is that tidal movements between habitats allow for greater resource partitioning and more species packing within habitats, hence an assemblage of seven species are depicted to utilize intertidal creeks rather than three in Figure 6.2. The temporal partitioning of habitat use by some species, may allow the habitats to support more species than otherwise possible. It also illustrates a mechanism for energy exchange among habitats, where cyclic movements provide trophic links among marsh, creek and bay communities (see discussion below).

Energy transfer between the marsh and marine waters

TROPHIC LINKAGE WITH THE SALT MARSH

In the past, direct consumption of plant materials by herbivores and, more importantly, by detritivores has been considered a primary pathway for energy exportation from the marsh into the surrounding waters because many species of fishes were found to consume large amounts of detritus (e.g. Darnell 1958, 1961, Jeffries 1972, Welsh 1975, Sibert et al. 1977, Naiman and Sibert 1979, Nixon 1980, Nixon and Oviatt 1973, Kneib 1984, Teal 1985). However, recent evidence suggests that many of these fishes extract little, if any, energy from detritus and the importance of direct consumption of detritus by fishes in energy exportation has been questioned (see reviews by Boesch and Turner 1984, and Mann 1988).

Because of the dubious importance of direct detritus consumption, research during the last two decades has focused on the role of microbial conditioning of detritus (see review by Mann 1988). It has been found that microbial (bacteria and fungi) colonization of detritus can result in improved nutritional value to animals. However, much of the energy from vascular plant detritus may be lost through microbial respiration because of the extensive conditioning required before animals can efficiently use the detritus. Contrastingly, macroalgae and phytoplankton are more efficiently utilized by animals (due to lower fibrous and higher nitrogen content) and require little or no microbial conditioning. In fact, research suggests algae (benthic and planktonic) may be the most important carbon source even in dense seagrass beds or salt marshes. Most recently, researchers have begun to suggest that dissolved organic matter (DOM), which is released both by living and decaying plants (vascular, macroalgae, phytoplankton), may play an even more important role than plant detritus (see Mann 1988).

Researchers have begun to shift emphasis from primary vascular plant production to total production where energy contained in detritus, associated decomposers, diatom-algal production, and vascular plant production within the intertidal marsh is transferred up through higher trophic levels via predation on intertidal benthic invertebrates (Odum and Heald 1975, Boesch and Turner 1984, Kneib 1984, Currin et al. 1984, Teal 1985). Natant fauna such as crabs, shrimps and fishes move up onto the intertidal marsh surface when it is inundated during flood tides and forage on benthic invertebrates (e.g. Butner and Brattstrom 1960, Welsh 1975, Virnstein 1977, Bell and Coull 1978, Kneib and Stiven 1982, Weisberg and Lotrich 1982, Helfman et al. 1983, Kneib 1984, Abrahams 1985, Kneib 1987, Marinelli and

Coull 1987, Coull et al. 1989). Studies of the carbon source for fishes, shrimps and other marsh invertebrates confirm that Spartina is one source of somatic carbon, but also suggest that carbon derived from phytoplankton and macroalgae sources may be more important (e.g. Odum and Heald 1972, Haines 1975, 1976a,b,1977, Haines and Montague 1979, Hackney and Haines 1980, Hughes 1980, Kneib et al. 1980, Peterson et al. 1980, Fry 1981, Marinucci 1982, Tenore et al. 1982, Mann 1988, Deegan et al. 1990). Energy assimilated by the intertidally foraging predators then becomes available to higher trophic levels through the food web, while detritus and nutrients passed out in excretion and feces are left more accessible to processing by decomposers and detritivores (See Frankenberg and Smith 1967, Tenore et al. 1982, and Kneib, 1984).

PATTERNS OF ENERGY EXPORTATION

The mechanisms by which energy from salt marshes is exported into coastal marine waters are poorly understood. Besides direct water transport of leaf litter, and suspended and dissolved organic matter, all mechanisms of energy exportation from the marsh involve the implicit assumption of trophic transfer of carbon derived from marsh production (both vascular and algal) through interconnecting food webs. The simplest trophic mechanism involves a "diffusion" of energy between overlapping communities (Fig. 6.3). It is difficult, however, to envision how a net one-way export from the marsh could occur by this mechanism. Alternatively, ontogenetic and cyclic migration patterns result in the direct transfer of energy between habitats though animal movements.

Detritus

Exportation into other water bodies can occur through the direct movement of suspended detritus and nutrients through water exchange (Teal 1962, Odum and de la Cruz 1967, Odum et al. 1973, Odum and Heald 1975, Odum 1980, Teal 1985). However, recent studies of salt marshes indicate that they tend to act as a sink for suspended organic and inorganic materials and, therefore, direct transport or "outwelling" of nutrients and detritus from salt marshes to coastal waters may not be as important as once thought (e.g., Erkenbrecher and Stevenson 1975, Haines 1975, 1977, 1979, Wolaver et al. 1980, Wolaver et al. 1985, Dame et al. 1984, Chrzanowski and Spurrier 1987, Spurrier and Kjerfve 1988, Wolaver et al. 1988). In fact net transport direction of nutrients, dissolved organic matter and particulate organic matter have been found to be highly variable between marshes, seasons, and between individual tidal creeks within a marsh (Shisler and Jobbins 1977, Marinucci 1982, Chalmers et al. 1985, Dame et al. 1986, Montague et al. 1987).

Ontogenetic migration

Ontogenetic migration can take one of two forms, season dependent and size dependent (see discussion in Chapter 5). Species may exhibit one or both of these patterns. Numerous researchers have suggested that substantial biomass may be exported from estuaries as fishes and invertebrates undergo seasonal migrations into coastal waters (Smith 1966, Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Welsh 1975, Hackney et al. 1976, Meredith and Lotrich 1979, Bozeman and Dean 1980, Weinstein et al. 1980, Weinstein and Walters 1981, Wiegert and Pomeroy 1981, Allen 1982, Conover and Ross 1982, Daiber 1982, Haedrich 1983, Boesch and Turner 1984, Currin et al. 1984, Kneib 1984, Vouglitois et al. 1987, Chapter 5). Less well known are the implications of size related movements between habitats to energy exportation from the marsh (Chapter 5). A strong tendency for large individuals of several species to "bleed off" out of marsh creeks and other shallow estuarine habitats has been noted for several fishes (Norris 1963, Yakupzack et al. 1977, Major 1978, Weinstein et al. 1980, Weinstein and Walters 1981, Conover and Ross 1982, Weinstein 1983, Weinstein and Brooks 1983, Weinstein et al. 1984, Deegan 1990, Chapter 5). Size dependent migrations of fishes represents a continual drain of carbon from the marsh and has been recently suggested to be a major pathway of energy export from the marsh (Chapter

5).

Since studies of nutrient and detritus transfer between tidal creeks and adjacent marshes have suggested that export through the creeks may not be a major pathway for energy exportation from the marsh (Dame et al. 1986, Chrzanowski and Spurrier 1987, see also my discussion above under the heading Detritus), transfer of energy through nekton movements may be of particular importance in this habitat. Because tidal marsh creeks are a primary interface between the salt marsh and open estuarine waters, and because they provide fish access to the marsh, numerous researchers have pointed out the need for research into the role of marsh creeks as fish habitat and in energy exportation from the marsh (Nixon and Oviatt 1973, Subrahmanyam and Drake 1975, Bozeman and Dean 1980, Weinstein et al. 1980, Currin et al. 1984, Weinstein 1984, Weinstein et al. 1984, Chapter 5). Tidal marsh creeks have been reported as important nursery grounds within the estuary (Cain and Dean 1976, Shenker and Dean 1979, Weinstein 1979, Bozeman and Dean 1980, Weinstein et al. 1980, Hodson et al. 1981, Weinstein and Brooks 1983, Rozas and Hackney 1984, Rozas and Odum 1987, Chapter 1), and some researchers have suggested that the abundant fishes utilizing the creeks as nursery grounds would effectively transfer large amounts of energy when they undergo seasonal migrations out of the creeks (Bozeman and Dean 1980, Currin et al. 1984, Weinstein 1984, Rozas and Odum 1987, Chapter

5). However, little has been done to enhance our understanding of the role of fish use of marsh creeks in this energy transfer, and direct studies quantifying the exchange of energy through immigration/ emigration of these resident fishes have been limited (Weinstein et al. 1984, Zimmerman and Minello 1984).

Two basic patterns of energy exportation through seasonal transfer appear to occur in New Jersey marsh creeks (Chapter 5, Fig. 6.4). In pattern A fishes are spawned either in the open estuary (e.g. *Pseudopleuronectes americanus*) or on the continental shelf (e.g. *Paralichthys dentatus*, *Pomatomus saltatrix*, *Mugil curema*) and recruit to marsh creeks during larval or early juvenile stages. Although some species may not be true residents of the creeks, they appear to utilize the creeks as a tidal foraging ground during a rapid growth period (e.g. *P. dentatus* Chapter 4, 5). Individuals which die in the creeks would represent an importation of biomass into the creeks. However, only biomass at immigration is imported regardless of when mortality occurs. Energy exported from the creeks would be the difference in biomass at emigration from biomass at immigration into the creeks. Although quantitative data are lacking, growth of most species exhibiting this pattern is so great that a net export of energy is likely (Chapter 5).

In a second pattern (B in Fig. 6.4), fishes spawn within marsh creeks (e.g., *Menidia menidia*, *Strongylura* marina, Fundulus majalis) and YOY leave the creeks either upon reaching a limiting size (M. menidia) or upon the onset of migration inducing seasonal conditions (e.g. cold water), or both (Chapter 5). In this case energy is exported through growth, but imported through egg mortality and through mortality of adult spawners. Again there is little quantitative information. However, Conover and Ross (1982) estimated that less than 1% of the YOY population of M. menidia survived the winter to spawn the following spring, suggesting a large one way export of biomass to the continental shelf. The fate of the adult fish after spawning is unclear (Chapter 5), but Conover and Ross (1982) indicate that few fish survive to a second spawning season. Because of their relatively large size, mortality of adult M. menidia may represent a significant return of energy to marsh creek habitat (Chapter 5).

Cyclic foraging migrations

Both tidal (Chapter 2) and diel (Chapter 3) cyclic foraging migrations appear to be important in the salt marsh. Energy exchange between the intertidal and subtidal marshes and the adjacent estuary can result from these cyclic foraging activities (Fig. 6.5). Marsh creeks are a major avenue of fish movements between the marsh and adjacent estuarine waters and, therefore, serve to energetically couple these areas. Several orders of energetic coupling may be identified. A primary coupling between the intertidal marsh and tidal marsh creek is established by the foraging activities of permanent and seasonally resident marsh creek fishes. The key to this model is the spatial separation of important foraging habitats from residence habitats due to the cyclic disturbance of the tides, or of diel changes in physical conditions. Fishes gain limited access to habitats with abundant food sources with the inundation of intertidal marsh areas on flood tides, but then must retreat to other areas due to physiological or behavioral limitations imposed by low tide conditions. For example, fishes foraging on the intertidal areas of the marsh would be forced to retreat into creeks and tide pools as the tide ebbs. Nixon and Oviatt (1973) estimated that foraging grounds were only available to predators 25 % of the time in a New England salt marsh. Because the subtidal marsh creek is used as a low tide refuge, it would be energetically coupled to the intertidal marsh foraging grounds. Energy would be exported from the intertidal foraging area as materials are consumed and incorporated into consumer biomass and transferred into the low tide habitat. Some of this energy would be entrained in the local low tide habitat through fish mortality (and local decomposition) and fecal deposition, while some would be exported out of the system through emigration of fishes into other areas and through predation by fishes coming from outside the primary coupling system. The primary coupling between the intertidal marsh and tidal creek has been basically implied in the discussions of transfer of energy between these areas through trophic interactions among detritivores, benthic infauna and resident natant predators (Nixon and Oviatt 1973, Odum and Heald 1975, Welsh 1975, Kneib 1984, Teal 1985).

Similarly, movements of fishes into, and out of, tidal marsh creeks result in a secondary energetic coupling where energy ultimately derived from the intertidal marsh and marsh creek is exported into the adjacent estuarine waters (Figure 6.5). This type of energy export can occur through emigration of seasonal residents of marsh creeks (nursery species), through the foraging activities of transient species, or through the movements of predators which regularly migrate between marsh creeks and adjacent estuarine waters with each tidal cycle. The secondary coupling of energy between tidal marsh creeks and adjacent estuarine areas has not been clearly addressed in the literature (although transfer by seasonally migrating fishes has been discussed briefly as indicated above). In this model, then, energy would be successively passed from the intertidal marsh into the marsh creek and then into the adjacent estuary through regular tidal movements of fishes between these adjacent habitats.

Energy transfer through materials passed along in fecal deposits may be an equally important pathway. The importance of reprocessed fecal materials in the detrital food web has been discussed previously (Frankenberg and Smith 1967, Nixon and Oviatt 1973, Odum and Heald 1975, Welsh 1975, Tenore et al. 1982, Kneib 1984, Teal 1985), but the physical transfer of organic energy from an area of foraging activity to another area through deposition of fecal materials has not been specifically examined in the estuarine habitat. This mechanism of transfer of energy from one area to another by a spatial segregation of foraging area and areas where feces are deposited has recently been recognized as important for marine systems such as coral reefs and artificial reefs (e.g. Bray et al. 1981, Meyer et al. 1983, Bray and Miller 1985, Meyer and Schultz 1985a, 1985b, Rountree 1990). For example, some coral reef fishes have been found to deposit fecal material upon the reefs after feeding in nearby grass beds, accomplishing a transfer of energy from grass beds to coral reefs (Meyer and Schultz 1985a, 1985b). Although the importance of energy exportation from marshes via direct consumption of detritus has been questioned by recent investigators, the fact that many fishes consume large quantities of detritus suggests that a transfer of energy through deposition of fecal materials within the subtidal creek by fishes feeding in intertidal areas may be an important pathway for energy exchange.

The primary coupling between the subtidal creek and intertidal marsh is best exemplified by Fundulus heteroclitus (Fig. 6.6). This species is well known to forage on the intertidal marsh during tidal inundation and tends to retreat to subtidal areas with the tide, though early life history stages may remain in small pools on the marsh surface (Baker-Dittus 1978, Weisberg et al. 1981, Kneib 1984, 1987). In fact, F. heteroclitus is more closely linked to Spartina production, based on carbon isotope studies, than any other species so far examined (Jeffries 1972, Kneib et al. 1980, Hughes and Sherr 1983). In New Jersey this species was found to undergo tidal movements into intertidal areas, but appears to utilize subtidal areas as a low tide refuge (Chapter 2, 3). Fecal deposition and mortality in the subtidal area would constitute an export of energy from the intertidal to subtidal marsh (Fig. 6.6).

Nocturnal movements of Menidia menidia into the intertidal marsh (Chapter 3), however, may result in a significant import of energy into the marsh. Menidia menidia appears to utilize shallow subtidal and intertidal marsh creek habitats as a nocturnal refuge rather than as a primary foraging ground. In fact, the species probably gets most of its food resource from pelagic zooplankton (see discussion in Chapter 3). If this pattern is confirmed, then deposition of fecal material in the shallow habitats by M. menidia (and potentially other species) during this nocturnal refuge, may result in a tremendous importation of nitrogen into the intertidal marsh. A similar mechanism of nitrogen enrichment of coral reefs refuge habitat by planktivores has also recently been suggested to be important to coral reef ecology (Meyer et al. 1983, Meyer and Schultz 1985a,b).

Trophic coupling between the subtidal marsh creeks and adjacent bay habitat is best illustrated by the behavior of *Paralichthys dentatus* (Fig. 6.6). Late juveniles of *P. dentatus* were found to undergo regular tidal movements into New Jersey marsh creeks to feed (Chapter 4, Szedlmayer and Able in prep.). Individuals captured in gill nets on ebb tide (assumed to be leaving the creeks) had significantly higher gut fullness values than those captured on flood tide (assumed to be entering the creeks). *Menidia menidia*, *Palaemonetes vulgaris*, *Crangon septemspinosa* and *Fundulus heteroclitus* were found to be the primary prey of *P. dentatus*. Although only *F. heteroclitus* has been shown to be closely linked to *Spartina* production (Kneib et al. 1980, Hughes and Sherr 1983; *Palaemonetes pugio* which is closely related to *P. vulgaris* may also be closely linked to marsh production Jeffries 1972, Welsh 1975, Hughes and Sherr 1983), foraging on these marsh species by *P. dentatus* is likely to represent a close trophic link to the salt marsh. Again, however, as mentioned above I am interested in mechanisms of energy transfer to coastal waters through trophic linkage to total marsh production, which includes algal and phytoplankton sources, rather than just vascular plant production. Fecal deposition and mortality while in the bay habitat result in an export of carbon from the subtidal creek to bay.

Evolution of marsh use

As I discussed above, the vegetated salt marsh tends to act as a sink for suspended organic particles, dissolved organic matter and even nutrients. Usually this is viewed in terms of potential export of terrestrial and marsh materials into adjoining estuarine and coastal waters. Implications to materials brought in from these areas have not be explored. For example, Dame and his colleagues (Dame et al. 1986), found that although no net transport of phytoplankton occurred in the marsh, composition changed from predominantly pelagic, to benthic forms from flood to ebb tide. They suggested that pelagic forms may have been removed through biofiltration, while benthic forms may have be suspended into the water column through tidal mechanical action (Dame et al. 1980, 1986).

Numerous studies have suggested that biofiltration may play an important role in energy cycling between the benthos and water column in shallow estuarine and marsh habitats (see Dame et al. 1980, 1986, Peterson and Black 1991). However, the importance of mechanical filtering of marine plankton in the marsh has not been investigated (Fig. 6.7). Phytoplankton and zooplankton (including fish larvae) carried into the marsh by the tides may get trapped in the shallow water, particularly during slack tide. Macro-algae and vascular plants would further trap water, and plankton, in the marsh. Rapid changes in water temperature, salinity and other physical conditions together with physical abrasion among plant stems, in the shallow marsh may result in high mortality of pelagic forms. Plankton which die would tend to be retained in the marsh. Further, plankton trapped in the shallows would be easy prey for benthic filter and deposit feeders, which may partially account for the abundance of these forms in the marsh.

Those larvae of marine fishes and invertebrates which could adapt to the harsh conditions in the shallow marsh would be in an environment with abundant food resources and with relatively low predation pressures from aquatic sources. However, increased body size with growth could lead to disadvantages, such as susceptibility to avian predation (see Kneib 1982, Power 1987), as well as increased energy, and space requirements. Hence, most resident marsh creek fishes achieve a small maximum size, while most species which utilize the marsh as a nursery also appear to emigrate at a relatively small size (Chapter 1, 5). In fact, most species emigrate from New Jersey marsh creeks by about 100 mm in length, which is also near the maximum size of marsh resident species such as _F. heteroclitus_ (Chapter 1,5).

Few large fishes are found in subtidal and intertidal marsh habitats (Chapter 1, 3). Most of these large species have body forms which allow maximum size in shallow water (e.g., the fishes Anguilla rostrata, S. marina, P. dentatus and the crab Callinectes sapidus). Species which have body forms pre-adapted to allow maximum size in shallow habitat (e.g. anguillaiform, or flattened bodies), and which can tolerate the variable physical conditions, could exploit the rich food resource (i.e., early life stages of nursery species and all stages of marsh residents) in the creek habitat.

Comparison with oceanic systems

Strong parallels in both patterns of community structure and patterns of trophic energy transfer can be found in literature on the oceanic communities. All the patterns which I describe for marsh/estuarine communities have parallels in deep sea communities. Though it is beyond the scope of this paper to provide a complete review of these patterns in deep sea literature, some brief examples are presented below. Vertical depth distributions of zooplankton and nekton are influenced by physiological tolerances to conditions and interspecific competition; size stratification can occur with depth; many organisms undergo vertical diel migrations, and ontogenetic migrations (usually from a pelagic larval/juvenile stage to demersal/benthic adults) are common (Marshall 1971, Longhurst 1976, Mauchline 1980, Young et al. 1980, Roe 1983, Wakefield and Smith 1990).

Just as estuarine scientists are concerned with processes of energy exportation from the highly productive marsh/estuary to coastal marine waters, marine scientists are concerned with processes by which energy moves from the highly productive surface waters of the photic zone to the benthos (in both shallow and deep seas). The importance of detritus or "organic rain" in the ocean has received considerable attention (Lohmann 1908 cited in Krey 1957, Bruun 1957, Fox 1957, Krey 1961, Parsons 1963, Krey 1967, Vinogradov 1971, McCave 1975, Honjo 1980, Stockton and Delaca 1982, Fowler and Knauer 1986, Alldredge and Silver 1988, Wakefield and Smith 1990). Merrett (1978) was apparently the first to suggest that ontogenetic vertical migration might be an important mechanism of trophic exchange of energy between deep sea layers. Ontogenetic transport of material in the deep sea has only recently been studied (Wakefield and Smith 1990).

The importance of cyclic diel vertical migrations to energy transfer has received much more attention in deep sea literature (Vinogradov 1953, Marshall 1971, Longhurst 1976). In fact, the hypothesized trophic linkage among estuarine habitats through tidal and diel migrations is reminiscent of Vinogradov's "ladder of migration" hypothesis for organic transport through vertical layers in the deep ocean (Vinogradov 1953, 1955 cited in Longhurst

1976). In patterns similar to the estuary, animals tend to move into shallow waters at night, and return to deeper waters during the day, and numerous researchers have debated whether these patterns result from foraging movements, or movements to escape predation (Longhurst 1976, Young et al. 1980, Mauchline 1980). Distributions of some species of fishes and squids have been suggested to be limited by countershading abilities (Young et al. 1980). Alternatively, diel movements may result from a strategy of feeding in warmer shallow depths, and returning to colder depths, where they remain in a lethargic state to gain a metabolic advantage (McLaren 1963, McAllister 1969, Clarke 1970, Marshall 1971, Youngbluth 1975, Mauchline 1980), as I have suggested for Paralichthys dentatus (see discussion above).

These two systems, estuarine and deep ocean, therefore, have two underlying similarities: 1) most primary production (i.e., all photosynthesis) occurs in a narrow band at shallow depths (coastal and photic zones, respectively), and 2) similar mechanisms operate to transport energy along a depth gradient. These parallels suggest to me a fascinating concept of community evolution resulting from increasing complexity of mechanisms to partition resources (Fig. 6.8). Since both these systems are overwhelmingly dominated by communities based on photosynthetic production, it is reasonable to assume that communities originally evolved at the source of production.

In their early evolutions, organic carbon in both systems would have been lost through gravity (sinking in water column in oceanic communities) or outwelling (i.e., net water flow in estuaries is seaward due to freshwater input, in estuarine communities). This means that a potential food source would be displaced from the production source towards deeper water.

Evolution of adaptations to exploit this resource could result in the patterns of energy exchange illustrated in Fig. 6.3 and discussed above. Some species might evolve the adaptation of undergoing cyclic migrations to obtain a bioenergetic advantage (also useful to survive fluctuations in food availability), or as a means to partition its resources among separate communities neither of which could support it alone. Ontogeny itself may have evolved as a mechanism to exploit deeper food resources. Few individuals reach large size because resources are less abundant. These processes would lead to a gradual expansion of increasingly complex and interconnected communities towards deeper water. Communities based on photosynthetic primary production would start out relatively simple, and concentrated in zones of optimum primary production (i.e., surface, and shallow shelf zones). Adaptations allowing organisms to move deeper in the water column would allow them to capitalize on resources available in detritus and organic rain. Hypothesized energetic benefits of movement into deeper water after feeding might allow organisms to survive through periodic short term flux in food availability. As has frequently been suggested, movement into deeper water with growth may be a mechanism to reduce intraspecific competition, and cannibalism (see my discussion above, Helfman 1978, Macpherson and Duarte 1991). Macpherson and Duarte (1991) examined trends between fish size and depth and concluded that movements towards deeper water during ontogeny result from benefits of extended lives and lower metabolism at lower temperature. They also describe this movement as often being a "diffusive" process. I propose that this trend evolved as a mechanism (illustrated in Fig. 6.8) for communities and organisms to efficiently utilize energy.

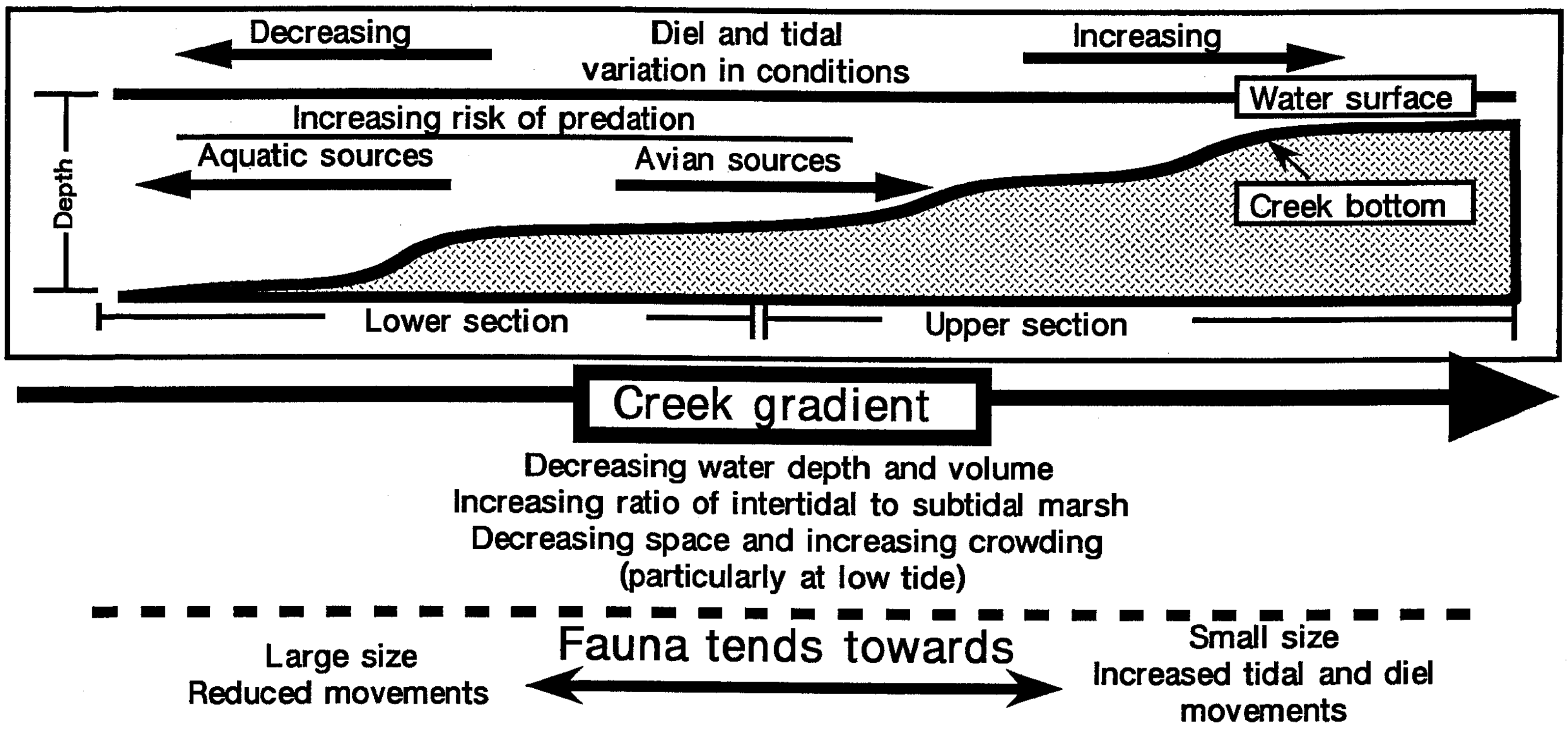


Figure 6.1. Schematic of hypothetical gradients in physical and biological conditions which may be formed along a creek mouth-to-headwater gradient. Assuming equal high tide densities, crowding in the subtidal creek at low tide would increase moving up the creek gradient. Risk of predation by aquatic predators would increase moving down the creek gradient, while risk of predation from avian sources may increase moving up the creek. Tidal drainage (ratio of intertidal to subtidal volume), and diel and tidal variation in environmental conditions would tend to increase moving up the creek gradient. In response to these gradients in physical and biological conditions, the prevalence of tidal and diel movement in the community would be expected to increase moving up the creek gradient, or from large to small creeks (see text for complete explanation). Additionally, fish size tends to be reduced moving up the creek, and to increase moving down the creek in response to ontogenetic release of aquatic predation pressures with size, and to increased space requirements with size.

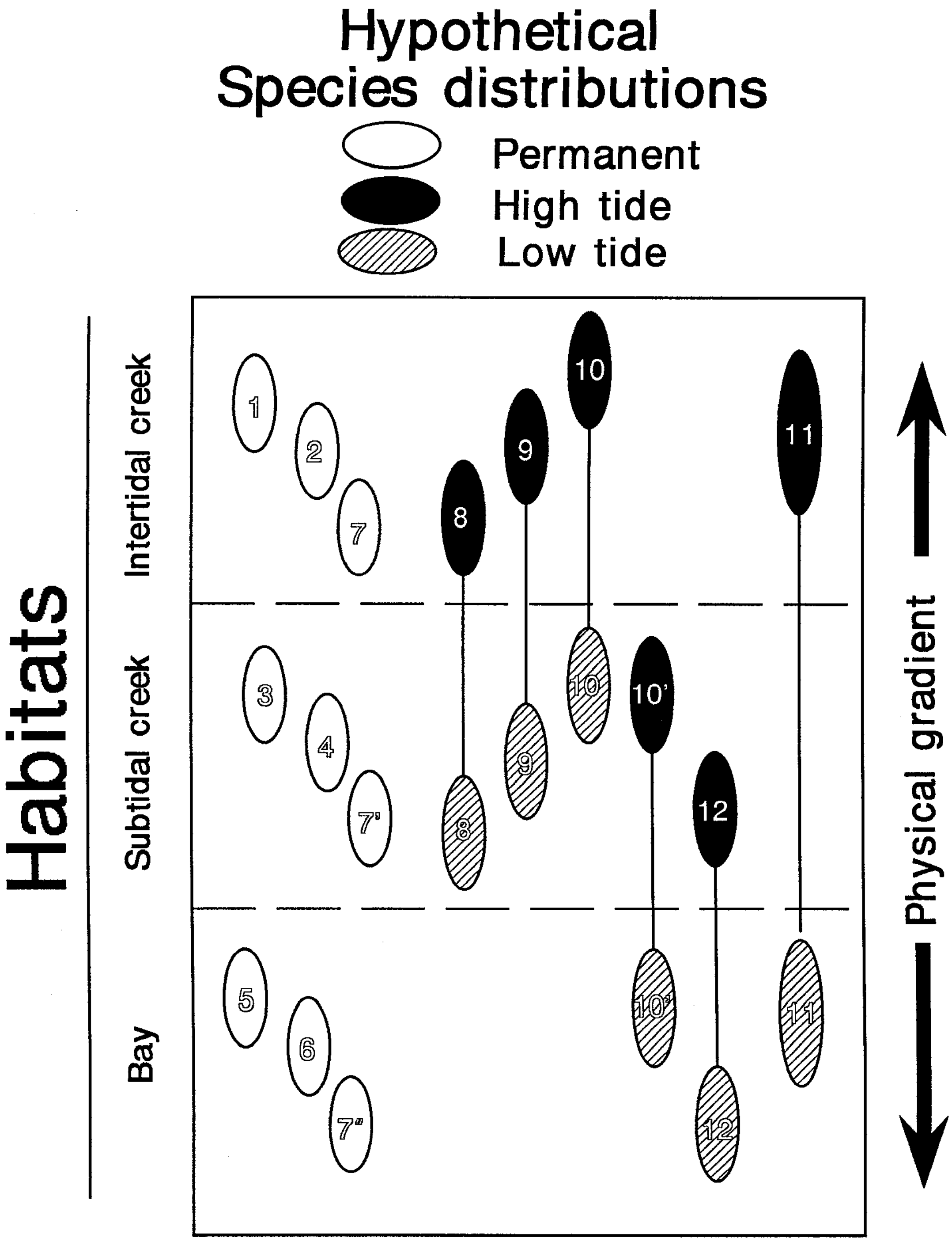


Figure 6.2. Hypothetical species distributions among bay, subtidal creek and intertidal creek habitats under the influence of tidal fluctuations in conditions (see text). Two basic types of distributions occur, 1) species are restricted within one habitat by the balances among physiological tolerances, competition and threat of predation (species 1-6); 2) mobile species move between habitats in response to tidal flux (species 8-12). During each tide stage distributions within each habitat of species 8-12 are regulated as in the first distribution type.

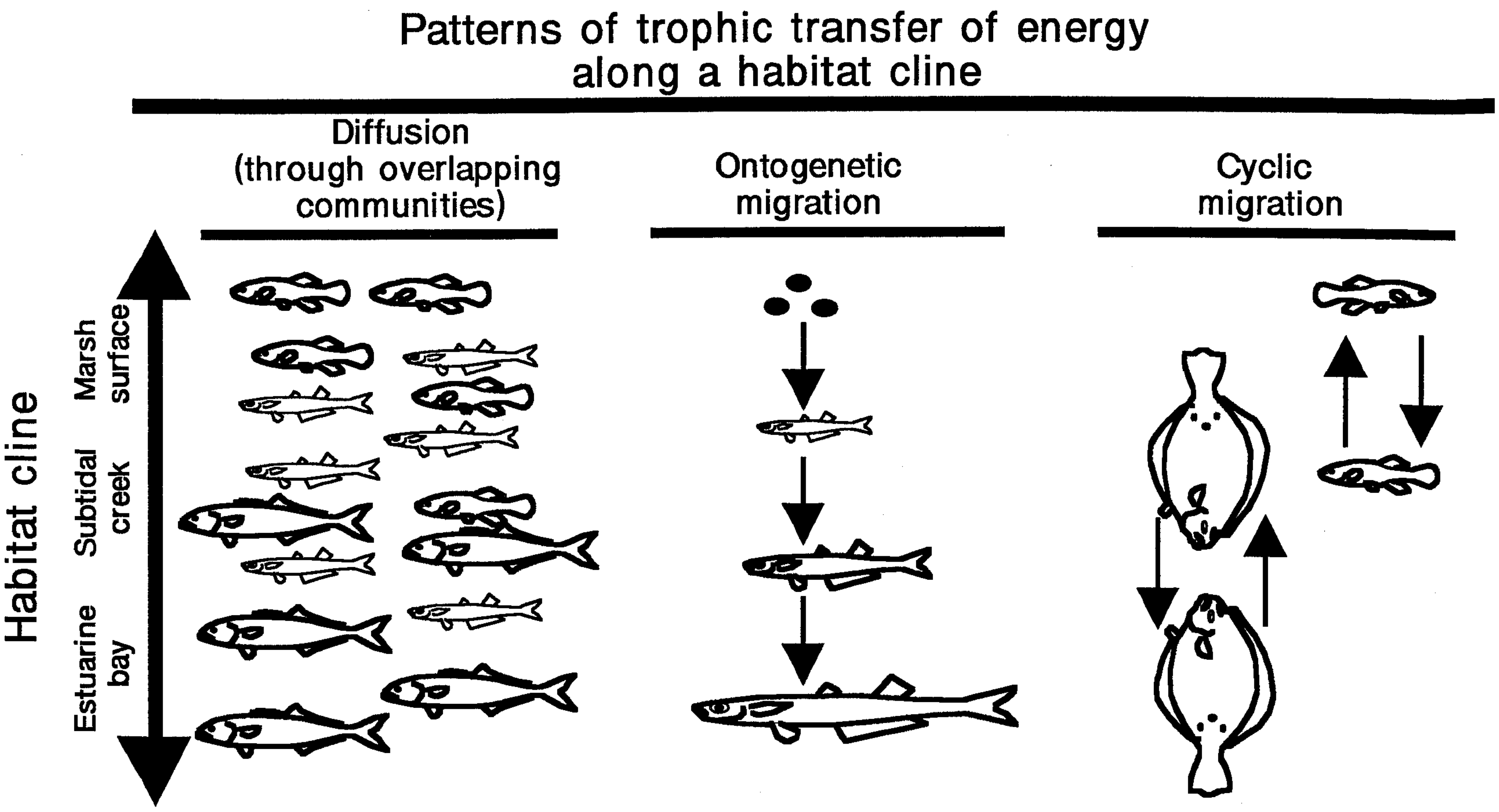


Figure 6.3. Patterns of trophic transfer of energy, derived from primary production on the marsh surface, through fish and invertebrate communities along an estuarine habitat cline. The simplest mechanism is through a diffusion of energy through the interconnecting food webs of spatially overlapping communities (estuarine bay, subtidal creek and marsh surface communities). Ontogenetic migration (including seasonal or size dependent movements, see text) of species between adjacent habitats results in the direct export of energy assimilated in somatic growth. Cyclic foraging migrations of species between habitats also results in the direct transfer of energy among habitats.

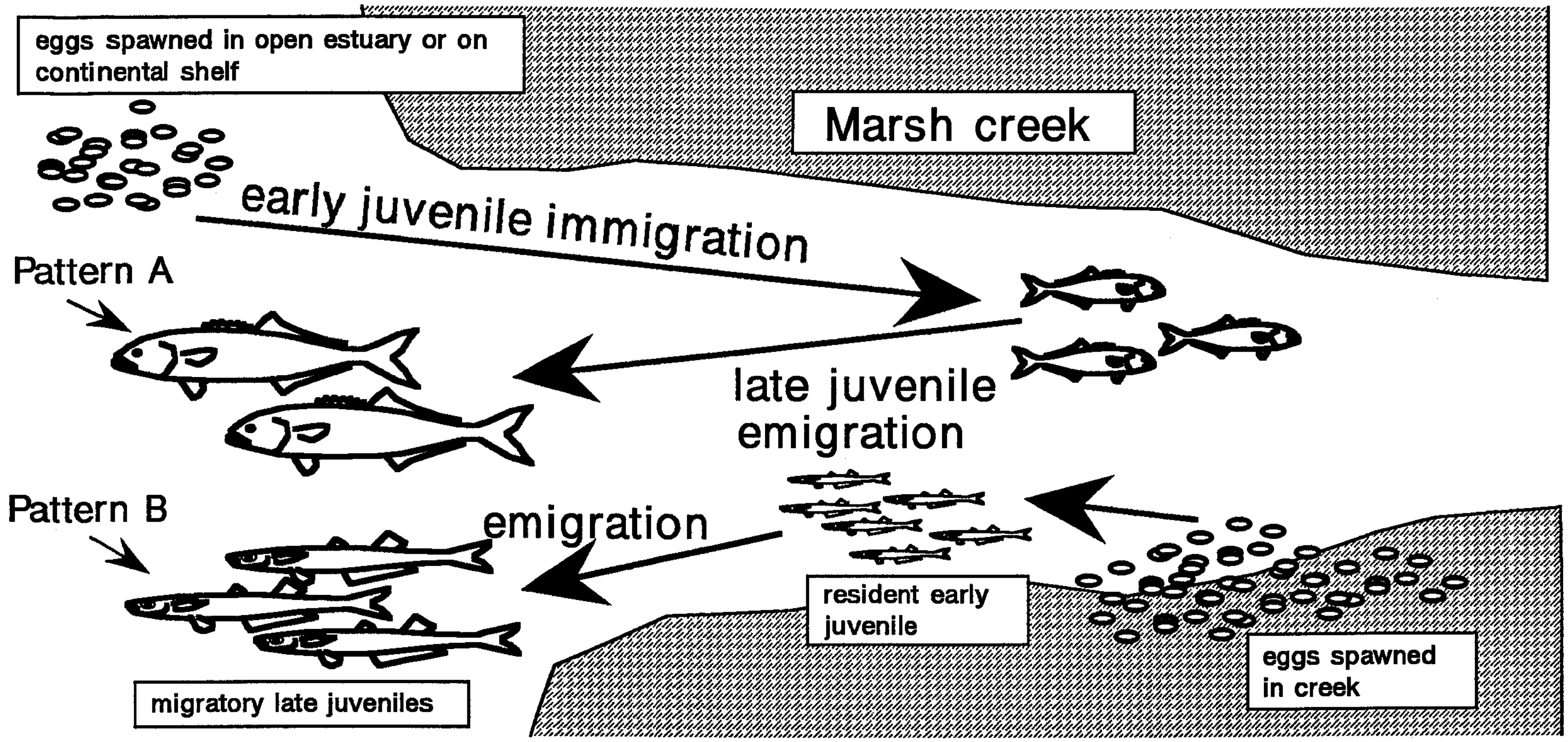


Figure 6.4. Two major patterns of energy export through seasonal movements of fishes occur in New Jersey marsh creek habitat. Pattern A: fishes are spawned outside of creek habitat, either in the open bay or on the continental shelf (e.g., *Pomatomus saltatrix*), and recruit into the creeks at a relatively large size. Pattern B: fishes are spawned in the creeks and emigrate as they grow (e.g. *Menidia menidia*). Net energy exported per fish is equivalent to somatic growth within the creek habitat, however energy imported into the creeks through fish mortality (juveniles in Pattern A, eggs and spawning adults in Pattern B) must be deducted from energy exported through juvenile emigration to determine net total energy exported.

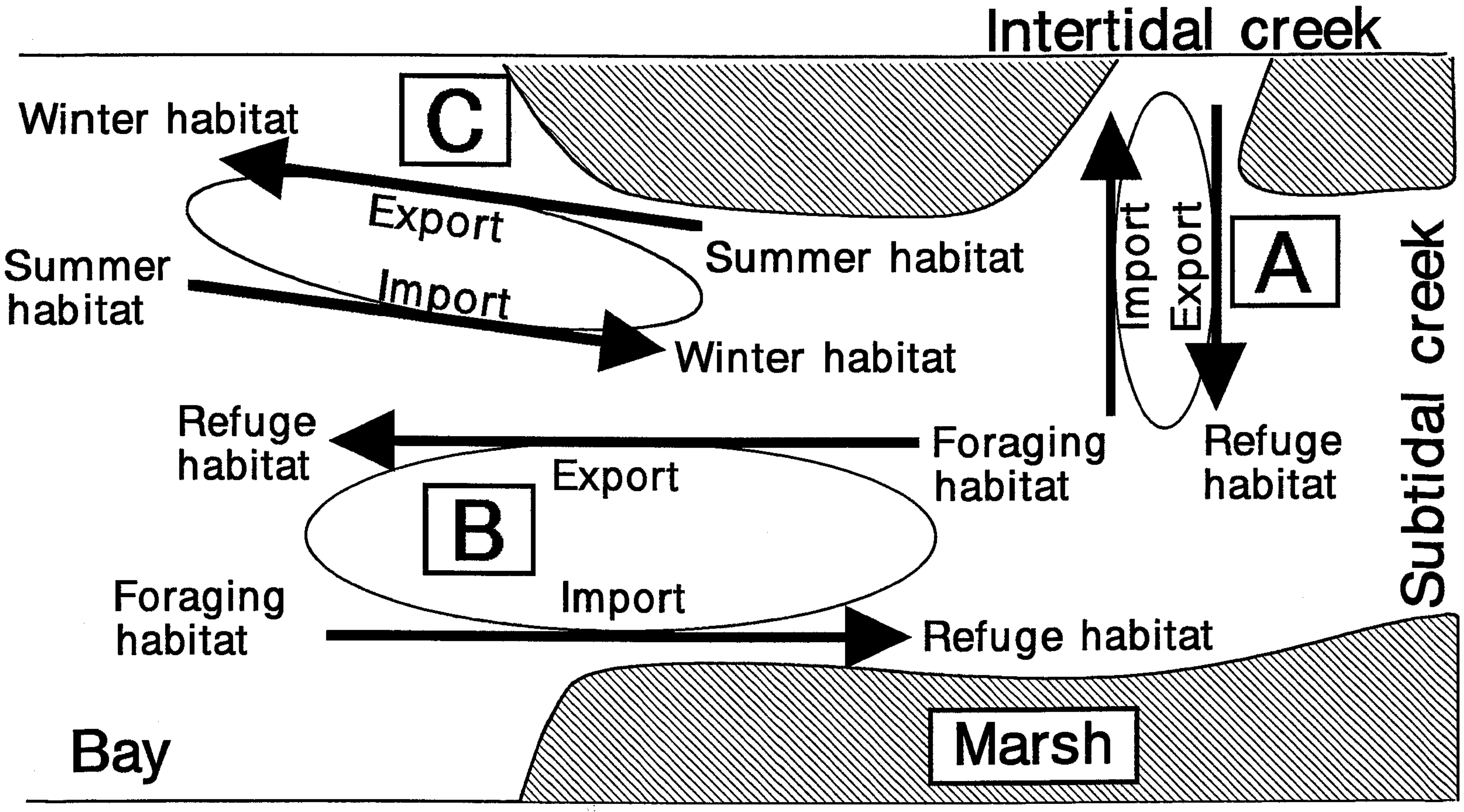


Figure 6.5. Schematic of energy flow among the intertidal marsh surface, subtidal marsh creek, and adjacent estuarine bay habitats. Trophic coupling between adjacent habitats results from seasonal movements, or diel and tidal foraging movements. Three orders of trophic coupling are indicated: A) a primary coupling between the intertidal marsh and subtidal marsh, B) a secondary coupling between the subtidal marsh and bay, and C) a seasonal coupling between the marsh and other habitats. The primarily and secondary couplings involve cyclic (diel and/or tidal) movements between adjacent foraging and refuge habitats. Refuge habitats serve as shelter from predation, or from stressful environmental conditions (e.g., low tide in intertidal habitats). Energy would tend to be removed from foraging habitats and deposited in refuge habitats through mortality and fecal deposition. For example, species which forage within the intertidal marsh would likely accomplish a net export of energy out of the marsh, while species which use the intertidal marsh as a refuge habitat would likely accomplish a net import of energy into the marsh (see text for complete explanation).

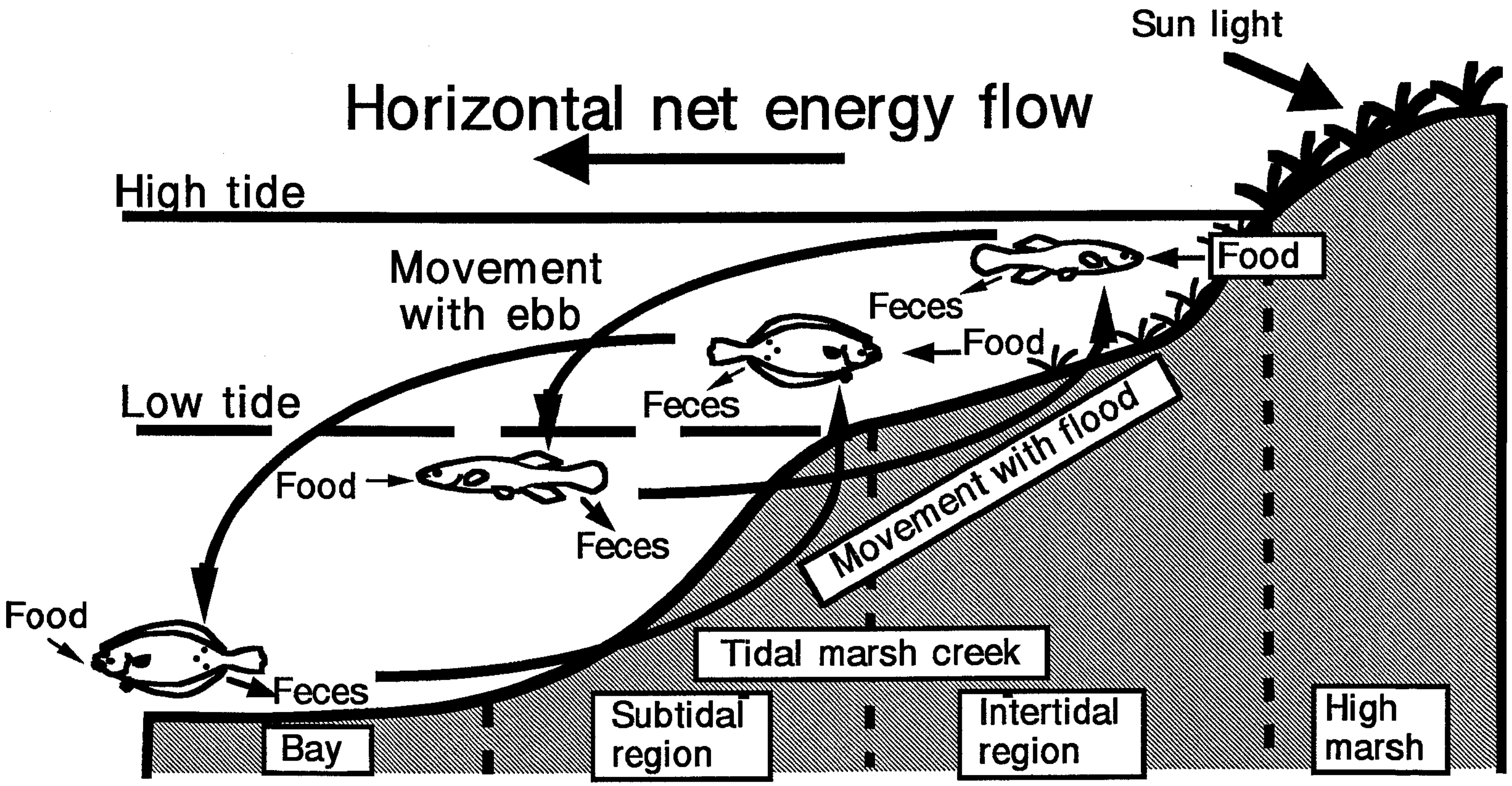


Figure 6.6. Hypothetical energy flow among New Jersey intertidal marsh, subtidal marsh and bay habitats resulting from foraging movements of *Fundulus heteroclitus* and *Paralichthys dentatus*. Foraging by *F. heteroclitus* in the intertidal marsh results in a transfer of energy (fecal materials and mortality) to the subtidal marsh where the species retreats at low tide, thus establishing a primary coupling between subtidal and intertidal marsh habitats (see Fig. 6.5 and text). Predation on *F. heteroclitus* during the tidal foraging activity of *P. dentatus* results in an export of energy from the subtidal marsh to the adjacent bay, establishing a secondary coupling between the bay and intertidal marsh habitats.

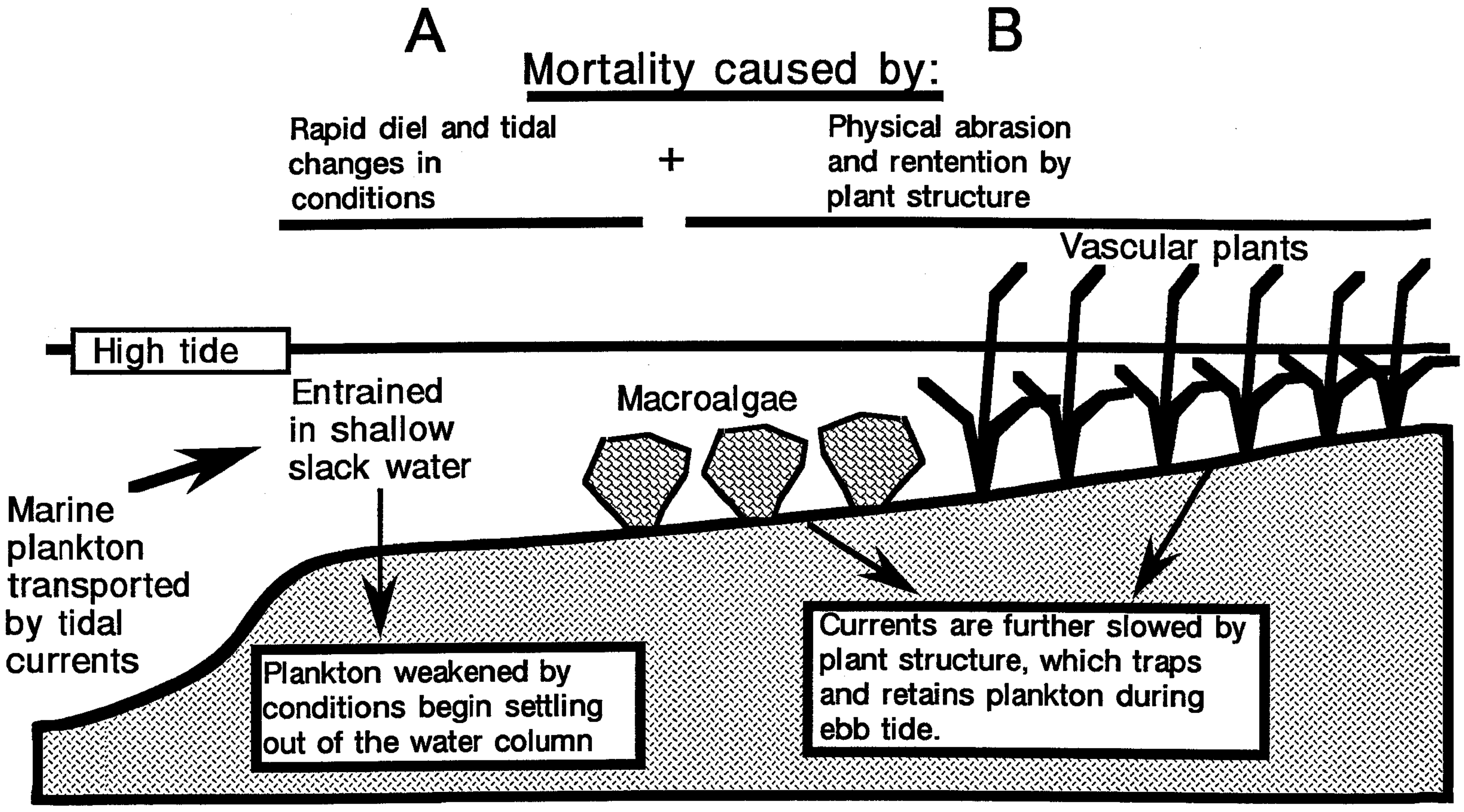


Figure 6.7. Biofiltration of marine plankton transported by tidal currents into shallow marsh habitats. Marine plankton transported into shallow marsh habitats are subject to numerous adverse conditions, including: the loss of suspension due to reduced current velocity, physical abrasion with the substrate and with plant structure, physical entrapment by plant structure (especially by macroalgae during receding tides), and stress due to rapid diel and tidal changes in water temperature, dissolved oxygen concentration, salinity, and other environmental conditions.

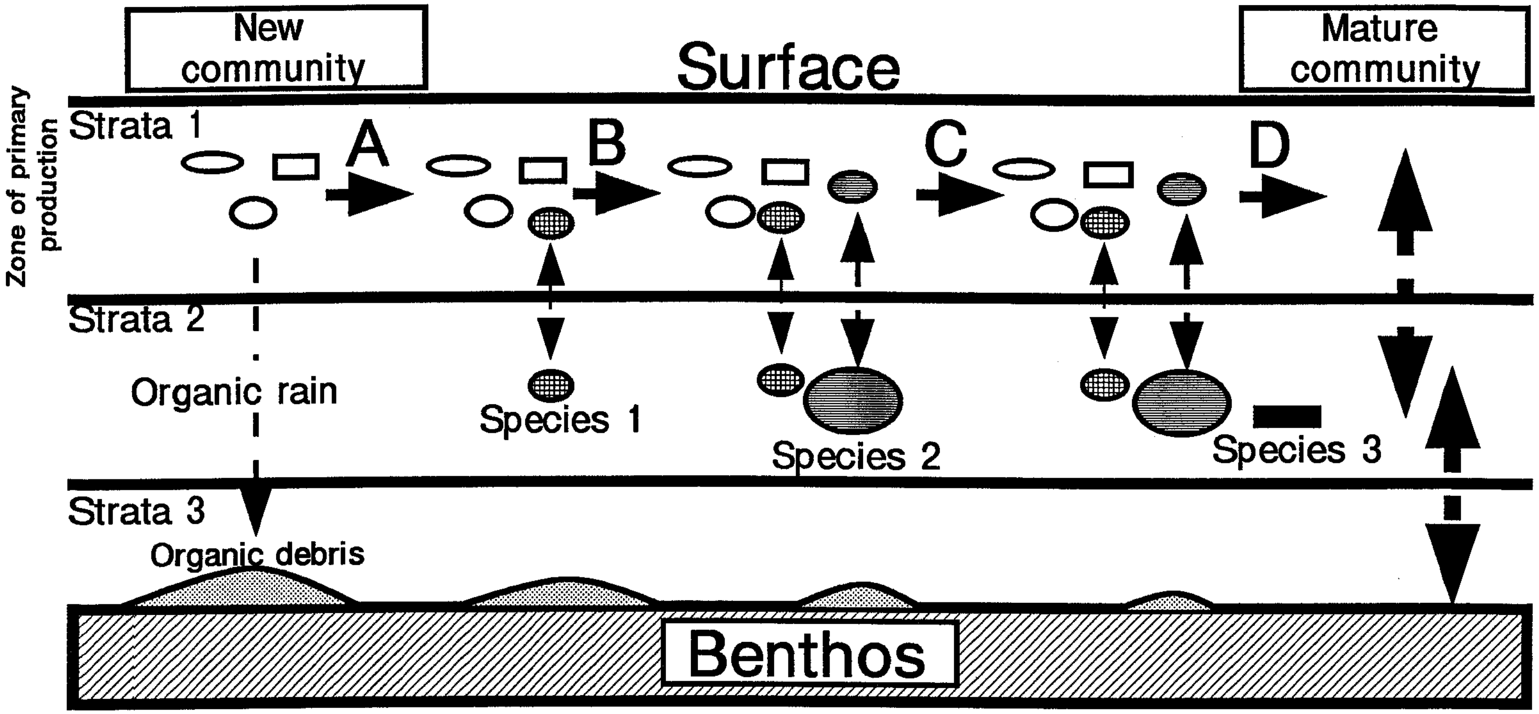


Figure 6.8. Hypothetical model of community succession resulting from the development of an increasing complexity of mechanisms to partition resources and conserve energy (carbon). Three arbitrary depth strata are depicted (strata 1=photic zone, strata 2=mid-water column, strata 3=benthos). Symbols represent different species. Vertical dashed arrows represent energy (carbon) flux through vertical migrations. Horizontal solid arrows represent community successional steps (presented in an arbitrary order). Four steps (A-D) in a succession from a new community towards a mature community are illustrated. Each step is characterized by the development of a new mechanism (species 1-3) to partition resources among species. In the new community, energy is constantly lost to the system through the sinking of organic materials to the benthos. In step A, species 1 develops the ability to undergo cyclic migrations between strata 1 and strata 2. This strategy has several possible advantages, including metabolic advantages (see text) and access to an unexploited organic rain resources. In step B, species 2 develops the adaptation of utilizing strata 1 and 2 at different life history stages. As more species begin utilizing strata 2, some species such as species 3 (Step C) become endemic to strata 2. Species 1 & 2 provide a trophic coupling (see Fig. 6.5 and text) between strata 1 and 2. The process continues until all three strata are interconnected by trophic couplings involving various patterns of trophic energy transfer such as diffusion, ontogenetic migration and cyclic migration among strata (see Fig. 6.3 and text). In the mature stage, carbon is conserved and is constantly cycled among strata through fish movements.

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