A

FEEDING PATTERNS OF SALT MARSH FISHES

by

KENNETH LYNK

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy, The City University of New York

2003

UMI Number: 3103137

UMI Microform 3103137

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

25 March 2003
Date

Chair of Examining Committee
Dr. Joseph Rachlin, Lehman College

August 7, 2003
Date

Richard L. Chappell
Executive Officer
Dr. Richard L. Chappell

Dwight Kincaid
Dr. Dwight Kincaid, Lehman College

Dr. Liesl Jones, Lehman College

Paul Maderson
Dr. Paul Maderson, Brooklyn College

Barbara L. Warkentine
Barbara Warkentine, SUNY Maritime College

David R. Franz
Dr. David Franz, Brooklyn College (Reader)

The City University of New York

Abstract

Feeding Patterns of Salt Marsh Fishes

by

Kenneth Lynk

Adviser: Dr. Joseph W. Rachlin

Salt marshes are widely recognized as faunal nurseries but feeding studies of salt marsh fishes have often focused on a single species (*Fundulus heteroclitus).* To accurately assess the feeding habits of salt marsh fishes, fish must be sampled after feeding inside the marsh and after feeding in the outer estuary because fish exit the marsh during outgoing tides and reenter with incoming tides. Three species (*Fundulus heteroclitus, Fundulus majalis, Menidia menidia)* were consistently collected with a fyke net and were subjected to intraspecific comparisons of diets between the salt marsh and the outer estuary using the modified form of Morisita's index. *Fundulus majalis* consumed gastropods (*Hydrobia sp., Littorina spp.*) frequently in the marsh and rarely outside the marsh. The bivalve *(Gemma gemma)* was consumed in both environments. Molluscs numerically dominated the diet across all sampling seasons and years. During fall, non-molluscan prey were almost excluded from the marsh diet and this led to a diet shift between the salt marsh and the outer estuary. *Fundulus heteroclitus* is known to feed actively during high tide periods and a higher proportion of empty guts at the end of low tides in this study reflects this pattern. Its diet is not dominated by a few prey taxa. For *Fundulus heteroclitus*, diet shifting between the marsh and the outer estuary appears to be related to its highly diversified diet. Diet overlap measures for *Menidia menidia* are seasonally influenced. Copepods numerically dominate the prey count during spring, early summer, and fall in the marsh and in the outer estuary. Diet shifting occurs in July when additional zooplanktivorous, nektonic and benthic prey are consumed. Consumption of seasonally available brachyuran megalops, ostracods and harpacticoids by smaller *Fundulus majalis* does not always lead to a measurable ontogenetic diet shift between size ranges from the same sample. Diet diversification in *Fundulus heteroclitus* increases with fish size and diet shifts between size ranges are measurable. Ontogenetic diet differentiation in *Menidia menidia* was minimal in spring and fall when copepods dominated the diets. A shift occurs in July, as smaller *Menidia menidia* continue to consume copepods while larger fish consume megalops.

Acknowledgments

The collections at the Caumsett salt marsh could not have occurred without the support of the Queens College Center for Environmental Education and Research. The Center is located within Caumsett State Park and it provided logistical and vehicular support for all collections. They also acted as a vital intermediary with the State Park Service. I also thank Mr. Paul Speranza, a friend and colleague, who withstood the brunt of the insect attacks while assisting in the field. The support of my wife Janet in the field and during the writing process sustained me over more the years and I can never adequately express my gratitude to her.

Table of Contents

Feeding Patterns of Salt Marsh Fishes

Introduction

Methods

Results

Discussion Page

Future Research Directions

List of Tables

List of Tables - continued Page

List of Figures

Appendices

Feeding Patterns of Salt Marsh Fishes

Introduction

Feeding Studies of Salt Marsh Fishes

Monospecific Studies

It is well known that salt marshes are important faunal nurseries. The diversity of juvenile taxa within a salt marsh is a consequence of the diversity of habitats. Subtidal marsh creeks act as nurseries for resident fish species, continental shelf spawned species, and shrimp (Roundtree and Able 1992a). Larval grass shrimp *(Paleomonetes pugio)* remain in aquatic refugia in the intertidal zone of salt marshes after the high tide recedes (Kneib 1987). Continuous occupation of intertidal habitats by zooplankton is ensured by a diversity of life history strategies (Houser and Allen 1996). Additional zooplankton enter the marsh with the incoming tides. Together, the internal production and tidal flux of invertebrates support fish populations of the marsh. This community of marsh fishes consists of small sized residents and transients. Piscivory is probably uncommon among marsh residents (personal observation), and while all fish species can potentially feed on a vast faunal array, detailed studies of feeding habits within salt marshes lag behind those of less saline environments. At the monospecific level, only the feeding habits of a single marsh resident species, *Fundulus heteroclitus* or the mummichog, have been reported in interrelated field studies (Weisberg et al. 1981, Rozas et al. 1988, Allen et al. 1994). These reports have been supplemented by studies which incorporate habitat manipulation (Weisberg and Lotrich 1982, Kneib 1986, Wiesberg 1986) and experimental protocols

(Vince et al. 1976, Cross and Stiven 1997). No other salt marsh resident species has received an equivalent level of attention.

Reports on the diets of wider ranging species have tended to avoid observations of diets within salt marshes. Winter flounder *(Pseudopleuronectes americanus)* have been collected from a variety of estuarine habitats for diet analysis (Pearcy 1962, Franz and Tanacredi 1992, Stehlik and Meise 2000) but ecologists have rarely ventured into the marsh for samples. No doubt this is partly due to the difficulties encountered when sampling fish in a marsh. Neighboring estuarine waters are easily seined or trawled. Less accessible salt marsh ponds with deep mucky bottoms are difficult to sample but these habitats could be congregating areas for young of year flounder. Young of year summer flounder, *Paralichthys dentatus,* use marsh channels as nursery and foraging habitats (Roundtree and Able 1992b). Surely other seasonal pisicivores forage in deep marsh channels. Migratory juvenile bluefish, *Pomatomus saltatrix,* inhabit local estuaries and prey on other fish species within the estuarine nursery (Richards 1976, Friedland et al. 1988, Juanes et al. 1993, Buckel and Conover 1997) but the species pursuit of prey into marshes (personal observation) where habitat structure can change prey vulnerabilities (Buckel and Stoner 2000) remains uninvestigated.

If the nursery function of salt marshes is widely accepted, then it follows that salt marshes can be viewed as feeding grounds for the earliest life history stages of resident and transient species. Yet, despite the vital role salt marshes play in the reproduction and survival of resident and migrant species, there is a dearth of monospecific reports on fish diets inside salt marshes. Even other members of the genus *Fundulus* have received scant attention. A single knowledge base for one species stands for salt marsh residents, while regular reports on the diets of seasonal species have not sufficiently recognized salt marsh contributions to the diets. This deficiency extends to the juvenile stages of several locally important recreational and commercial species.

Multispecies Studies

Observations of feeding habits at the multispecies or community level are infrequent. Certainly, no single taxonomic grouping of salt marsh fishes has received the attention bestowed upon the inland centrarchids. The feeding habits of *Fundulus heteroclitus* have tended to be reported in isolation from other species, even though it occurs in sympatry with other members of the genus *Fundulus.* It is not uncommon to collect different *Fundulus spp.* within a single sample and comparative diet studies can be readily conducted (Baker-Dittus 1978). The delineation of a study's boundaries can depend on the species richness of a marsh. The guild concept was applied in a study of four seasonal zooplanktivorus fish species in a salt marsh creek in South Carolina. Here spatial partitioning of the water column occurred when two species occupied the creek. The vertical axis was divided between surface species and bottom species. *Menidia menidia* switched from occuppying the entire water column to surface waters when bay anchovies *(Anchoa mitchilli)* migrated into the creek. Different copepod and insect species were preferred by different fish species and all species strongly selected fiddler crab megalops in summer and fall (Allen et al. 1995).

Smaller marshes may not contain recognizable guilds or even sympatric conspecifics if species richness is relatively low. In a small marsh, the entire fish community can be the level of investigation but this has not been achieved to date. Until ecologists venture into the marsh and sample multiple species or sample species exiting the marsh, little can be said about the differential use of resources by salt marsh fish species and this is a major gap in our knowledge of salt marsh ecology.

Habitat Shifting

Tidally Induced Habitat Shifts

Fish movements within a salt marsh and between a salt marsh and the outer estuary are influenced by tidal cycles. *Fundulus heteroclitus* uses the elevated marsh surface as a feeding ground when tidal inundation is high enough to allow marsh surface access (Weisberg and Lotrich 1982, Weisberg et al. 1981, Weisberg 1986). Mummichogs moving onto the marsh surface in Virginia had an average gut fullness of 10% while fish exiting the surface averaged 80% (Rozas et al. 1988). For *Fundulus heteroclitus*, marsh surface feeding appears essential for normal growth (Weisberg and Lotrich 1982). Even after the tide recedes, larval and juvenile mummichogs remain in pockets of water effectively isolated from swimming piscivores (Kneib 1986). *Fundulus heteroclitus* can numerically dominate the marsh surface nekton (Kneib 1997a). Similarly, *Fundulus grandis*, the gulf killifish, and *Fundulus parivpinnis,* the California killifish, consumed a greater volume of food on the marsh surface than in subtidal areas (Rozas and Lasalle 1990, West and Zedler 2000). Besides habitat shifting within the marsh, another tidally induced habitat shift occurs between the marsh and the outer estuary. Typically, in intertidal areas, fish enter a salt marsh with the incoming tide from a less vegetated estuarine habitat. This habitat is often connected to a larger estuarine water body, or to the sea, via an inlet. Fish species display different seasonal peaks of movement between the marsh and adjacent open water habitats (Nixon and Oviatt 1973). Since feeding studies of marsh fishes are rarely attempted, there is limited data on changes in feeding habits as species move between the marsh and outer estuarine habitats. As fish move between habitats, they are exposed to different arrays of prey items and there is a potential for a diet shift or increased feeding activity. A higher percentage of age-0 sea bass, *(Dicentrachus labrax)* exiting a salt marsh during outgoing tides contained stomachs with food than bass entering the marsh through the same channel during incoming tides (Laffaille et al. 2001). But the movements of fish species between a salt marsh and the outer estuary tends to be uneven. Over the same twelve hour tidal cycle the species entering the marsh with the incoming tide may not match species exiting the marsh with the outgoing tide. Even when species match, the size ranges can differ markedly. This mismatch between incoming and outgoing tides may not be entirely due to sampling error. Since these movements are relatively uninvestigated, there is no basis to assume that these are passive cyclic movements with the tides.

Coastal Migrations

Superimposed on these two tidally dependent habitat shifts, are seasonal migrations of fish species towards coastal environments from offshore locations. It has been proposed that a "trophic relay" of salt marsh production from intertidal to subtidal habitats occurs when large migratory piscivores consume fish and invertebrates exiting marsh creeks and channels on the ebbing tide (Kneib 1997b). Eventually, this relay connects salt marsh production to even deeper estuarine waters. Bay anchovies collected in the open waters of Delaware Bay carry isotopic signatures characteristic of salt marshes (Weinstein et al. 2000). Anchovies are a common prey of migratory piscivores (Hartman and Brandt 1995). It is also likely that a significant portion of zooplanktivorous fishes emigrating from coastal estuaries into the ocean do not survive and return to estuaries the following spring. This represents an additional export of coastal production to the open ocean (Allen et al. 1995). Furthermore, planktonic trophic transfer within an estuary has been observed to be greatest when seasonally migrating larval and juvenile fishes are in estuarine residence (Mallin and Pearl 1994). When all migrants move offshore, there is a potential for a significant transfer of estuarine production to the open ocean. With abundant concentrations of small fishes and invertebrates, salt marshes may play a unique role in this transfer. The abundance stems from the salt marsh acting as a nursery and a residence for older individuals. The salt marsh even "feeds" pelagic predators in neighboring estuarine environments through the export of young fish and invertebrates. Quantitative assessments of trophic export from salt marshes are not available and are not likely to be very meaningful until feeding studies of fish entering and leaving the marsh are undertaken.

Diet and Habitat Shifting

The marsh contains more physical barriers to movement than other aquatic environments. Restrictions on movement can limit prey consumption. While tidal inundation holds the potential for a wider range of habitat for all species within a marsh, it is unlikely that all fish species have equal access to all habitats even during extreme high tides. *Fundulus majalis* is not known to feed extensively on the marsh surface

(Werme 1981, Weisberg 1986). Since previous studies have demonstrated that *Fundulus heteroclitus* feeds on the elevated surface, its consumption of prey can differ markedly from fish restricted to lower elevations including sympatric conspecifics. As species exit the salt marsh, species specific responses to the array of prey outside the marsh can differentiate feeding patterns even more.

For an individual species, differences in diet between the marsh and the outer estuary can be manifested in different ways. Interrelated diet changes include: taxon disappearing from the diet, a change in water column position when feeding, a decrease in overall prey consumption, or changing to a piscivorous diet. The expression of a diet shift, between the marsh and outer estuary, is not predictable. The approach taken here is to measure diet overlap between the salt marsh and the outer estuary for an individual species using a general index of diet overlap (Horn 1966). A feeding shift can be identified if a diet overlap measure falls below a predetermined level, then attributing diet dissimilarity to the appearance or disappearance of taxa is required. Attribution in this case is not completely synonymous with cause since several taxa in concert may cause the shift, but if a pattern of diet difference between the marsh and outer estuary can be identified, then that pattern is likely to be a major factor in the measurable difference in diet between the two environments. The first major question of this thesis is: Do diets shift as fish move between the salt marsh and outer estuary ?

Since fish feeding is size structured, ontogeny is a potential complicating factor when two groups of unequally sized fish are compared. If the size range for a species within a single sample is very wide, simply aggregating all diet observations from the sample can obscure ontogenetic diet shifts. Teasing out ontogenetic diet effects requires examination of diet data from selected size ranges of fishes. Therefore, the second major intraspecific question to be asked is: Can a diet shift be identified between selected size ranges ? When this question is applied to fish in a single sample, then the size range is divided into an upper and lower range.

The two major questions to be tested here address gaps in our knowledge of salt marsh ecology. This is a multispecies study. A multispecies description of fish diets in the salt marsh is rare in itself, but incomplete. Comprehensive diet descriptions require assessments of feeding outside the marsh. The inclusion of ontogenetic considerations is unusual even for the well-studied mummichog diet and adds to the completeness of the diet descriptions.

Methods

Study Site

The study site is a salt marsh located on the north shore of Long Island (figure 1) in the Village of Loyd Harbor, Suffolk County at the border with Nassau County ($40^0 53'$ N: $73^0 29'$ W). The marsh is within the confines of Caumsett State Park. A barrier beach separates the northeast face of the marsh from Long Island Sound. This beach is occasionally breached by storms and subsequently repaired. Upland forest bounds the east to southeast marsh border. The only freshwater surface flow into the marsh is a small intermittent creek. The central marsh surface is dominated by *Spartina alterniflora* with patches of *Spartina patens* around the periphery. The marsh is not directly linked to Long Island Sound. An elongate, sandy-bottomed lagoon lies between the marsh and the Sound. The long axis of the lagoon is north to south and a barrier beach, interrupted by a boat channel, separates the lagoon from Long Island Sound. The boat channel is the lagoon's sole connection to the Sound. South of the boat channel, the barrier beach is partly supported as a rocky jetty. In reference to the marsh, the far southern section of the lagoon is quite deep and is known as the sand hole. The name is apparently derived from past excavations of sand from this area. At the northern end of the lagoon, a cobblestone beach along the marsh edge is exposed at low tide. The lagoon is the only marsh outlet and most flow between the two habitats is through a channel which is subtidal in the middle. The entire lagoon is commercially clammed which is an indication of the low level of pollutants despite its proximity to Long Island Sound.

Landward, at the eastern boundary of the marsh, a narrow band of *Phragmites* borders a drainage ditch but *Phragmites* invasion is limited to this single small stand.

Manmade geometric drainage patterns are common among Long Island salt marshes but at Caumsett, a natural branching drainage pattern has been retained across the marsh surface. Fly Island is a distinctive feature within the marsh. This island of mature trees, within the main channel, is surrounded by salt marsh.

Since this study requires multispecies samples, the Caumsett salt marsh is more likely to match this requirement than similarly sized channellized marshes along the shores of Long Island. It is assumed that the drainage system at Caumsett and the clean waters around the marsh will contain a naturally occurring fish fauna which is less impacted in its diversity by human activities than less pristine marshes. The relatively moderate size of the marsh increases the likelihood that numerically dominant species can be collected at a single sampling location.

The collecting gear used in this study is a fyke net. A fyke net is a series of suspended hoops surrounded by netting with a large squared opening. The netting has a mesh of 1.0 x 0.5 cm. The net is staked in a channel and two extended wings guide fish into the mouth of the net. As fishes enter the squared mouth, tidal flow tends to move the fish towards the distal end. Fish are essentially funneled through the five suspended, interior hoops towards the closed cod end. The cod end can be opened or closed with a drawstring. An exterior frame raises the netting off the substrate and this precludes any bottom feeding while fish are entrapped in the net. Once the net is removed from the channel, the cod end is opened and the trapped fish are collected.

Field Collections

Tidal sampling

The main channel was not used as a sampling location, rather, a narrow intertidal creek was selected as a sampling site because its location and configuration was more suitable for deploying the collecting gear. The creek width was completely encompassed by the extended wings of the net (see figure 2). The creek substrate is a mix of sand, cobblestones and shell fragments. The *Spartina alterniflora* marsh surface bounds one side of the sampling area within the creek and the opposite bank consists of a sandy beach. The beach allowed easy deployment and retrieval of the net. The creek penetrates deep into the marsh and connects with other marsh habitats through rivulets and open flows of water through the *Spartina.*

During extreme low tide, the water within the creek drains below ankle depth. Fish are effectively excluded from the sampling area at this time. As a consequence, when the net is set, it collects fish either entering or leaving the marsh, depending on the directional placement of the mouth and wings of the net. It does not collect fish lingering in the creek between tides. Fish entering the marsh from the lagoon were collected by setting the fyke net with its mouth facing the lagoon. The net was retrieved when incoming tidal flow was waist to chest deep. For outgoing tidal samples, the net was set with its mouth facing the marsh. Basically, the net was turned around. During outgoing tides, the net was retrieved either when it was obviously full of fish or when it no longer effectively collected fish. The amount of time that the net was left in the water was variable but never exceeded two hours. A fixed sampling period was not practical and would not have provided useful data such as catch per unit effort, because the volume of water flowing through the creek over a fixed unit of time varies widely with the lunar cycle and seasons.

Extreme high tides were avoided. When early attempts were made to collect samples during full and new moon tides, the net could not be set against swiftly moving outgoing tides in the creek until waters levels were so low that a sizeable sample could not be collected once the net was staked. Retrieving the net during rapidly rising incoming tides was hazardous. Waters were unworkable at these times. The net was set and retrieved during daylight hours. The net was not in the creek after dusk. Samples were collected from April through November in 1998, from April through October in 1999 and from March through June in 2000. Twenty-four samples were collected during the incoming tides and nineteen samples were collected during outgoing tides. On thirteen days, the incoming and outgoing samples were collected over the same twelve hour tidal cycle. This accounted for twenty-six of the forty-three samples. There were only a few days within each month when the timing and heights of tides permitted collecting both types of samples on the same day. Sometimes, weather conditions closed out these days. Some samples consisted of zero to a few fish and additional sampling trips were undertaken in an attempt to balance species representation between incoming and outgoing samples. Questions of diet shifting between habitats cannot be addressed unless species are collected in both tidal directions over relatively short time intervals. One week or less was considered an acceptable interval. This accounts for the uneven number of incoming and outgoing samples.

Weisberg et al. (1981) considered 15 fish per sample to be acceptable in a study of the feeding habits of *Fundulus heteroclitus*. In other reports on the feeding habits of estuarine fishes, 10 juvenile salmon per species (Shreffler et al. 1992), 10 or more summer flounder larvae (Grover 1997), and 10 gobies per habitat (Swenson and McCray 1996) were all considered sufficient numbers for dietary analysis. In a study of zooplanktivorous fishes in salt marsh creeks, 10-20 individuals per species per sampling date were analyzed and species area curves, adapted for prey consumption, indicated that the diets of each of the four species was sufficiently characterized in qualitative and quantitative terms by this range of individuals (Allen et al. 1995). Therefore, for the fyke net samples, twenty-five fish per species per sample was considered adequate for diet analysis. If a species size range appeared relatively wide in a sample, then additional fish were selected for ontogenetic comparisons. Generally, excess fish were taken beyond those needed. If ten or less individuals of a species were collected in the fyke net, then all members of the species were taken but the lower limit for reporting diet results for a species was ten individuals per sample. All fish were immediately stored in a 10% formaldehyde solution and transferred to 70 - 75 % ethyl alcohol after a minimum of two weeks.

Treatment of Fish and Gut Contents

For each fish subject to gut content analysis, standard length measurements (.001 m) and mass measurement (.01g) were recorded and the entire gut was removed. Statview 5 was used to plot standard length size distributions (appendices 1 to 6). Prey from guts were enumerated to the lowest practicable taxonomic level. For marsh feeding fish, thirty-four prey were identified to the genus level. For fish feeding in the outer estuary, twenty-four prey were identified to the genus level. There was overlap in identifications between the two environments (appendix 7). Keys covering geographic regions of various sizes were used in the identifications of fish and invertebrates (appendix 8).

Prey items from a fish species were pooled into taxonomic groups. When practical, mass measurements were taken on pooled gut contents. Even on a pooled basis, surface to volume ratios introduce wide variations in mass measurements due to water evaporation from very small prey. Prey from different fish species within a sample were not pooled together. Infrequently occurring small sized taxa were placed into a mixed taxa pool. Pooled prey were placed in pre-weighed boats. Excess liquid was allowed to evaporate from the weighing boats and paper toweling was used to soak up excess liquid from the boats and from the prey. Prey tissue remained moist when mass measurements were taken (.001 g). If prey mass measurements were not recorded, then prey were simply identified to the lowest practicable taxonomic level and counted.

Data Analysis

Horn's modification of Morisita's index of similarity (see figure 3) is an appropriate measure of diet overlap when prey are grouped into various taxonomic categories (Krebs 1999, Horn 1966). Based on simulations, Wolda (1981) strongly recommended Morisita's index over other similarity indices. He concluded that the index is less influenced by differences in sample size and taxonomic diversity than comparable indices. Since fish are feeding in two different habitats in this study, prey diversity is likely. In addition, wide variations in sample sizes of fish are to be expected A robust index is needed. The index ranges from 0 to 1. As diets become similar, the index approaches 1. It has been accepted that meaningful or significant diet overlap occurs when the index is above .60 (Zaret and Rand 1971, Labropoulou et al. 1998). This is a reasonable cutoff for this study but use of the word significant is avoided here because of the statistical connotations. The term biologically meaningful overlap (Rachlin and Warkentine pers. comm.) is adopted for overlap measurements greater than .60. If the Morisita index falls below .60, then the result indicates that biologically meaningful diet overlap is not evident. To avoid the repetition of awkward terminology, the term diet shift is also used in this case. The index was used for intraspecific comparisons between incoming and outgoing tides. Incoming samples are synonymous with samples from the outer estuary and outgoing samples are synonymous with marsh samples.

In addition, two types of size effects were investigated. One comparison was to measure the degree of diet overlap between similarly sized fishes when feeding in the marsh and in the outer estuary. This comparison was needed to distinguish size versus habitat effects when fish fed in two different environments. Ontogeny was the focus of the second size effect. If a species size range within a sample exceeded 40 mm, then the size range was divided into two equivalent size ranges of smaller and larger individuals and Morisita's index was applied to these two groups, but if this 40+ mm size range contained a large gap which indicated a strong bimodal size distribution, then this gap was used as a guide for size range division. Forty millimeters was considered wide enough to "capture" ontogenetic diet shifts within samples for the species known to inhabit the Caumsett salt marsh. When size ranges were divided, the number of fish within each division of the range was a minimum of ten with one exception (see **Results**-*Fundulus majalis*).

Results

Fyke Net Samples

Water temperatures in the channel ranged from 9.5^0 C in March 2000 and 10^0 C in April 1998 and 1999 to maximum temperature levels in early to mid-August of 24^0 C to 25^0 C . By November, temperature again dropped as low as 10.5^0 C. The number of fish opened for gut contents analysis was 1,663. Four species, *Fundulus heteroclitus, Fundulus majalis, Menidia menidia,* and age-0+ *Pseudopleuronectes americanus* appeared frequently in samples from late spring into fall, but only the first three species were collected regularly in incoming and outgoing samples. Winter flounder *(Pseudopleuronectes americanus)* were rarely collected in incoming samples and questions of diet shifting within this species could not be addressed.

Other species were collected when the fyke net was deployed. Two stickleback species, *Gasterosteus wheatlandi* and *Gasterosteus aculeatus* appeared in spring samples as early as March. The ripe condition of these seasonal species indicated that the marsh was a breeding ground. By June, sticklebacks were no longer taken in samples. A few sand lances, *Ammodytes americanus,* were collected in 1998 and 1999, but in spring 2000 hundreds appeared in one fyke net sample. Relatively high numbers of young of year bluefish were collected in a pair of summer 1998 samples and appeared in additional 1998 samples but bluefish were rare in 1999. Forty-four sheepshead minnows *(Cyprinodon variegates)* were trapped in the fyke net in July 1999 during an incoming tide. In 1998 and 1999 Atlantic menhaden, *Brevoortia tyrannus,* were collected from August through the fall. Rarer species were the four beard rockling *(Enchleyopus cimbrius)*, northern pipefish *(Syngnathus fuscus)*, white perch *(Morone americana)*, butterfish *(Peprilus tricanthus)*, striped bass *(Morone saxatilis)*, and tautog *(Tautoga onitis)*. Only a few individuals represented each of these species over the course of the entire study period. Seining of the lagoon and the marsh produced no additional species.

Monospecific Results

Fundulus majalis

Fundulus majalis, the striped killifish, was rarely collected during early to mid-spring. Relatively large-scale movements between the salt marsh and the outer estuary appeared to commence in June. Striped killifish were collected consistently in summer samples but sporadically in fall samples. Movements of *Fundulus majalis* through the creek continued into November. A larger size range was collected in incoming samples. In one outgoing sample (August 1999), nine exceptionally large fish were opened for gut contents analysis. This was the single exception to a minimum count of ten fish for diet analysis set forth in the Methods section. The Queens College Marine Biology Laboratory assisted with the identification of molluscs in the diet of this species.

Gastropods, *Hydrobia sp.* and *Littorina spp.*, dominated the counts of prey in outgoing samples across seasons and sampling years (tables 1 to 3). *Littorina* taxa included *Littorina littorea* and *Littorina obtusata*. *Hydrobia sp.* and *Littorina spp.* were absent from one pair of samples (table 4). Standard lengths of fish in this pair were smaller than other samples. Two outgoing samples contained the gastropod *Melampus bidentatus* but it was always found among the shells of the more common genera. Gastropods almost dropped out of diet when the species fed outside the marsh. When all sampling years are combined, and fish not subjected to Morisita's comparison are included with the compared fish, 73% of 172 fish exiting the marsh contained gastropods in their guts, but only 7% of 198 fish entering the marsh contained gastropods. Most of the incoming fish containing gastropods were in a November 1998 sample. Seventy-five fish from that sample were opened for gut content analysis and five of the larger fish contained gastropods. The bivalve *Gemma gemma* was present in 40% of the fish leaving the marsh and 66% of the fish entering the marsh. On a sample basis, the proportional representation of mollusc mass was often higher than all other prey taxa combined for fish feeding in the marsh, but other prey taxa contributed substantially to the total prey mass when fish fed outside the marsh.

Three pairs of samples were subjected to measurements of diet overlap using the simplified Morisita's index (table 5). Only one pair indicated a measurable diet shift had occurred between the outer estuary and the salt marsh. This was the November 1998 pair. Diets did not shift during the summers of 1998 and 1999. When similarly sized fish were compared between the two environments, a shift occurred in the summer of 1998 but diets overlapped in November 1998. Two out of six ontogenetic comparisons indicated diets had shifted between size ranges.

Fundulus heteroclitus

Very few mummichogs were collected in the sampling channel in April 1998 and April 1999. On May 10, 1999, both tidal directions contained mummichogs and the species continued to appear through the summer and fall of 1998 and 1999 but they were not present in all samples during these seasons. The maximum standard length of mummichogs was less than striped killifish (75 mm versus 100 mm respectively) but *Fundulus heteroclitus* appeared in higher numbers in samples than *Fundulus majalis.*

No taxa consistently dominated the mummichog diet even on a seasonal basis. The diet was highly varied (tables 6 through10). Four Morisita comparisons between incoming and outgoing samples indicated that diets overlapped in May 1999 and July 1999 but in the summer and fall of 1998 diets shifted between the two environments (table 11). When similarly sized fish between samples were compared, larger fish shifted diets between the salt marsh and the outer estuary in July 1999 but no shift occurred in the diets of the smaller fish from the same pair of samples. Similarly sized fish from a pair of November 1998 samples also shifted diets. Within samples, five out of six ontogenetic comparisons indicated that diets shifted between size ranges. The single exception was within a July 1999 sample.

Menidia menidia

Menidia menidia was the most commonly collected fish species in the fyke net. Its earliest seasonal appearance was on March 29, 2000. During previous sampling years, it was collected in April, but not in May, and continued to appear in samples until November in 1998 and in 1999. Ripe adults were common in the fyke net in spring of all sampling years but young of year were not observed emerging from the marsh until June. The recently hatched fish were small enough to pass through the fyke net mesh but were collected with a scoop net for positive identification. Scooped fish were not subject to diet analysis. The species fed as a zooplanktivore from spring into the summer and in the fall. During mid-summer, the mysid, *Neomysis americana,* was consumed along with benthic taxa (tables 12 through 18).

Six out of seven paired comparisons were based on incoming and outgoing samples collected on the same day (table 19). Diet shifting occurred on two dates in July 1998 and on one date in July 1999. Similarly sized fish also shifted diets on one of these dates (July 9, 1998). Three ontogenetic comparisons are reported. Again, diet shifting was associated with a July sample and was not observed in September 1998 and November 1998 samples.

Pseudopleuronectes americanus

Winter flounder were not present in samples from March through April in any sampling year or in a pair of May 1999 samples. Flounder were also absent from an incoming May 2000 sample. Seasonally, the earliest appearance of the species in the fyke net was on May 31, 2000 during an outgoing tide when 48 fish were collected. These were also the smallest fish collected (mean standard length = 28 mm). In 1998 and 1999, the species began appearing in June samples. Most fish were collected in outgoing samples. An exception to this pattern occurred in November 1998 when fourteen fish were collected during an incoming tide. The only other incoming sample containing a high number of flounder was on June 19, 2000 when 34 flounder were collected in the fyke net. Over all sampling years, 238 flounder were collected exiting the marsh and 65 were collected entering the marsh. Flounder numbers peaked in 1999. In three outgoing samples, between June and August of that year, 101 age-0+ winter flounder were collected.

Discussion

Intraspecific Patterns

Fundulus majalis

The frequent consumption of *Gemma gemma* by *Fundulus majalis* at Caumsett is consistent with observations at Sapelo Island, Georgia, where surf clams (*Donax spp.* and *Mulinia spp.*) contributed the highest percent occurrence and estimated prey volume to the species diet. Gastropods were not reported in the diet of fishes from this sandy beach environment (Harvey 1998), but Werme (1981) reported that *Hydrobia* and *Gemma* together were estimated to occupy thirty percent of total food volume in striped killifish collected in a salt marsh in Massachusetts. These last two studies and my findings provide evidence that bivalves and gastropods are common contributors to the diet of striped killifish but gastropod consumption is associated with salt marshes. Suitably sized gastropods may be concentrated in the marsh. The diminishment of gastropods in the diet during periods of feeding outside the marsh did not always lead to a diet shift because of the high frequency of *Gemma gemma* in the diets of fish in the marsh and in the outer estuary plus other prey were common to both environments.

The low level of overlap for the November 1998 pair of samples was most likely due to a simplification of the diet in the marsh (table 3). Marsh fish consumed an exclusive diet of molluscs except for one isopod in one fish. The marsh sample consisted of relatively large fish. Between the same two samples, overlap in the diets of similarly sized fish is partly attributed to the consumption of harpacticoid copepods in fish less than 45 mm outside the marsh. The omission of these smaller fish from the comparison of similarly sized fish had an elevating effect on the index, but the overlap in this comparison is primarily attributed to the fact that this was the single sample from the outer estuary where large striped killifish had consumed *Hydrobia sp.* and *Littorina spp.* Diet similarity was positively influenced by gastropod consumption in both environments. In the outer estuary, gastropod consumption by larger fish and harpacticoid consumption by smaller fish also explains the apparent dietary partitioning between size ranges within the November 1998 sample.

Apparent ontogenetic diet shifts did not always lead to overlap indices below .60. In the August 3, 1998 within sample comparison, 60% of the fish in the lower size range contained copepods. The copepods were predominantly harpacticoids. None of the fish in the upper size range from this sample contained copepods, but high numbers of amphipod and bivalve taxa were shared between the size ranges. The lower range is not congruent with the size range of fish feeding on copepods, rather, a shift away from copepods appears to occur somewhere within the lower size range. The June 19, 2000 sample demonstrates the seasonality of ontogenetic diet shifting. Here, 44% of the smaller fish from the outer estuary contained brachyuran megalopa. None of the fish in the upper size range contained megalopa, but again diets overlapped. The elimination of megalopa had minimal impact on the overlap measure because the megalopa did not occur in high numbers in the guts.

Ontogenetic diet shifting is indicated by one of the three Morisita indices for marsh feeding fish. For marsh feeding fish, larger fish are more likely to consume gastropods and less likely to consume harpacticoid copepods. This factors into the low levels of ontogenetic overlap within the August 6, 1999 sample (tables 2 and 5). Only three of eleven fish in the smallest size range of this sample contained gastropods.

Whereas nineteen out of twenty-six from the mid-sized range contained gastropods and nine out of nine fish of the upper size range consumed gastropods. This was the only sample with a three-way subdivision. Over 50% of the prey in the smallest size range were harpacticoid copepods or ostracods. These were rare in the mid-size range and absent from the upper size range. Diet dissimilarity between the lower and mid-size range is partly attributed to a shift away from the consumption of smaller prey. The September 2, 1998 marsh sample displays a similar gastropod consumption pattern. In the smaller fish, nineteen out of twenty-four fish contained gastropods but thirteen out of fourteen fish of the larger fish contained gastropods. Across seasons and sampling years there was a general tendency for gastropod consumption to increase with fish size. The high level of ontogenetic overlap of the September 2, 1998 sample was most likely due to a narrowing of the diet (table 2). Fish of all sizes consumed molluscs, mainly gastropods, in high proportions. Diet overlap on July 8, 1999 is the final evidence for a relationship between gastropod consumption and fish length (table 4). These were the smallest striped killifish collected and none of the fish leaving the marsh contained *Littorina spp.* or *Hydrobia sp.*. Harpacticoids and ostracods dominated the diets in both tidal directions.

Unlike Caumsett, rivers and creeks flow into other marshes on the north and south shores of Long Island and the diet at Caumsett is not necessarily typical of Long Island coastal habitats. Variations in salinity regimes are likely to modulate molluscan prey availabilities. A high reliance on polychaetes and small crustaceans and a low incidence of "hard shelled" prey was observed in striped killifish collected from the Patuxent River Estuary. Samples were collected between late spring and early fall (Bakker-Dittus, 1978). Still, if gut contents are accepted as evidence of resource availability, the salt marsh appears to provide a stable dietary resource for striped killifish in the form of molluscs and if the species retreats into salt marshes during fall and winter, then molluscs could assume a seasonal support role across a variety of coastal habitats. These dietary staples, *Hydrobia sp.*, *Littorina spp.* and *Gemma gemma*, may be vital to the sustainability of marsh populations of *Fundulus majalis*.

Fundulus heteroclitus

For mummichogs, it is tempting to conclude that same day comparisons will yield similar diets between the marsh and outer estuary if fish are similarly sized. This certainly appears to be the case for two out of the four comparisons between the marsh and outer estuary (table 11 - May and July 1999) but the similarities lie within a restricted overall size range of 26 to 46 mm. All fish of the May 10, 1999 samples fall within this size range, and copepods numerically dominated the diets in both tidal directions (table 9). Amphipod taxa were the most common prey of the smaller size fish in the July 8, 1999 samples (table 10). The shift in diet on July 8 is partly attributed to the sheer variety of prey items in the guts of fish leaving the marsh. Analysis of the July 8 samples was complicated by the high numbers of empty guts in incoming fish. Twenty-six out of fifty incoming fish had empty guts while all outgoing guts on that date contained identifiable prey. When all samples over all years are tallied, 30% and 7% of all mummichog guts collected during incoming and outgoing tides respectively had empty guts or guts with unidentifiable debris. Fish collected during incoming tides at Caumsett were trapped at the end of a low tide period. The feeding activity of mummichogs has been reported to increase during high tide periods even when the tide does not inundate the marsh surface (Weisberg et al. 1981, Allen et al. 1994). Therefore, with 15 out of 25 fish falling into the empty gut/debris category and a relatively low number of prey items in the remaining fish of the August 3, 1998 incoming sample, the low Morisita index for the August 3/July 27 pair cannot be simply ascribed to samples being taken on different days or diet shifting, if feeding activity is partly suppressed at low tide outside the marsh. All of the fish leaving the marsh on July 27 contained identifiable prey at the end of a high tide (table 6).

The remaining pair of samples was taken in November 1998 (table 7). Here, differences in copepod consumption was partly responsible for diet disimilarity. On November 8, harpacticoids numerically dominated the diets of fish entering marsh but harpacticoids were restricted to fish below 44 mm standard length. The within sample ontogenetic Morisita index for this date reflects this. Fish leaving the marsh on November 13 had consumed cyclopoid and calanoid copepods in addition to harpacticoids.

Three samples were not paired with samples from the opposite tidal direction (table 8). In the September 2, 1998 sample, 8 out 25 smaller fish contained debris in the guts and the total prey count for the smaller fish was relatively low. This indicates a suppression of feeding within the smaller size range and this cannot be discounted as a factor leading to the low overlap index for this date. All of the larger fish contained identifiable prey. Fish leaving the marsh on August 6, 1999 also exhibited an ontogenetic diet shift. Again, the larger fish also contained a more varied assortment of taxa. Finally, ontogenetic diet shifting was evident in the June 19, 2000 sample. Prey items from the upper size range were absent from the lower range (*Menida menidia, Balanus sp., Limulus polypheums, Gemma gemma, Pagurus longicarpus*, Araneae, Acarina).

It does seem that taking samples on the same day in both tidal directions is needed to adequately assess diet overlap between habitats for *Fundulus heteroclitus.* Unlike its conspecific, *Fundulus majalis,* the mummichog is not relying on dietary staples which are consistent major contributors to the diet across seasons and sampling years, rather, the mummichog appears ready to switch to other prey including resources which may be restricted to the marsh surface. If mummichog diets are more likely to change significantly over short time intervals than stripped killifish diets then a shorter time interval between samples is desirable.

Menidia menidia

The Morisita indices above .60 were based on copepod dominated diets in spring, early summer and fall (table 19). Harpacticoids were never prominent (tables 12,15,16,17). For *Menidia menidia,* diet overlap between the salt marsh and the outer estuary appears to be a function of season more than standard length. Diet shifting in midsummer coincided the incorporation of additional zooplanktivorous, nektonic and benthic prey into the diet (tables 13,14,18). Since copepods were not identified to lower taxonomic levels, the possibility exists that different copepod taxa were consumed between the marsh and the outer estuary.

Copepod dominated diet sometimes masked other potential diet shifts. The incoming and outgoing November 1998 samples were separated by five days. Twenty out of twenty-five fish entering the marsh had consumed erythrocytic shaped invertebrate eggs and the eggs constituted 39% of all prey. Only six out of fifty fish leaving the marsh contained these eggs and the eggs represented only 2% of all prey (table 16). An index incorporating frequency of occurrence might have indicated a diet shift in this case. It is possible that egg densities simply decreased in all waters during the five days between samples. The high level of ontogenetic similarity in the November marsh sample is attributed to the consumption of copepods by all fish and few other prey types. Diets overlapped on September 25, 1998 (table 15), but when similarly sized fish from the same two samples were compared, the similarity index decreased. This is attributed to the high frequency of egg consumption among incoming fish less than 49 mm but few eggs were in the guts of similarly sized fish from the marsh. Diet overlap during midsummer amply demonstrates that same day incoming and outgoing samples do not automatically lead to higher levels of diet overlap. Three pairs of July diets over two sampling years indicated that diet shifted between the marsh and outer estuary (tables 13,14,18). Zooplankton were still the numerically dominant prey on July 9, 1998 except zoea outnumbered copepods and occurred in more guts in the incoming samples but the reverse was true in the outgoing sample. The extreme level of ontogenetic dissimilarity within the outgoing sample of this date can be related to copepod consumption by twenty-two of the fish in the lesser size range but none of the larger *Menidia* contained copepods instead megalopa were the dominant prey. Copepods are known to be more frequently consumed by smaller *Menidia* (Cadigan and Fell 1985). On July 27, 1998, 67% of the prey in fish entering the marsh consisted of erythrocytic shaped eggs and the mysid, *Neomysis americana*. A diet shift between habitats was measurable. None of the fish leaving the marsh that day contained mysids or eggs. The 40 mm cutoff point for ontogenetic diet overlap may have left a shift within the incoming sample undetected. The fish with mysids were within a 43-60 mm size range whereas 11 out of 16 fish smaller than this size range contained the eggs. None of the larger fish contained these eggs. Besides the absence of mysids and eggs in the diets of fish leaving the marsh, the dissimilarity between incoming and outgoing samples on July 27 can be partly attributed to 20 out of 46 fish exiting the marsh with no food in their guts and copepods being common prey in those with food. On this day, a large number of young of year bluefish chased the *Menidia* out of the marsh and it is tempting to speculate that feeding suppression occurred as a consequence of predator presence. Diet shifting on July 8, 1999 appears to be related to a shift from *Neomysis americana* consumption in 8 out of 11 incoming fish to one mysid in 15 outgoing fish. During July, *Neomysis americana* consumption was higher in fish from outside the marsh in two separate sampling years. It can be concluded that this mysid is a seasonally predictable prey in the outer estuary.

Pseudopleuronectes americanus

Limited evidence seems to support the proposition that young of year winter flounder do not range over wide distances during the summer. Movements of marked fish presumably in response to increased water temperatures in shallow areas was followed by the return of some marked fish to those areas on a later date when temperatures cooled (Pearcy 1962). Within a period of a few weeks in the summer, marked fish in a channel in Waquoit Bay, Massachusetts tended to remain within 100 m of the release site (Saucerman and Deegan 1991). With these studies in mind, it is possible that young of year flounder exiting the Caumsett salt marsh do not venture further then the lagoon outside the marsh until an undetermined amount of time has passed or until the fish have reached a certain level of development.

To my knowledge, no study has intercepted winter flounder moving between a salt marsh and the outer estuary. The results of the fyke net samples suggest a seasonal directionality to the movements. More than 3.5 times more fish were collected leaving the marsh than entering the marsh and this was despite the higher number of incoming samples. Since juveniles were not collected in early to mid-spring samples and were missing or were few in number in most incoming samples, there is limited evidence for reentry into the marsh for over-wintering, although, a gradual to late fall entry and a winter exit is plausible. The higher number of fish collected exiting the marsh could be due to a high summer mortality outside the marsh, leaving fewer flounder to re-enter the salt marsh but no flounder larger than 59 mm was ever collected in the fyke net so there is no evidence for overwintering.

Winter flounder diets were dominated numerically and on a weight basis by a variety of amphipod and polychaete taxa. The diet at Caumsett is typical for the species. Amphipods are commonly reported as important prey items (Pearcy 1962, Franz and Tancredi 1992, Stehlik et al. 2000). If the years 1998 and 1999 are used as a guide, then amphipods are the most frequently consumed prey taxa in June to early August and are major contributors to total prey weight during this period, but initially in May, amphipods may not be the dominant food item in the diet of Caumsett winter flounder. The smallest flounder were collected on May 31, 2000 (size range 23-31 mm). For this sample, one polychaete family, Spionidae, was the major dietary item in terms of weight. Spionids were only outnumbered by cyclopoid and calanoid copepods. Similarly, spionids were reported as a major prey item of flounder between 15 and 49 mm in a New Jersey estuary in May (Stehlik and Meise 2000).

Feeding Patterns of Salt Marsh Fishes

Habitat and Diet

Three species display varying degrees of diet shifting when moving between the marsh and the outer estuary and for all species there is a temporal influence. Across the seasons, *Fundulus majalis* does not deviate much from a pattern. While feeding outside the marsh from summer through fall, gastropods almost disappear from the diet. This is truly a habitat induced diet change with minimal seasonal influence, but it does not necessarily lead to a measurable diet shift between the two habitats unless the species has largely restricted itself to molluscs in the marsh. This appears to be the case in the fall. In September 1998 and November 1998, fish in a size range from 49-86 mm, inside the marsh consumed a diet of molluscs and little else. Across seasons, copepods were usually harpacticoids but the restriction of harpacticoids to smaller fish size ranges indicates that juveniles are staying close to the bottom along with adults.

Fundulus heteorclitus reportedly congregates in the upper reaches of marsh creeks during winter and disperses into the lower creek, onto mudflats, and into channels with the onset of warmer temperatures (Lotrich 1975, Halpin 1997). The late spring exit of mummichogs from the Caumsett salt marsh support these finding and they appear to apply to *Fundulus majalis* as well, but the evidence does not support the position that movements out of the marsh are foraging excursions for mummichogs. Several previously cited studies and this one indicate that *Fundulus heteroclitus* cycles through periods of high and low levels of feeding. These levels correspond to tidal level and probably reduce diet similarity measures when the species is outside the marsh during low tide. The consumption of terrestrial arthropods by *Fundulus heteroclitus* does not appear to be a chance occurrence in a single sampling year. Spiders appeared in the diet during the summers of 1998 and 1999. Intact spinnerets were observed in several fishes and in one case, juveniles were observed with an adult of the family Araneidae. Spiders and mites have been previously reported in the diet of *Fundulus heteroclitus* (Kneib 1986, Allen et al. 1994). Plant hoppers in the family Delphacidae were also observed as prey. This family commonly occurs on salt marsh plants along Long Island Sound (Weiss 1995). These arthropods, along with the decapods, did not completely supplant other taxa while the species fed in the marsh

Both *Fundulus spp.* are consuming prey in the marsh which are absent or less abundant outside the marsh, if, gut contents is accepted as evidence of resource abundance. This is an indication that salt marshes are the primary feeding grounds for these species even when they spend considerable periods of time outside the marsh. These conspecifics share a reliance on marsh resources and, to some extent, have partitioned those resources. The decapods and terrestrial arthropods in the guts of mummichogs were not observed in the guts of striped killifish, while gastropods and bivalves were never dominant in the diets of mummichogs. Marsh contributions to the diets of both species are readily identifiable and distinguishable. Marsh resources are likely to lead to considerably higher concentrations of *Fundulus spp.* than can be found in other estuarine environments.

Warkentine and Rachlin (1989) reported on the winter diet of *Menidia menidia* when the species is offshore and concluded that the species fed at the bottom of the water column. Allen et al. (1995) reported that silversides in salt marsh creeks have a preference for larger prey when it is available. Cadigan and Fell (1985) categorize

Menidia menidia as an opportunistic feeder citing the species consumption of a variety of prey during the year. The results presented here indicate that the Atlantic silverside feed in the water column when zooplankton densities are presumably high but can readily take advantage of other inhabitants of the nekton and benthos. Samples of fish entering the marsh during the summer of 1998 illustrate this point. On July 24 the diet of twenty-four out of twenty-eight fish was exclusively nereids but this was followed by a completely different diet on July 27 without nereids and high in mysids. Later that same summer in August, thirteen out of twenty-one individuals contained pennate diatoms as the sole dietary item. All of these fish had fed in the outer estuary and no conclusion can be drawn about the locations of feeding but the species appears to be "flexible" during summer foraging but assumes a zooplanktivorus diet in spring and fall. As was the case with *Fundulus majalis*, diet dissimilarity between the marsh and the outer estuary appears to be related to a reduced frequency of specific prey in the diet after switching habitats, except with *Menidia menidia* the prey was *Neomysis americana* and it was consumed more frequently in the outer estuary than in the marsh.

It is reasonable to assume that *Menidia menidia* is often more concentrated within a salt marsh than in surrounding estuarine waters. This is based on the abundance of the species in the fyke net and its spawning behavior in salt marshes (Middaugh 1981, Cadigan and Fell 1985). It was interesting to watch the behavior of the smallest *Menidia* as they passed through the fyke net mesh. These schools attempted to swim back into the marsh during outgoing tides. Tidal movements literally pushed the schools backwards out of the marsh. For *Menidia*, marsh resources may be vital to the survival of recently hatched fish and less important later in life. The salt marsh concentrations of *Menidia* and *Fundulus spp.* probably extends to other species as well. While *Psuedopleuronectes americanus* was not tested for diet shifting, it is worth noting that the stomachs of age-0+ winter flounder exiting the salt marsh in May, June, and July were bulging full of prey. Average counts of amphipods and polychaetes were much higher than counts in other fish species. There are likely to be distinct advantages for this species if its young of year concentrates and feeds in salt marshes during the earliest stages of development.

Ontogeny and Diet

All three fish species tested for diet shifting passed through ontogenetic diet shifts and, for all species, small fish consumed small prey at higher frequencies than larger fish within the same sample but the prey sometimes differed among the three species at relatively high taxonomic levels. One common feature among the species was that the prey was seasonally available.

As *Fundulus majalis* grows it eliminates harpacticoid copepods, ostracods, and brachyuran megalopa from its diet during different seasons but a measurable diet shift was not always indicated by Morisita's index. With growth, *Fundulus heteroclitus* includes a wider array of prey taxa in its diet. This extension includes prey of terrestrial origins. Diet shifts between size ranges is attributed to this diversification of the diet. As *Menidia menidia* grows, the frequency of copepod and invertebrate egg consumption is reduced seasonally and in July larger fish consume *Neomysis americana*, but the size range of *Menida* containing this mysid probably depends on the size distribution of the mysid population (see **Future Research Directions** – *Menidia menidia*). During juvenile stages, all species function to some extent as seasonal zooplanktivores but as summer approaches the two *Fundulus spp.* are more likely to switch to alternative prey than *Menidia menidia.* The Atlantic silverside probably switches when zooplankton densities reach minimum levels and larger silversides switch sooner than smaller silversides. Presumably they can take advantage of the summer availability of larger prey.

Habitat shifting and ontogenetic diet shifting are interactive processes (see figure 4). The frequency of occurrence of gastropod consumption in *Fundulus majalis* tends to increase with fish size but this only occurs in the marsh. For *Fundulus heteroclitus,* ontogenetic diet shifting may be more pronounced inside the marsh if feeding is suppressed during low tide periods outside the marsh. Certainly, in the outer estuary the higher frequency of occurrence of *Neomysis americana* in larger *Menidia* than in smaller *Menidia* links habitat to diet ontogeny. Within the salt marsh, ontogenetic habitat shifts are potentially linked to ontogenetic diet shifts. Understanding these linkages requires more detailed studies of salt marsh fishes at the monospecific level

Future Research Directions

Fundulus majalis

Fundulus majalis consumption of salt marsh gastropods presents several potential lines of research. *Melampus bidentatus* resides within the Spartina of the low and high marsh. Within the vegetation, small individuals (< 7mm shell height) are consumed by *Fundulus heteroclitus* (Rozas and Zimmerman 2000, Vince et al. 1976). Size selection of gastropods by *Fundulus majalis* is also likely. At Caumsett, several gastropod species were abundant in the striped killifish diet . Bivalves in the diet were primarily confined to *Gemma gemma.* Molluscs are well suited for field studies of prey densities and prey size distributions and *Fundulus majalis* presents the rare opportunity to study the effects of a predator on several prey species. The potential for a variety of studies exists if striped killifish are collected for gut contents analysis in habitats where prey data is obtained. Questions pertaining to prey size selection, regulation of prey populatons, and prey refugia come to mind. Habitat manipulation using fish exclosures can provide direct evidence of predation effects on mollusc populations. Striped killifish are easily collected within the marsh by seining during low tides. Yet, few feeding studies have been performed on this common species. Assessing the importance of molluscs to its diet requires additional studies in a variety of estuarine habitats. It has been proposed in this thesis that molluscs are important to the survival of *Fundulus majalis* if the species retreats into salt marshes during colder periods.

Fundulus heteroclitus

At the monospecific level, additional monospecific studies of the mummichog's feeding habits may be productive, but time might be better spent on the diets of other salt marsh species. Studies of the feeding habits of mummichogs and its sympatric conspecifics could eventually lead to a knowledge base which parallels the extensive studies of the freshwater *Lepomis spp.*.

Pseudopleuronectes americanus

Even degraded estuaries support populations of juvenile winter flounder (Pearcy 1962, Meise et al. 1999, Franz and Tancredi 1992). The habitat requirements of juveniles has been the subject of several studies. No doubt the attention is due to the commercial importance of the species. Preferred habitats for the species can include coves (Poole 1966), shallow embayments with mud covered by live bivalves or shell litter (Howell et al. 1999), muddy silty unvegetated shallow areas in upper Narrangansett Bay, Rhode Island (Meng and Powell 1999) and in the Chesapeake, where the species tends to concentrate in the upper bay, it is most common on muddy or vegetated bottoms (Murdy et al. 1997). Recent attempts to identify habitat variables favoring juvenile growth have not been successful (Phelan et al. 2000). Juvenile growth has actually been observed to be slightly better in a degraded estuary than in a relatively pristine one (Meise et al. 1999). One possible explanation is that high levels of nutrient loading indirectly support secondary production of specific amphipod prey species that are consumed by juvenile flounder (Franz and Tancredi 1992). Despite all of the attention given to the habitat preferences and requirements of this species, the role of the salt marsh in the earliest stages of young of year development remains unknown. Simply identifying the habitats within the salt marsh where the juveniles congregate is a good starting point. Then the movements between the marsh and the outer estuary deserve attention. This transition from a salt marsh habitat to the more open waters of the outer estuary can be viewed as a tradeoff. The food supply in the two habitats is probably unequal in terms of quality and quantity, and piscivorous fishes are more likely to be encountered in the deeper estuarine water outside the marsh. Winter flounder, within the size range observed at Caumsett, are a common prey of summer flounder (Manderson et al. 2000). Flounder could be responding to the summer heating of the shallow waters (Pearcy 1962, Crawford 1990) within the salt marsh. Water temperatures in partially isolated shallow bodies of water in salt marshes might be less buffered against rapid temperature change than shallow areas in more open marine environments, but the species began exiting the Caumsett salt marsh as early as May and temperature alone is not likely to fully explain these movements. Still, any study of winter flounder movements cannot ignore temperatures in different habitats. This particular lagoon is called the sand hole because of a deep pocket towards the middle. The deeper water is a potential thermal refuge. There is also the possibility that movement out of the marsh is triggered by ontogenetic development or a combination of ontogenetic and environmental factors. Photoperiod is a consideration. Additional studies incorporating fyke net sampling, seining, otolith analysis and perhaps fish marking could clarify the relationships among flounder movements, ontogeny, and habitat variables. The fyke net in particular, is an effective sampling tool for the smaller size classes of this species. Fish can be observed and even counted when the water is very shallow. In contrast to fish schooling higher in the water column, when individual winter flounder were observed entering the net, there was no indication of any avoidance behavior. Many flounder were observed following the substrate and simply swimming above the bottom of the net frame. Besides basic studies of flounder movement between the marsh and the lagoon, a question worth investigating is: Does predator presence in the lagoon correlate with winter flounder movements back into the marsh ?

Menidia menidia

In two July samples in two different sample years the mysid, *Neomysis americana*, was a major prey item in the diet of *Menidia menidia* while feeding in the outer estuary, but there was a difference in the standard lengths of silversides consuming the mysid. On July 27, 1998, fish below 43 mm did not consume mysids, whereas the size range of the July 8, 1999 sample was from 36-53 mm and mysids were consumed by 16 out of 25 fish including the smallest fish. Smaller mysids can be consumed by smaller fish, but at what point does mysid growth outpace *Menidia* growth? Assuming mysids can be collected along with *Menidia*, the potential for a predator's growth "tracking" a prey's growth can lead to inquiries on this particular predator/prey relationship. If an indirect means of measuring the size of *Neomysis americana* in the gut of *Menidia* can be developed, then the size distribution in the guts can be compared to the size distribution of mysids collected in the field. The question posed is: Does the feeding of *Menidia menidia* within the size distribution of *Neomysis americana* shift towards the lower end of that distribution as the summer progresses ?

Multispecies Studies

Utilization of salt marsh habitats by fishes remains an underdeveloped field of inquiry. It may not be practical to study all species feeding habits in a large marsh but large marshes offer the opportunity for guild studies or studies of coastally migrating species. Studies of this latter group can open the door to an assessment of trophic transfer from the salt marsh to the outer estuary. Observations of habitat partitioning among salt marsh fish species can certainly shed some light on interspecific diet differences. Little is known about the distribution of species among the different habitats within a salt marsh. The distribution of an individual species may depend on its ontogenetic stage. In addition, the species inhabiting the marsh change seasonally. One can easily envision a study where the distributions of all species within a salt marsh are described both ontogenetically and seasonally. A relatively low number of species were observed in residence at the Caumsett salt marsh. Residence for a salt marsh can be defined as using the marsh for reproduction or as a nursery. This definition excludes short-term transients. The few resident species observed at Caumsett brings to mind the species area curve. Since marshes have well defined boundaries, there is a potential for its application to salt marsh fishes.

Salt marshes have been under protection for a long time now and marsh restoration is an active field. Restoration efforts include the realignment of canalized drainage patterns to a more natural state. Drainage ditches are practically absent from the Caumsett salt marsh and it retains a natural pattern of drainage and standing water. I saw the large numbers of post-larval fishes in those shallow bodies of water on the surface of the Caumsett marsh. There is a need to quantify the effects of manmade geometric drainage patterns on fish species diversity. Naturally draining marshes such as Caumsett provide a baseline for development of a species diversity metric correlated with overall marsh size. Without proper metrics and baseline data, the impact of restoration efforts on the fish community is difficult to measure and even the most well-meaning restoration efforts are undertaken in the absence of a broad foundation of ecological knowledge

Table 1. Proportional representation of *Fundulus majalis* prey in fish entering the salt marsh on August 3, 1998 (incoming) and from fish exiting the salt marsh on July 27, 1998 (outgoing)

Taxa	Outer Estuary and Marsh			Ontogeny	
	Incoming	Outgoing	Incoming	Incoming	
	mm 40-55&70-90	mm 32-51	mm 40-51	mm 40-55	mm 70-90
Gastropoda					
Hydrobia /Littorina spp.		.316			
Bivalvia					
Gemma gemma	.210	.209	.158	.148	.460
Annelida					
Polychaeta					
Nereidae					
Neresis succinea		.007			
unidentified nereids		.039			
unidentified polychaetes	.007		.010	.009	
Arthropoda					
Crustacea					
Ostracoda					
Cypridina	.002		.004	.002	
Copepoda					
harpacticoids	.224	.016	.293	.301	
other copepods	.031	.014	.042	.042	
Isopoda	.006		.005	.005	.007
Amphipoda					
Gammarus mucronatus	.319	.263	.297	.290	.405
Corophium sp.	.017				
Melitidae		.020			
other amphipods	.165	.088	.189	.178	.128
eggs		.029			
unidentifiable	.002		.002	.002	

Table 2. Proportional representation of *Fundulus majalis* prey in fish exiting the marsh on two dates (outgoing) and entering the marsh on a third date (incoming)

Taxa	Ontogeny Samples						
	Sept. 2,1998 Outgoing mm		Aug. 6, 1999 Outgoing mm			June 19, 2000 Incoming mm	
	49-74	75-100	24-45	49-65	86-100	42-65	76-93
Nemertea						.005	.064
Nematoda				.006			
Mollusca							
Gastropoda							
Hydrobia ./Littorina spp.	.734	.864	.017	.354	.601		.011
Melampus bidentatus		.015			.036		
Bivalvia							
Gemma gemma	.266	.109	.421	.177	.073	.564	.542
Annelida							
Polychaeta							
Phyllodocidae							
Eteone sp.							.021
Spionidae						.032	
Nereidae						.009	
Neresis diversicolor						.005	.032
unidentified nereids		.003					
unidentified polychaetes					.012	.193	.053
unidentified annelid						.009	
Arthropoda							
Crustacea							
Ostracoda			.298	.024			
Copepoda						<.001	
harpacticoids			.253	.003			
Isopoda							
Edotea montosa				.003		.009	
Cyathura polita					.012		
Amphipoda							
Gammarus mucronatus						.037	.170
Corophium sp.				.035			
other amphipods		.009	.011	.236	.024	.018	.064
Brachyuran megalopa						.105	
Insecta						.005	
Chelicerata							
Limulus polyphemus				.162		.004	
eggs					.242	.005	.032

Table 3 Proportional representation of *Fundulus majalis* prey in fish entering the salt marsh from the outer estuary on November 8, 1998 (incoming) and from fish exiting the marsh on November 13, 1998 (outgoing)

Taxa	Outer Estuary and Marsh			Ontogeny	
	Incoming mm	Outgoing mm	Incoming mm	Incoming mm	
	30-90	65-89	67-90	30-60	60-90
Mollusca					
Gastropoda					
Hydrobia/Littorina spp.	.144	.953	.370		.348
Bivalvia					
Gemma gemma	.538	.038	.284	.703	.305
Annelida					
Polychaeta					
Nereidae					
Neresis diversicolor	.002		.004		.004
Neresis succinea					
unidentified nereids	.011		.029		.027
unidentified polychaetes	.010		.012		.024
Arthropoda					
Crustacea					
Ostracoda	.021			.035	
Copepoda					
harpacticoids	.152			.259	
Isopoda					
Sphaeroma quadridentatum	.069	.009	.177	.003	.163
Amphipoda					
Gammarus mucronatus	.016		.041		.039
other amphipods	.027		.062		.066
unidentifiable	.010		.021		.024

Table 4 Proportional representation of *Fundulus majalis* prey in fish entering the salt marsh (incoming) and exiting the marsh (outgoing) on July 8, 1999

Taxa	Outer Estuary and Marsh	
	Incoming mm 27-41	Outgoing mm 28-40
Nemertea	.082	
Nematoda		.009
Mollusca		
Gastropoda		
Skeneopsidae planorbis	.016	.017
Bivalvia		
Gemma gemma	.049	.034
Annelida		
Polychaeta		
Nereidae		.009
Phyllodocidae		
Eteone sp.		.005
unidentified polychaetes	.004	
Arthropoda		
Crustacea		
Ostracoda	.245	.409
Copepoda		
copepods (not harpacticoids)	.043	
harpacticoids	.440	.452
Isopoda		
Cyathura polita		.009
Amphipoda		
Melitidae		
Gammarus mucronatus	.045	.034
Corophium sp.	.003	
other amphipods	.071	.022
Mandibulata		
Insecta		
Homoptera	.002	

Table 5. Modified Morisita's index (C_H) for *Fundulus majalis* (N = 346 fish). Dates on left refer to all samples across the row. Marsh samples are collected during outgoing tides and outer estuary samples are collected during incoming tides. Under **size range comparisons, between samples** are diet overlap measures between the outer estuary and the salt marsh of similarly sized fish and **within sample ontogeny** are diet overlap measures of different size ranges within a sample. Biologically meaningful diet overlap>.60

Samples			Size Range Comparisons				
			Between Samples		Within Sample Ontogeny		
Marsh Date with Size Range	Outer Estuary Date with Size Range	C_H	Size Ranges In/Out	C_H	Size Ranges	In or Out	C_H
Aug 3, 1998 40-55&70-90mm	July 27, 1998 32-51mm	.65	40-51mm/32-51mm	.57	40-55mm/70-90mm	In	.67
	Sept. 2,1998 49-100mm				49-74mm/75-100mm	Out	.97
Nov. 8, 1998 30-90mm	Nov. 13, 1998 65-89mm	.25	67-90mm/65-89mm	.63	30-60mm/60-90mm	In	.53
July 8, 1999 27-41mm	July 8, 1999 28-40mm	.94					
	Aug 6, 1999 24-65&86-100mm				24-45mm/49-65mm 49-65mm/86-100mm	Out Out	.32 .69
June 19, 2000 42-93mm					42-65mm/76-93mm	In	.92

Table 6. Proportional representation of *Fundulus heteroclitus* prey in fish entering the salt marsh on August 3, 1998 (incoming) and for fish exiting the salt marsh on July 27, 1998 (outgoing)

Taxa	Outer Estuary and Marsh	
	Incoming mm 55-71	Outgoing mm 56-73
Nematoda	.233	.086
Mollusca		
Gastropoda		
Hydrobia sp.	.033	.052
Littorina obtusata		.080
Bivalvia		
Gemma gemma		.035
Melampus bidentatus		.149
Annelida		
Polychaeta		
Nereidae		
Neresis diversicolor		.006
Neresis succinea	.033	
unidentified nereids		.034
unidentified polychaetes		.006
Arthropoda		
Crustacea		
Cirripedia		
Balanus improvisus		.025
Isopoda		
Edotea montosa		.017
Cyathura polita		.012
Amphipoda		
Gammarus mucronatus	.101	.170
Microdeutopus gryllotalpa		.046
other amphipods		.154
Mysidacea		.006
Decapoda		
Palaemonetes pugio	.033	
Crangon septemspinosa	.033	.006
Panopeus herbstii	.067	
Pagurus longicarpus	.333	
Brachyuran decapod		.006
Megalopa larva		.012
Chelicerata		
Limulus polyphemus		.046
Mandibulata		
Insecta		.012
Chordata		
Menidia menidia	.067	
unidentified fish	.033	
Algae	.033	.012
Plant		.017
Unidentifiable		.017

Table 7. Proportonal representation of *Fundulus heteroclitus* prey in fish entering the salt marsh on November 8, 1998 (incoming) and in fish exiting the marsh on November13, 1998 (outgoing)

Taxa	Outer Estuary and Marsh			Ontogeny	
	Incoming	Outgoing	Incoming	Incoming	
	mm	mm	mm	mm	
	30-75	23-45	30-48	30-45	50-75
Nematoda		.006			
Mollusca					
Gastropoda		.041			
Annelida					
Polychaeta					
unidentified polychaetes	.004	.006	.005	.005	
Arthropoda					
Crustacea					
Ostracoda	.004		.005	.005	
Copepoda					
harpacticoids	.713	.272	.877	.882	
other copepods		.515			
Isopoda					
Gnathia cerina		.006			
Edotea montosa		.065			
Amphipoda					
unidentified amphipods	.004	.071			.017
Insecta – pupae	.187				.810
Chordata					
Menidia menidia	.008				.035
unidentifiable		.018	.050	.049	
Algae	.076		.058	.054	.138
Plant	.004		.005	.005	

Table 8. Proportional representation of *Fundulus heteroclitus* prey in two samples of fish exiting the salt marsh (outgoing) and one sample of fish entering the salt marsh (incoming)

Taxa	Ontogeny Samples					
	Sept. 2, 1998 Outgoing mm		Aug 6, 1999 Outgoing mm		June 19, 2000 Incoming mm	
	30-45	57-73	27-48	50-75	37-55	56-73
Nemertea			.032		.088	.065
Nematoda		.079				
Mollusca						
Gastropoda						
Melampus bidentatus		.630				
Hydrobia sp.		.011				
Littorina sp.	.029	.045				
Bivalvia						
Gemma gemma	.172	.011		.037		.022
Annelida						
Polychaeta						
Nereidae						
Neresis diversicolor		.011			.118	
unidentified nereids	.029	.011		.018	.053	.022
unidentified polychaetes	.114			.092	.035	.065
Arthropoda						
Crustacea						
Ostracoda	.172		.170			
Harpacticoids			.490			
other copepods	.057					
Cirripedia						
Balanus improvisus				.055		
Balanus sp.					.018	.110
Isopoda						
unidentifiable isopod				.018		.022
Amphipoda						
Gammarus mucronatus			.072	.204		
other amphipods	.258		.013	.018	.140	.130
Mysidacea		.011			.195	.130
Decapoda						
Palaemonetes pugio						
Pagurus longicarpus		.011				
Pagurus sp.				.018		.022
Uca sp.		.023				
Brachyuran decapod	.026			.165	.018	.065
Megalopa larva					.195	
unidentifiable crustecean		.045				
Insecta		.022				
Chelicerata						
Limulus polyphemus				.038		.043
Aracnida						
Araneae	.086	.079				.043
Araneidae			.014	.038		
Acarina				.038		.022

Table 8 - continued

Chordata						
Menidia menidia				.054		.065
fish eggs				.075	.070	.022
Algae		.011	.072	.019		.022
Pennate Diatoms			.111			
Plant				.038	.035	.065
Unidentifiable	.057		.026	.075	.035	.065

Table 9. Proportional representation of *Fundulus heteroclitus* prey in fish entering (incoming) and exiting (outgoing) the salt marsh on May 10, 1999

Taxa	Outer Estuary and Marsh	
	Incoming mm 30-44	Outgoing mm 26-44
Nemertea	.002	
Nematoda	.025	.005
Mollusca		
Gastropoda		
Skeneopsis planorbis	.002	
Hydrobia sp.		<.001
Annelida		
Polychaeta		
Nereidae		
Neresis diversicolor		<.001
unidentifiable nereids		<.001
unidentifiable polychaetes	.004	.002
Arthropoda		
Crustacea		
Copepoda		
harpacticoids	.063	.064
other copepods	.793	.835
Isopoda		
Jaera marina		.082
Amphipoda		
unidentifiable amphipods	.002	.010
Zoea	.100	<.001
Mandibulata		
Insecta	.009	
Unidentifiable		.002

Table 10. Proportional representation of *Fundulus heteroclitus* prey in fish entering the salt marsh (incoming) and exiting the salt marsh (outgoing) on July 8, 1999

Taxa	Outer Estuary and Marsh					
	Incoming mm 25-71	Outgoing mm 27-70	Incoming mm 25-46	Outgoing mm 27-43	Incoming mm 49-71	Outgoing mm 49-70
Nemertea	.167	.162			.229	.269
Nematoda		.003		.009		
Mollusca						
Gastropoda						
Melampus bidentatus		.003				.006
Bivalvia						
Modiolus modiolus	.021		.077			
Annelida						
Polychaeta						
Nereidae						
Neresis diversicolor		.007		.009		.006
Neresis succinea		.003				.006
unidentified nereids		.034		.017		.045
unidentified polychaetes	.042	.058	.077	.059	.028	.056
Arthropoda						
Crustacea						
Cirripedia						
Balanus sp.	.021		.077			
Isopoda						
Jaera marina		.003		.009		
Sphaeroma quadridentatum	.021	.017	.077	.042		
Amphipoda						
Gammarus mucronatus	.333	.207	.384	.491	.314	.017
Microdeutopus gryllotalpa	.083	.027			.114	.045
Corophium sp.	.125	.058		.034	.172	.073
other amphipods	.104	.176	.154	.254	.086	.123
Decapoda						
Brachyuran decapod		.003		.009		
Chelicerata						
Limulus polyphemus	.083	.207	.154	.025	.057	.326
Arachinida						
Araneae		.003		.009		
Mandibulata						
Insecta		.003		.008		
Delphacidae		.006		.017		
unidentified arthropod		.010		.008		.011
eggs		.010				.017

Table 11. Modified Morisita's index (C_H) for *Fundulus heteroclitus* (N = 429 fish). Dates on left refer to all samples across the row. Marsh samples are collected during outgoing tides and outer estuary samples are collected during incoming tides. Under **size range comparisons, between samples** are diet overlap measures between the outer estuary and the salt marsh of similarly sized fish and **within sample ontogeny** are diet overlap measures of different size ranges within a sample. Biologically meaningful diet overlap > .60

Samples			Size Range Comparisons				
			Between Samples		Within Sample Ontogeny		
Marsh Date with Size Range	Outer Estuary Date with Size Range	C_H	Size Ranges In/Out	C_H	Size Ranges	In or Out	C_H
Aug. 3, 1998 55-71mm	July 27, 1998 56-73mm	.27					
Nov. 8, 1998 30-75mm	Nov.13, 1998 23-45mm	.43	30-48mm/23-45mm	.42	30-45mm/50-75mm	In	.01
	Sept. 2, 1998 30-73mm				30-43mm/57-73mm	In	.03
May 10, 1999 30-44mm	May 10,1999 26-44mm	.98					
July 8, 1999 25-71mm	July 8, 1999 27-70mm	.86	25-46mm/27-43mm 49-71mm/49-70mm	.90 .56	25-46mm/49-71mm 27-43mm/49-70mm	In Out	.68 .21
	Aug. 6, 1999 27-75mm				27-48mm/50-75mm	Out	.08
June 19, 2000 37-73mm					37-55mm/56-73mm	In	.57

Table 12 Proportional representation of *Menidia menidia* prey in fish entering the salt marsh (incoming) and exiting the marsh (outgoing) on June 23, 1998

Taxa	Outer Estuary and Marsh	
	Incoming mm 58-93	Outgoing mm 19-41
Nemertea	<.001	
Arthropoda		
Crustacea		
Cladocera		
Evadne sp.	.004	
Podon sp.		.020
other cladocerans	.004	.047
Ostracoda	.002	.062
Copepoda		
copepods (not harpacticoids)	.964	.866
Amphipoda		
Gammarus mucronatus	.001	.001
other amphipods	.003	.001
Mysidacea		
Neomysis americana	<.001	
Nauplius	<.001	
Zoea	.017	.002
unidentifiable	.005	

Table 13. Proportional representation of *Menidia menidia* prey in fish entering the salt marsh (incoming) and exiting the salt marsh (outgoing) on July 9, 1998

Taxa	Outer Estuary and Marsh			Ontogeny	
	Incoming mm 20-43	Outgoing mm 24-101mm	Outgoing mm 24-43	Outgoing mm 24-62	Outgoing mm 63-101
Annelida					
Polychaeta					
Nereidae		.002			.026
unidentified polychaetes		.003			
Arthropoda					
Crustacea					
Cladocera	.002	.003		.004	
Ostracoda	.013	.052	.022	.055	
Copepoda					
copepods (not harpacticoids)	.105	.809	.881	.868	
Amphipoda					
Melita nitida	.002				
Gammarus mucronatus	.006	.021	.010	.006	.316
Corophium sp.		.012	.017	.012	
other amphipods	.038	.005	.005	.002	.052
Caprella sp.		.001		.002	
Mysidacea					
Neomysis americana	.002	.003		.002	
Decapoda					
Crangon septemspinosa		.003	.005	.002	
Nauplius		.003		.002	
Zoea	.779	.032	.044	.033	
Megalopa	.002	.032			.474
Mandibulata					
Insecta					
Coleoptera					
Chrysomelidae larvae	.002				
Chordata					
Menidia menidia		.010			.132
eggs	.147				
unidentifiable	.002	.011	.016	.012	

Table 14. Proportional representation of *Menidia menidia* prey for fish entering the salt marsh (incoming) and exiting the salt marsh (outgoing) on July 27, 1998

Taxa	Outer Estuary and Marsh	
	Incoming mm 23-65	Outgoing mm 28-65
Arthropoda		
Crustacea		
Copepoda		
copepods (not harpacticoids)	.270	.782
Amphipoda		
Gammarus mucronatus	.008	.090
other amphipods	.038	.002
Mysidacea		
Neomysis americana	.217	
unidentifiable crustacean		.017
Zoea		.042
Chelicerata		
Acarina		.008
eggs	.467	
undentifiable		.059

Table 15. Proportional representation of *Menidia menidia* prey in fish entering the salt marsh (incoming) and exiting the marsh (outgoing) on September 25, 1998

Taxa	Outer Estuary and Marsh			Ontogeny	
	Incoming mm 39-96	Outgoing mm 40-52	Incoming mm 40-54	Incoming mm 39-66	Incoming mm 67-93
Annelida					
Polychaeta					
Maldanidae	<.001		.002	.001	
unidentified polychaetes	<.001				.001
Arthropoda					
Crustacea					
Ostracoda		.002			
Copepoda					
copepods (not harpacticoids)	.775	.972	.481	.630	.871
Amphipoda	.015		.002	.001	.023
Mysidacea					
Neomysis americana	.004				.006
Nauplius	.006	.001	.016	.013	.002
Brachyuran zoea	.004	.003	.010	.007	.002
Parafavella sp.	.006	.018	.021	.015	
eggs	.170	.004	.415	.291	.093
Pennate Diatoms	.018		.051	.042	
unidentifiable	.002		.002		.002

Table 16. Proportional representation of *Menidia menidia* prey in fish entering the marsh on November 8, 1998 (incoming) and in fish exiting the marsh on November 15, 1998 (outgoing)

Taxa	Outer Estuary and Marsh		Ontogeny	
	Incoming mm 44-57	Outgoing mm 49-99	Outgoing mm 49-74	Outgoing mm 75-99
Arthropoda				
Crustacea				
Ostracoda	.003			
Copepoda				
copepods (not harpacticoids)	.601	.983	.980	1.00
Amphipoda				
Gammarus mucronatus	.002			
unidentifiable	< .001			
eggs	.394	.017	.020	

Table 17. Proportional representation of *Menidia menidia* prey in fish entering the salt marsh (incoming) and fish exiting the salt marsh (outgoing) on April 5, 1999.

Taxa	Outer Estuary and Marsh	
	Incoming mm 52-63	Outgoing mm 52-85
Arthropoda		
Crustacea		
Ostracoda	.022	.369
Copepoda		
copepods (not harpacticoids)	.888	.630
unidentifiable	.001	
fish eggs	.089	<.001

Table 18. Proportional representation of *Menidia menidia* prey in fish entering the salt marsh (incoming) and exiting the marsh (outgoing) on July 8, 1999

Taxa	Outer Estuary and Marsh	
	Incoming mm 52-63	Outgoing mm 52-85
Nematomorpha	.036	
Annelida		
Polychaeta		
Nereidae		
Neresis diversicolor		.028
Arthropoda		
Crustacea		
Copepoda		
Amphipoda		
Gammarus mucronatus		.028
other amphipods	.071	.055
Mysidacea		
Neomysis americana	.821	.055
Zoea		.194
unidentifiable crustacean	.036	
Mandibulata		
Insecta	.036	

Table 19 Modified Morisita's index (C_H) for *Menidia menidia* (N = 449 fish). Dates on the left refer to all samples across the row. Marsh samples are collected during outgoing tides and outer estuary samples are collected during incoming tides. Under **size range comparisons, between samples** are diet overlap measures between the outer estuary and the salt marsh of similarly sized fish and **within sample ontogeny** are diet overlap measures of different size ranges within a sample. Biologically meaningful diet overlap > .60

Samples			Size Range Comparisons				
			Between Samples		Within Sample Ontogeny		
Marsh Dates with Size Range	Outer Estuary Dates with Size Range	C_H	Size Ranges In/Out	C_H	Size Ranges	In or Out	C_H
June 23, 1998 58-93mm	June 23, 1998 19-41mm	.99					
July 9, 1998 20-43mm	July 9, 1998 24-101mm	.17	20-43mm/24-43mm	.05	24-62mm/63-101mm	Out	.01
July 27, 1998 23-65mm	July 27, 1998 28-65mm	.44					
Sept 25, 1998 39-96mm	Sept. 25, 1998 40-52mm	.95	40-54mm/40-52mm	.69	39-66mm/67-93mm	In	.92
Nov. 8, 1998 44-57mm	Nov. 13, 1998 49-99mm	.81			49-74mm/75-99mm	Out	.99
April 5,1999 52-63mm	April 5,1999 52-85mm	.90					
July 8, 1999 33-53mm	July 8, 1999 33-50mm	.13					

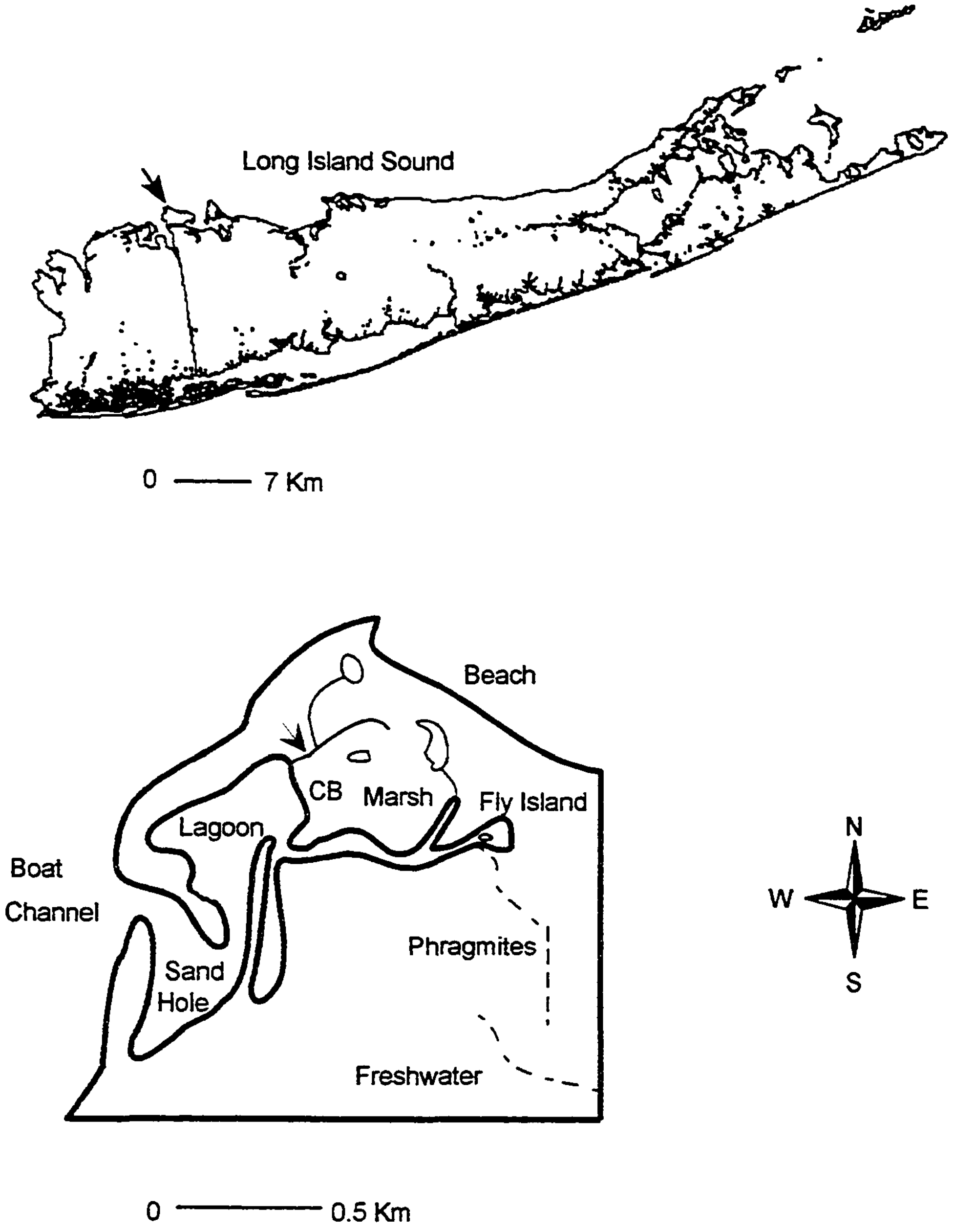


Figure 1 Arrow in upper map is the location of Caumsett salt marsh at the northern end of the border of Nassau County (left) with Suffolk County (right). In the lower map, the arrow indicates the sampling site. CB = cobblestone beach

Figure 2 Fyke net is set during low tide to collect fish entering the marsh.

$$C_H = \frac{2\sum_i^n p_{ij}\, p_{ik}}{\sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2}$$

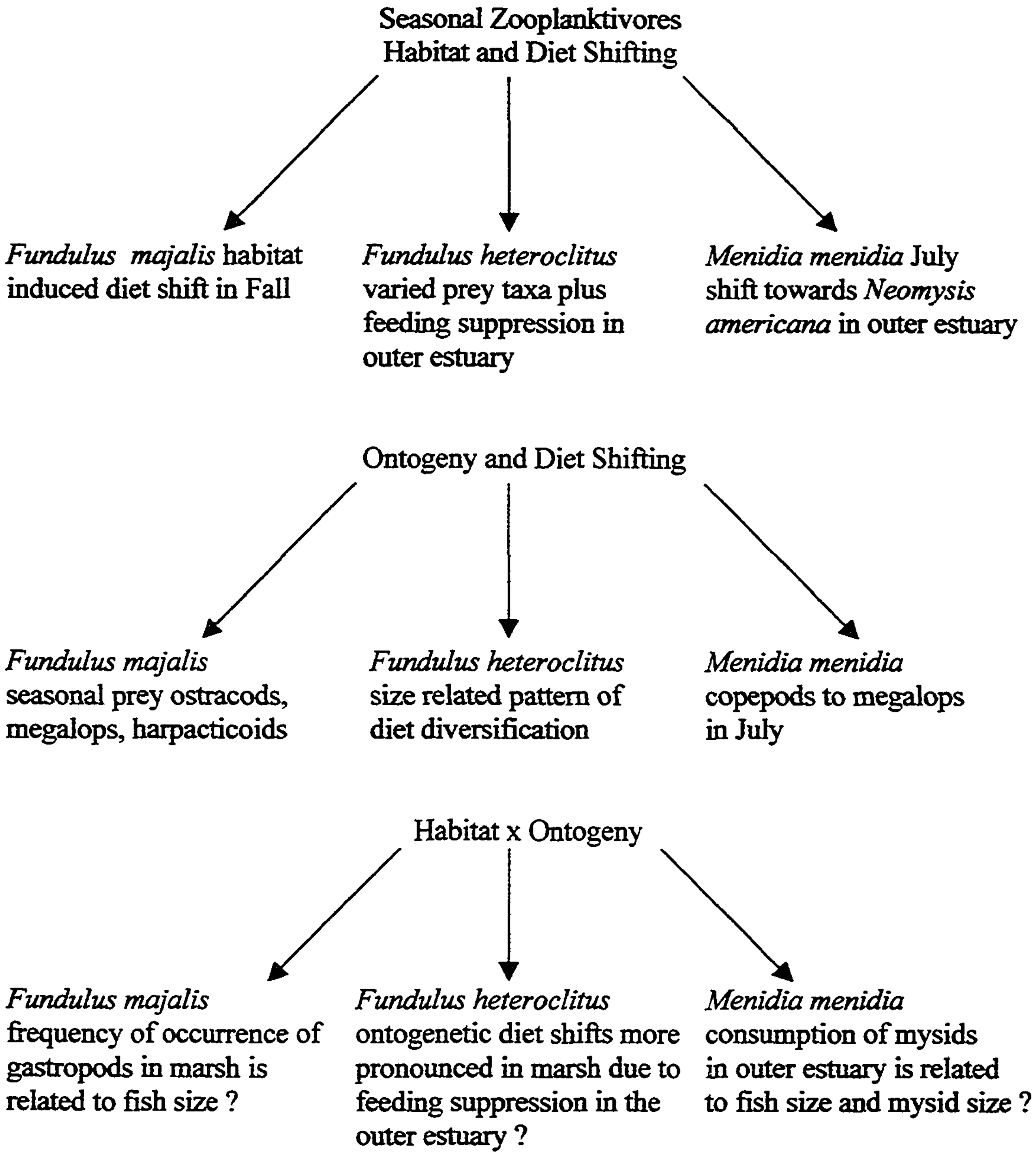
C_H = Modified Morisita's index of niche overlap between species *j* and and species *k*

p_{ij} = Proportion resource *i* is of the total resources used by species *j*

p_{ik} = Proportion resource *i* is of the total resources used by species k

n = Total number of resource states

Figure 3 Morisita's index as modified by Horn (1966)



Seasonal Zooplanktivores
Habitat and Diet Shifting

Fundulus majalis habitat induced diet shift in Fall

Fundulus heteroclitus varied prey taxa plus feeding suppression in outer estuary

Menidia menidia July shift towards *Neomysis americana* in outer estuary

Ontogeny and Diet Shifting

Fundulus majalis seasonal prey ostracods, megalops, harpacticoids

Fundulus heteroclitus size related pattern of diet diversification

Menidia menidia copepods to megalops in July

Habitat x Ontogeny

Fundulus majalis frequency of occurrence of gastropods in marsh is related to fish size ?

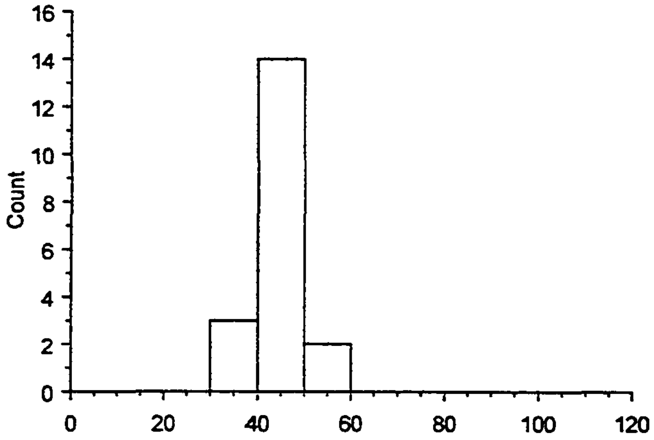
Fundulus heteroclitus ontogenetic diet shifts more pronounced in marsh due to feeding suppression in the outer estuary ?

Menidia menidia consumption of mysids in outer estuary is related to fish size and mysid size ?

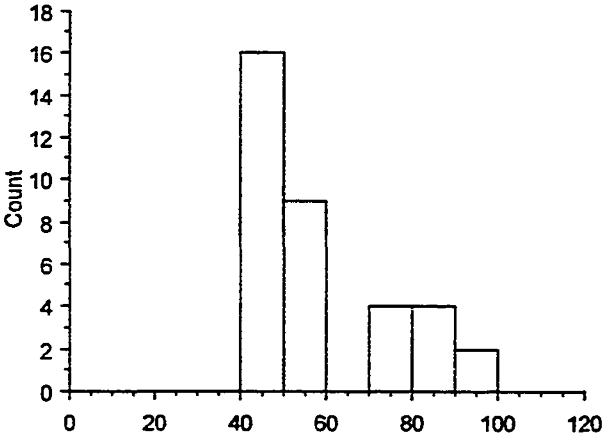
Figure 4 Summary of habitat and ontogenetic diet shifts for three species of salt marsh fishes

Appendix 1
Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

July 27, 1998 n = 19

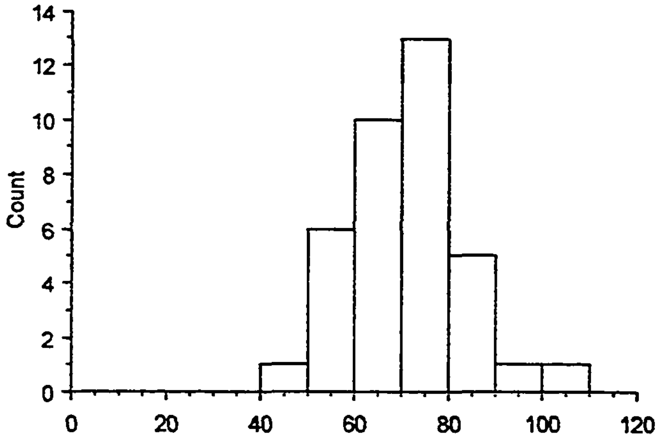


August 3, 1998 Incoming n = 35

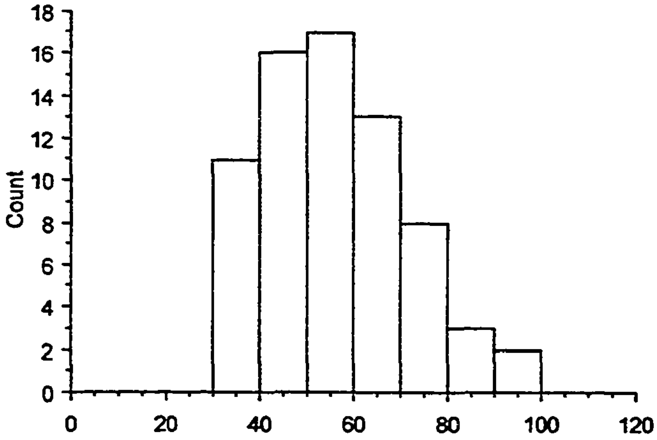


Appendix 1 (continued)
Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

September 2, 1998 Outgoing n = 37

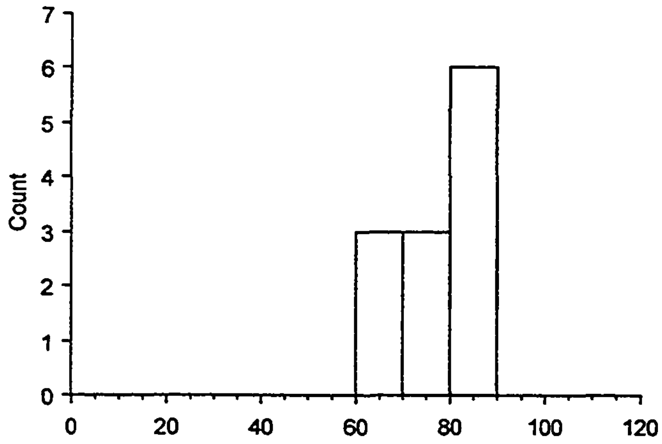


November 8, 1998 Incoming n = 70

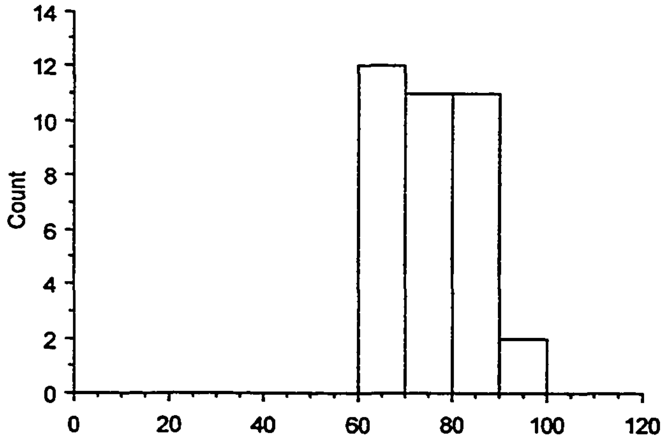


Appendix 1 (continued)
Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

November 13, 1998 Outgoing n = 12

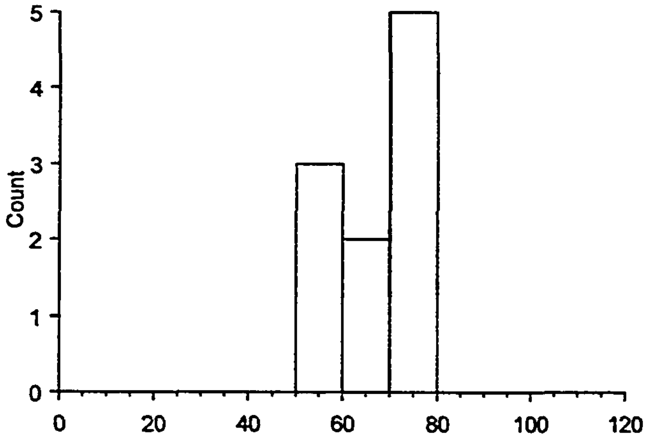


June 10, 1999 Outgoing n = 36

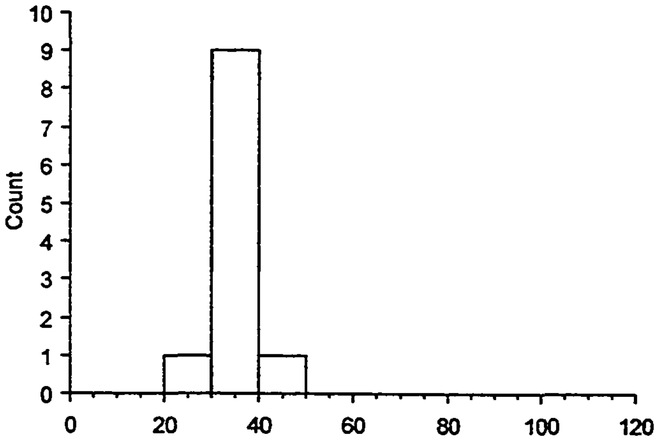


Appendix 1 (continued)
Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

May 10, 1999 Outgoing n = 10



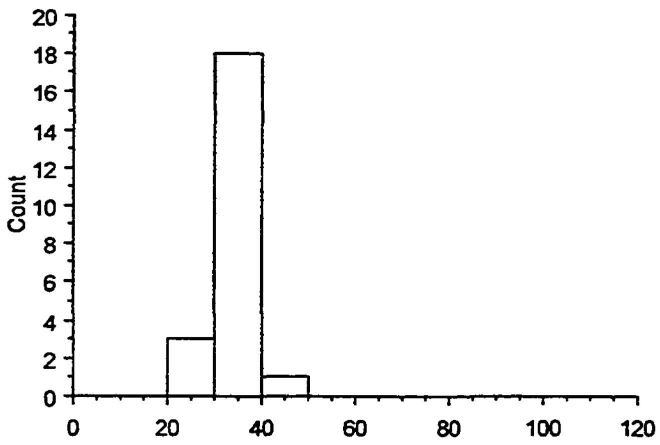
July 8, 1999 Outgoing n = 11



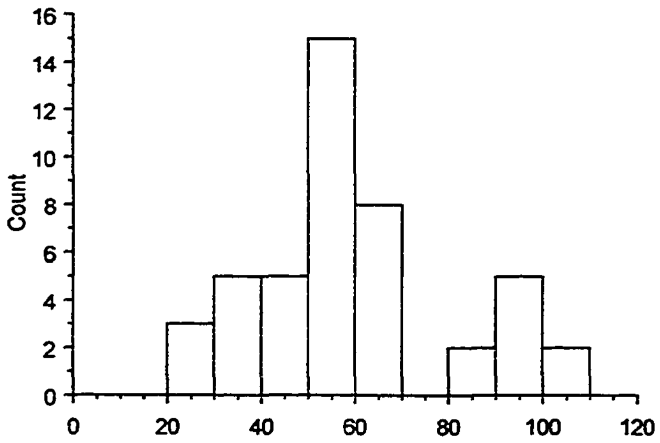
Appendix 1 (continued)

Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

July 8, 1999 Incoming n = 22

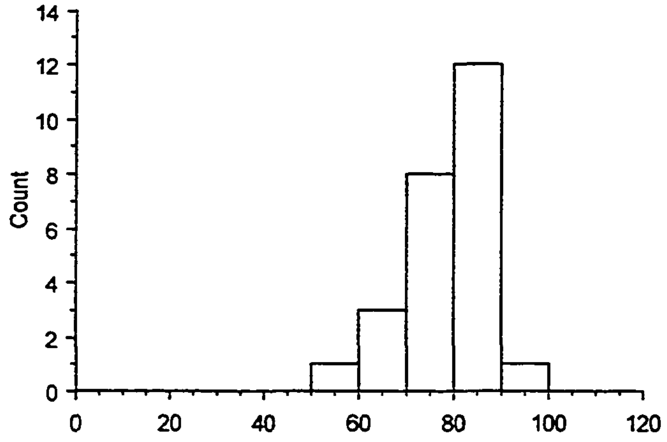


August 6, 1999 Outgoing n = 45

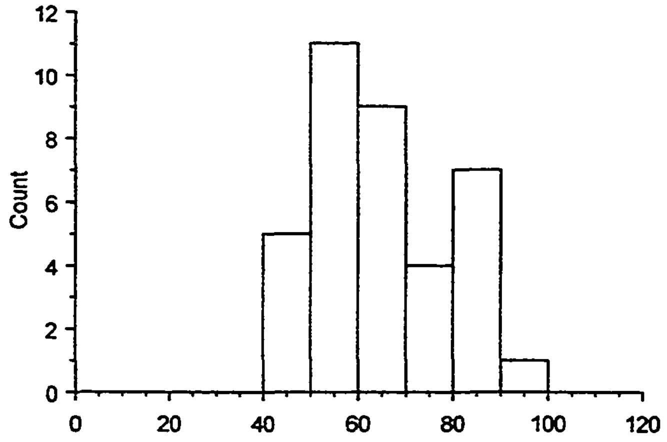


Appendix 1 (continued)
Standard length histograms (mm) of *Fundulus majalis*
Intervals include lowest value.

October 18, 1999 Incoming n = 25

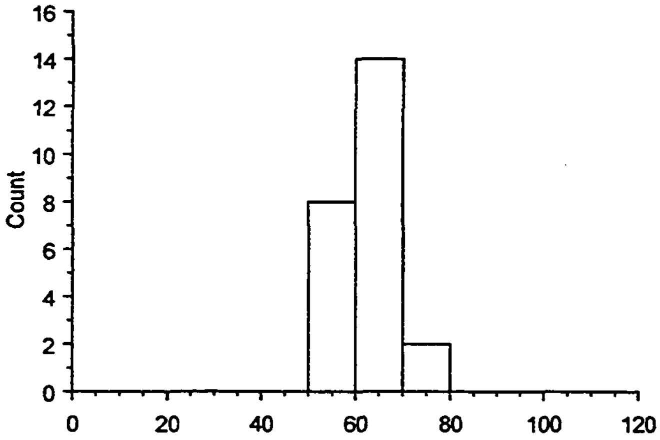


June 19, 2000 n = 37

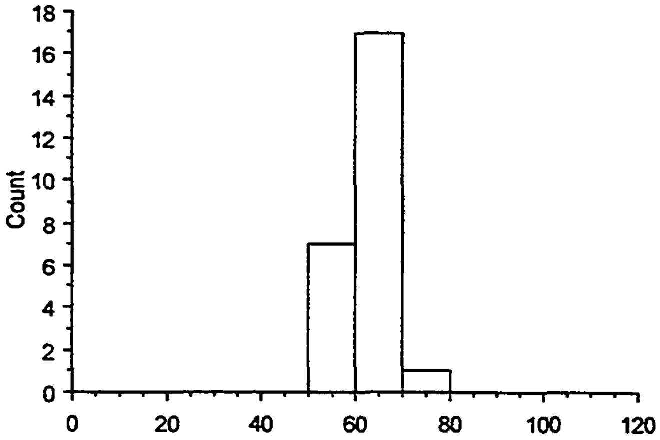


Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

July 27, 1998 Outgoing n = 24

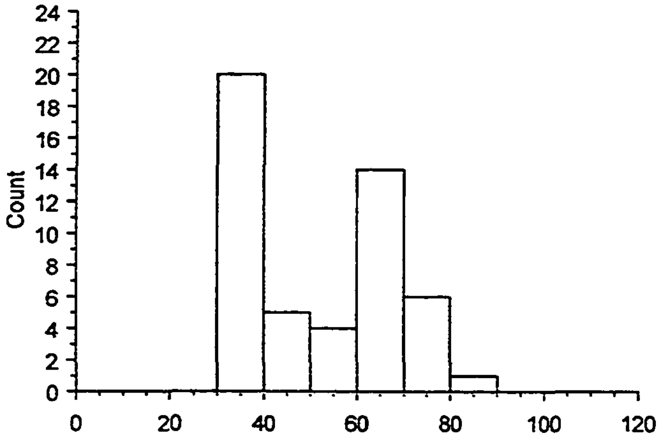


August 3, 1998 Incoming n = 25

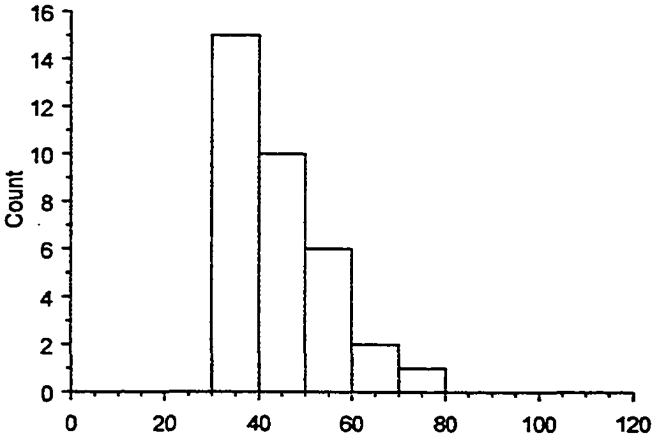


Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus* (continued)
Interval includes lowest value.

September 2, 1998 Outgoing n = 50

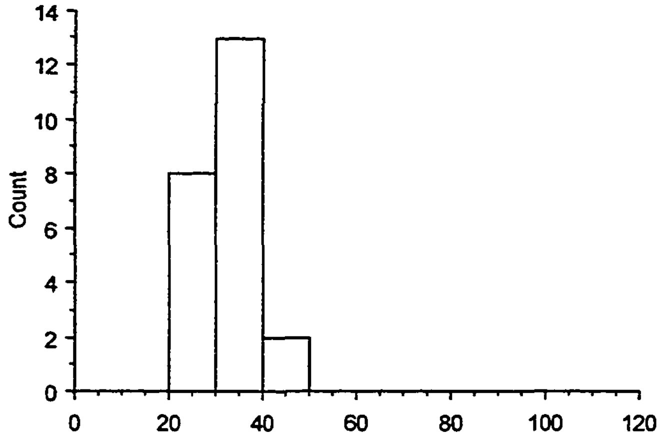


November 8, 1998 Incoming n = 34

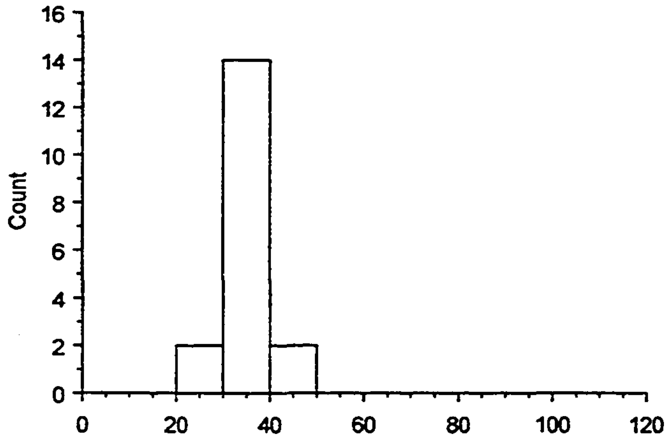


Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

November 13, 1998 n = 23



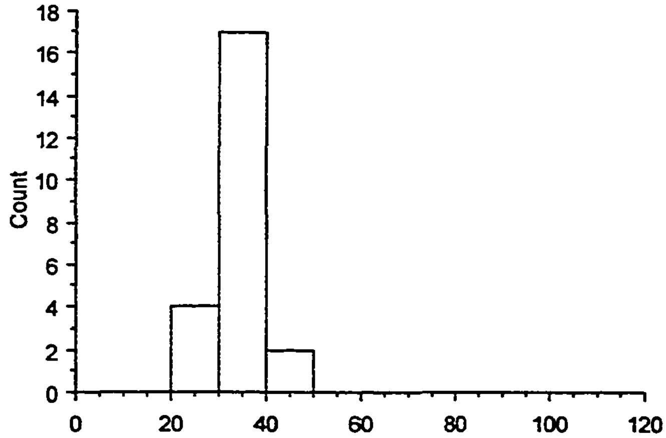
May 10, 1999 Incoming n = 18



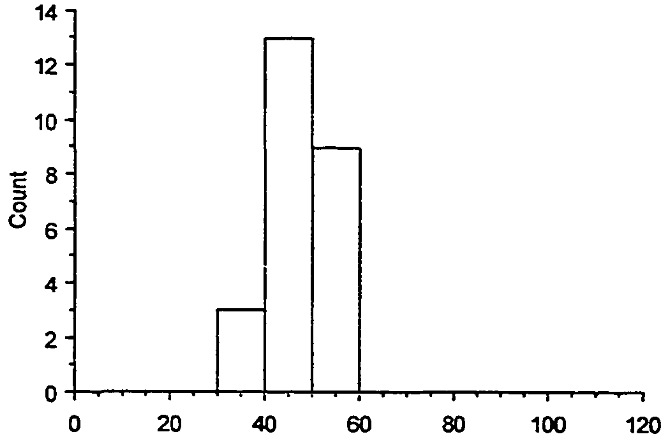
Appendix 2 (continued)

Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

May 10, 1999 Outgoing n = 23

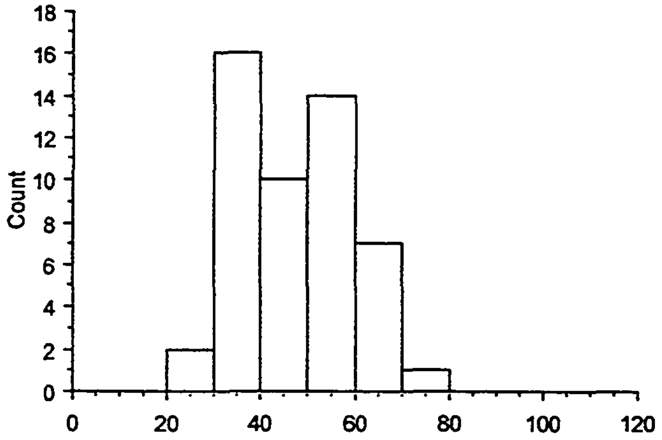


June 10, 1999 Outgoing n = 25

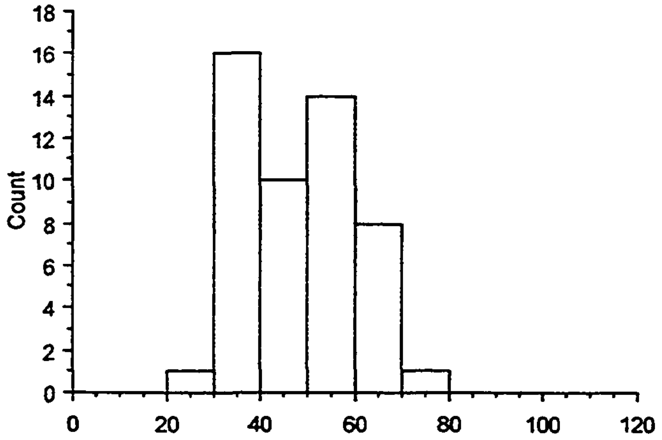


Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

July 8, 1999 Outgoing n = 50

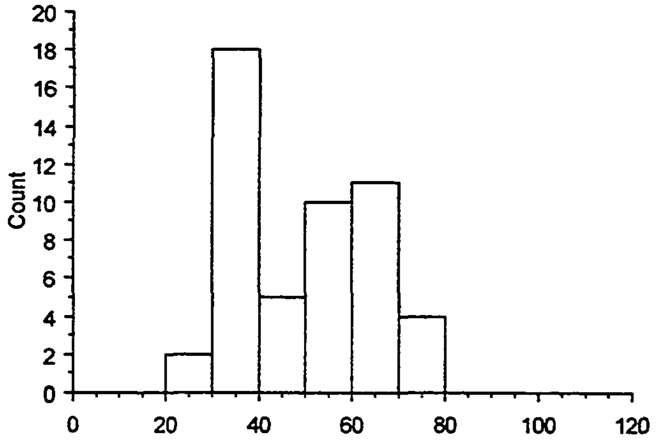


July 8, 1999 Incoming n = 50

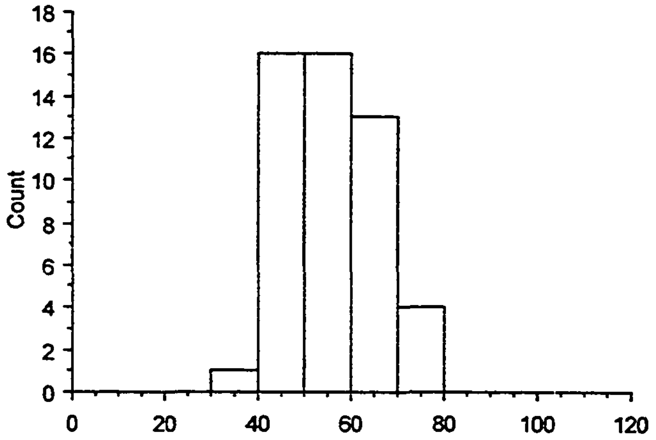


Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

August 6, 1999 Outgoing n = 50

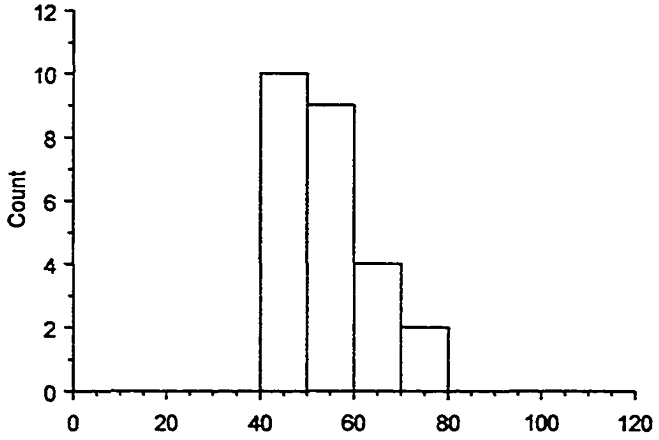


June 19, 2000 Incoming n = 50



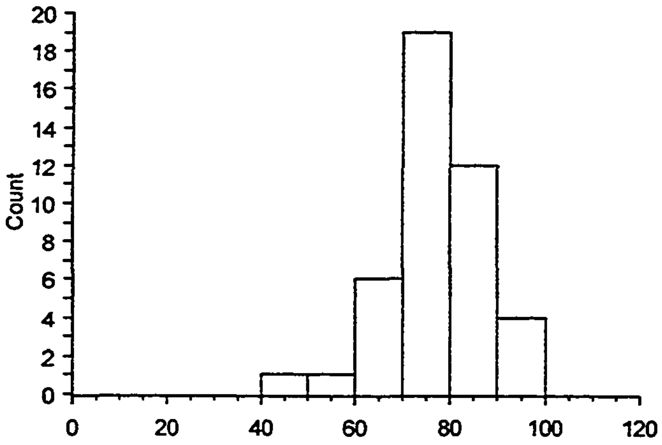
Appendix 2 (continued)
Standard length histograms (mm) of *Fundulus heteroclitus*
Interval includes lowest value.

October 18, 1999 Incoming n = 25

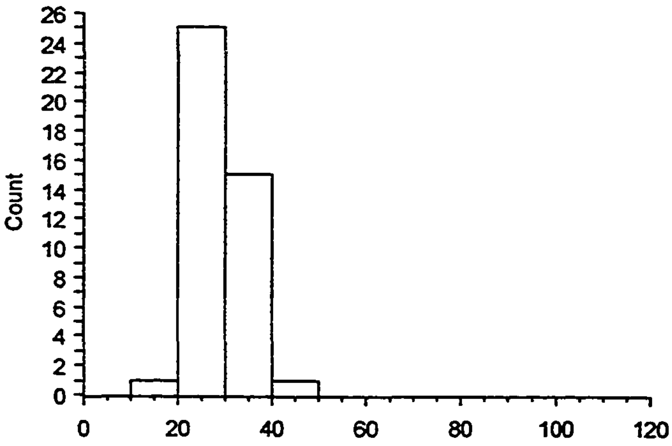


Appendix 3
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

June 23, 1998 Incoming n = 43

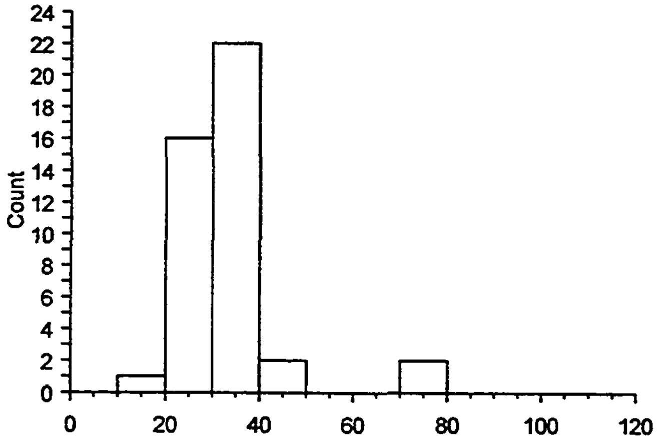


June 23, 1998 outgoing n = 42

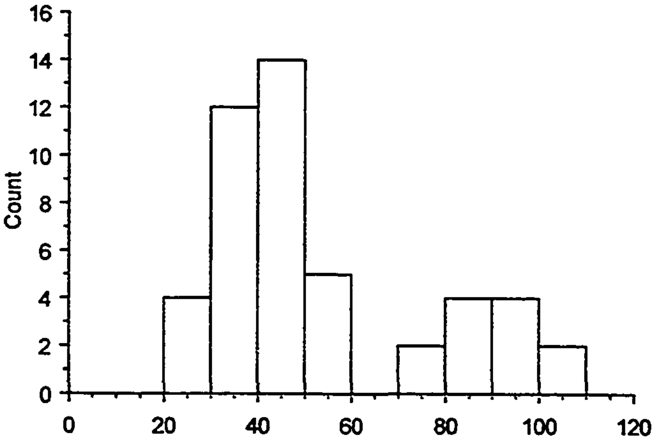


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

July 9, 1998 Incoming n = 43

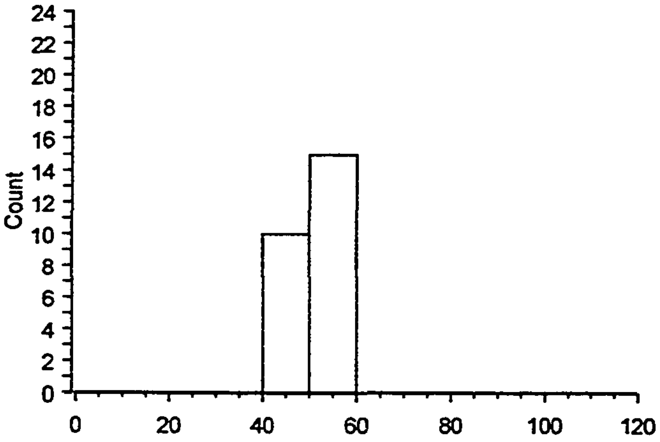


July 9, 1998 Outgoing n = 47

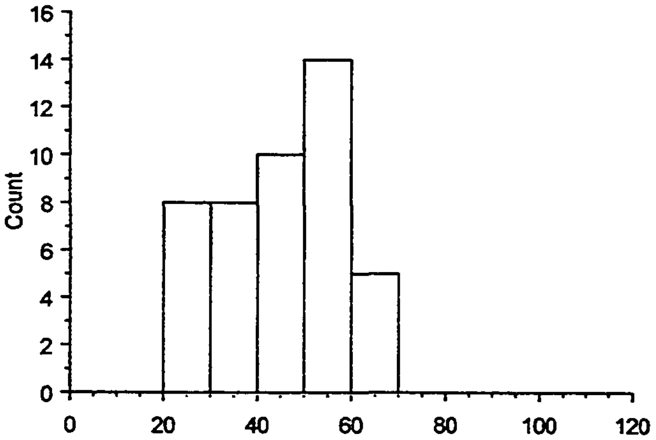


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

July 24, 1998 Incoming n = 25

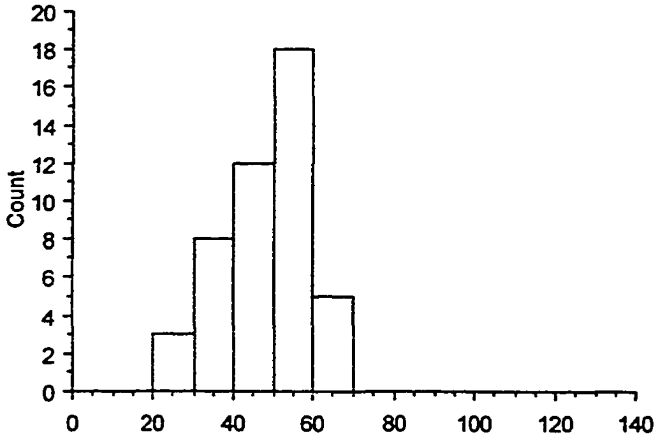


July 27, 1998 Incoming n = 45

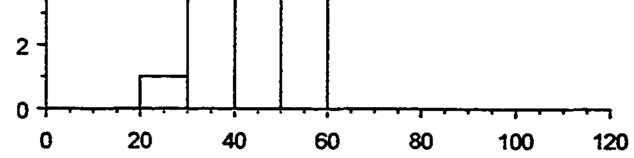


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

July 27, 1998 Outgoing n = 46

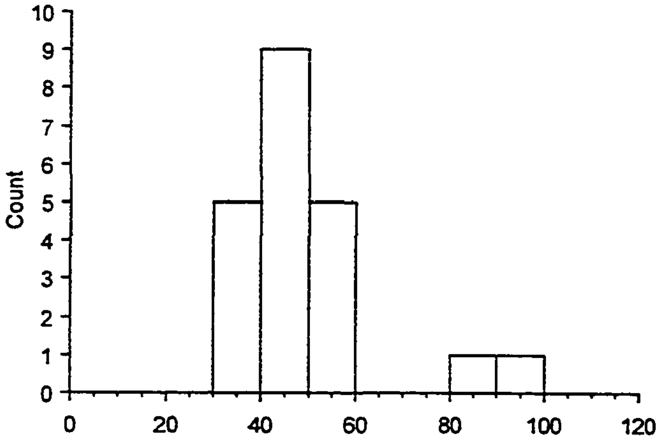


August 3, 1998 Incoming n = 25

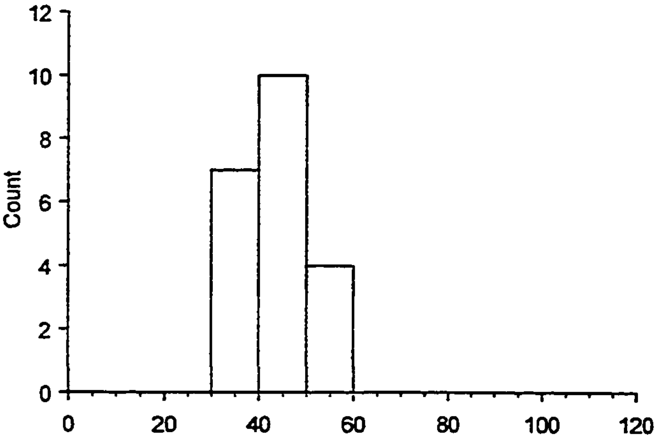


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

August 12, 1998 Incoming n = 21

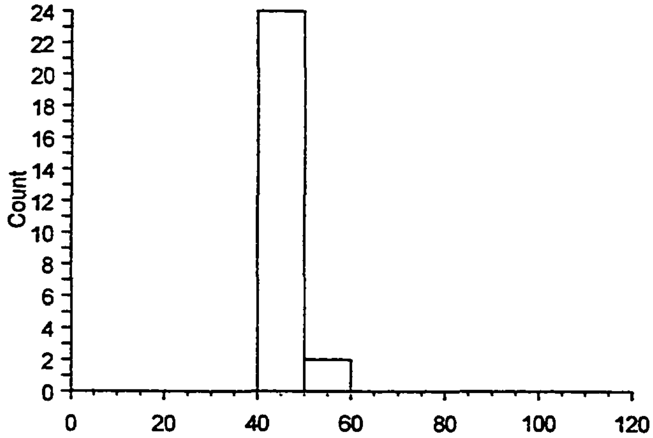


September 2, 1998 Outgoing n = 21

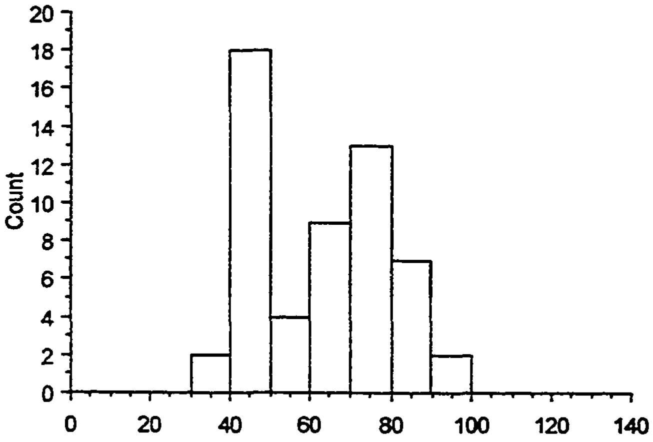


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

September 25, 1998 Outgoing n = 26

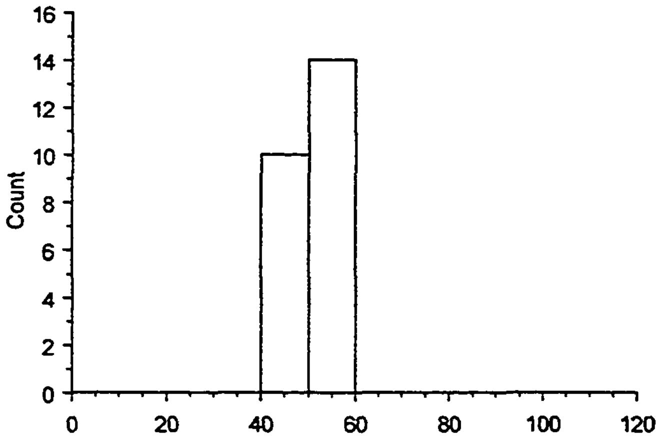


September 25, 1998 Incoming n = 55

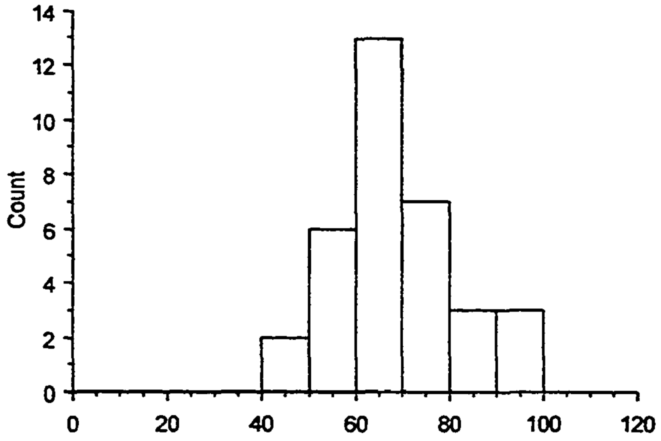


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

November 8,1998 Incoming n = 24



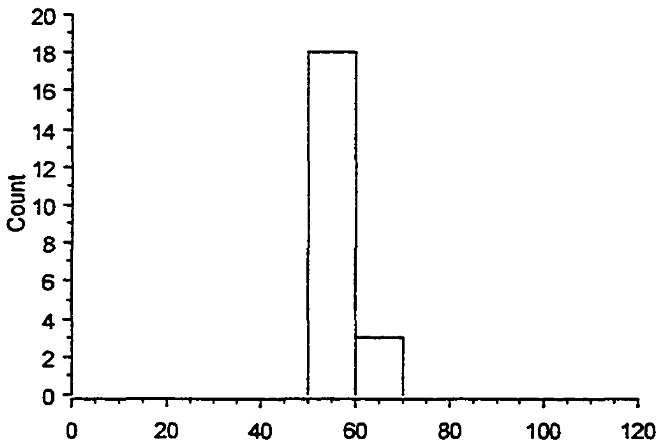
November 13,1998 n = 34



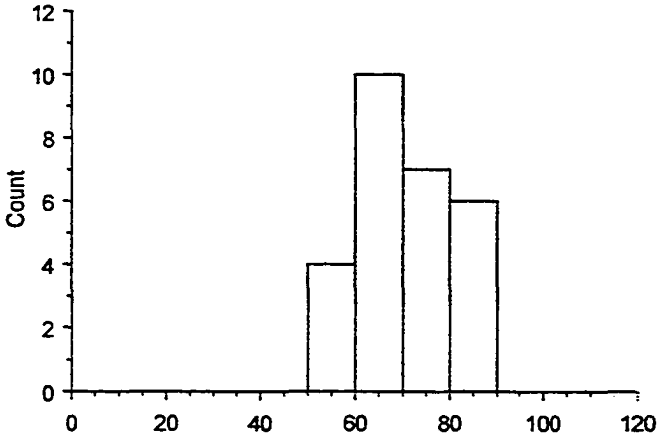
Appendix 3 (continued)

Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

April 15, 1999 Incoming n = 21



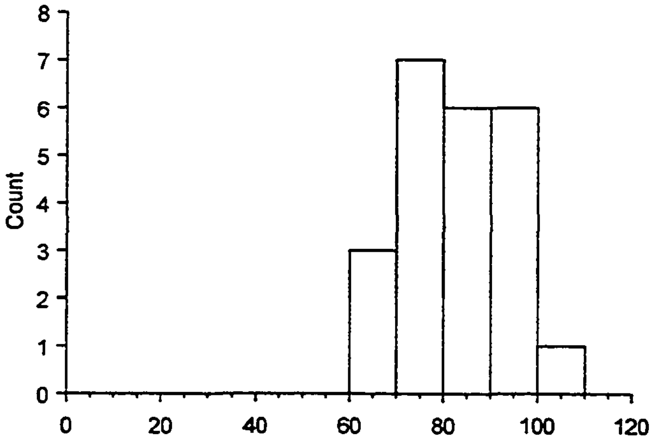
April 15, 1999 Outgoing n = 27



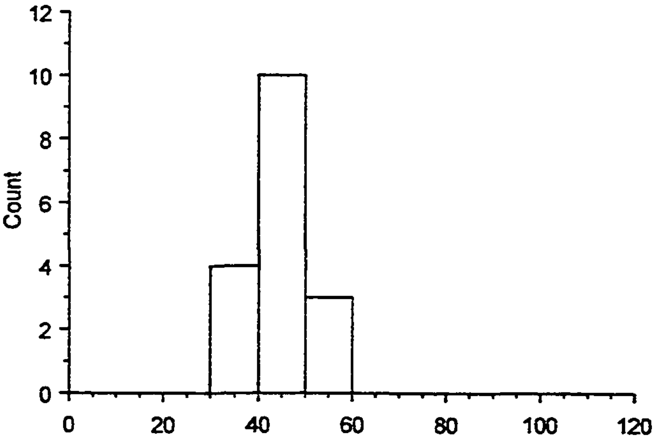
Appendix 3 (continued)

Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

June 10, 1999 Outgoing n = 23



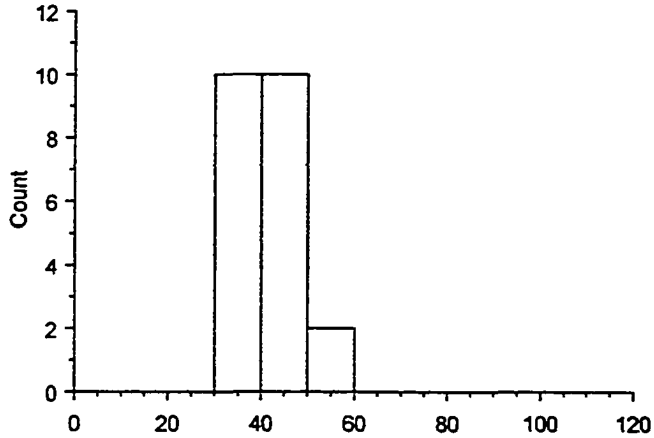
July 8, 1999 Outgoing n = 17



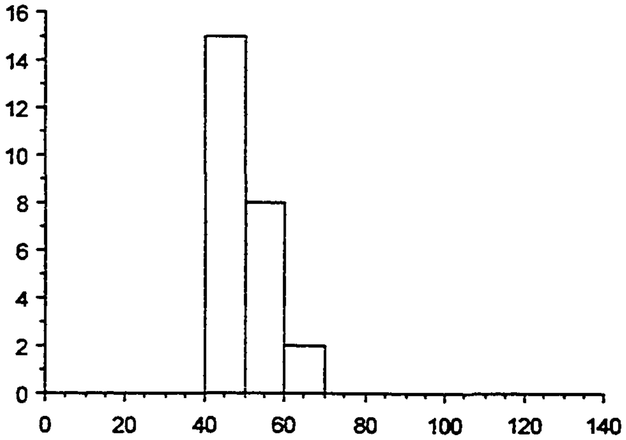
Appendix 3 (continued)

Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

July 8, 1999 Incoming n = 22

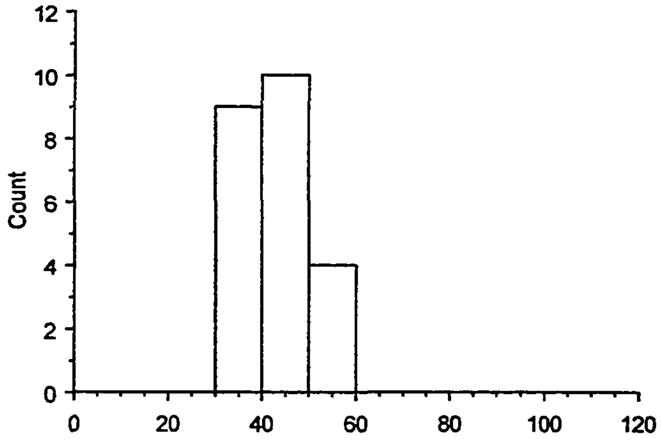


August 6, 1999 Outgoing n = 25

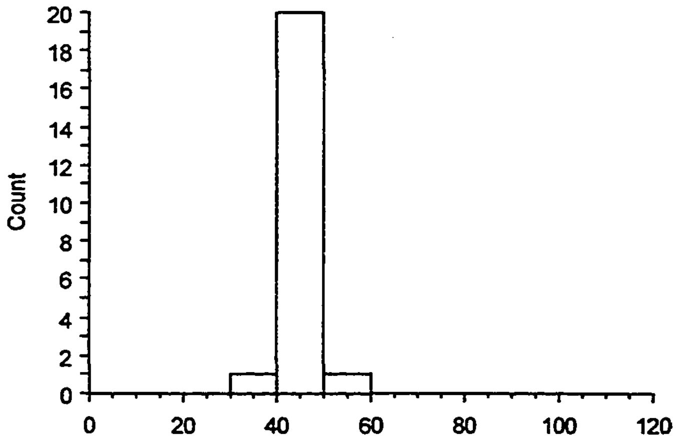


Appendix 3 (continued)
Standard length histograms (mm) of *Menidia menidia*
Interval includes lowest value.

September 2, 1999 Outgoing n = 23

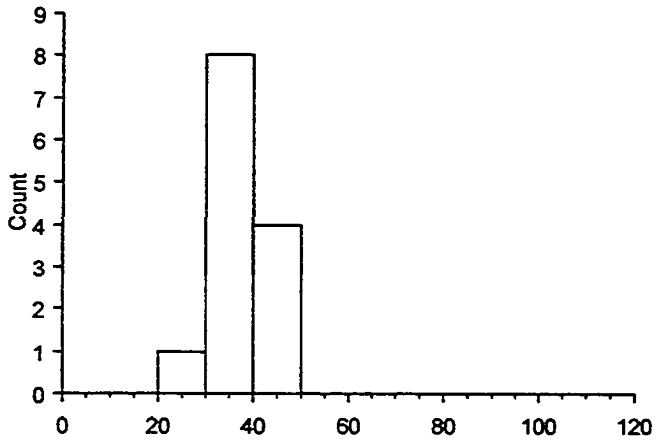


October 18, 1999 Incoming n = 22

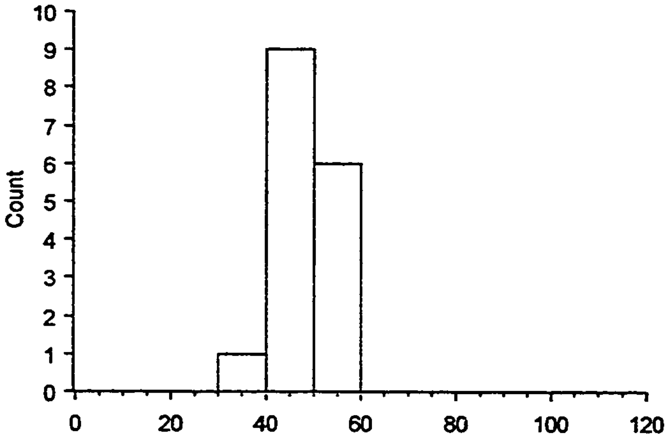


Appendix 4
Standard length (mm) histograms of *Pseudopleuronectes americanus*
Interval includes lowest value.

June 23 and July 9, 1998 (pooled) Outgoing n = 13



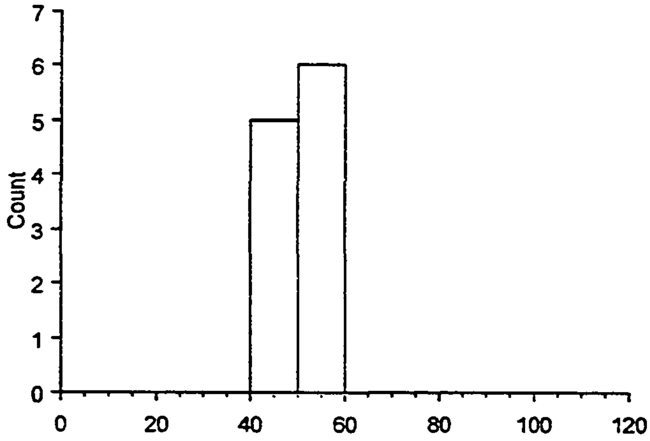
July 27, 1998 Outgoing n = 16



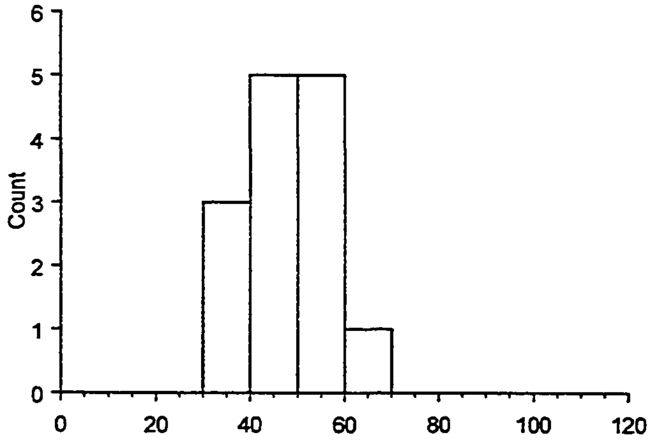
Appendix 4 (continued)

Standard length (mm) histograms of *Pseudopleuronectes americanus*
Interval includes lowest value.

September 2, 1998 Outgoing n = 11

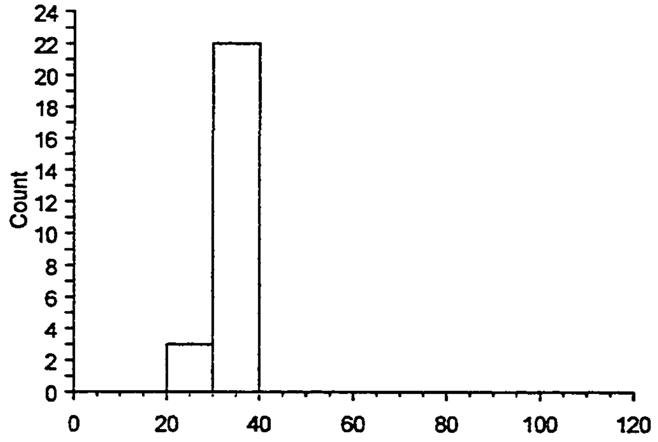


November 8, 1998 Incoming n = 14

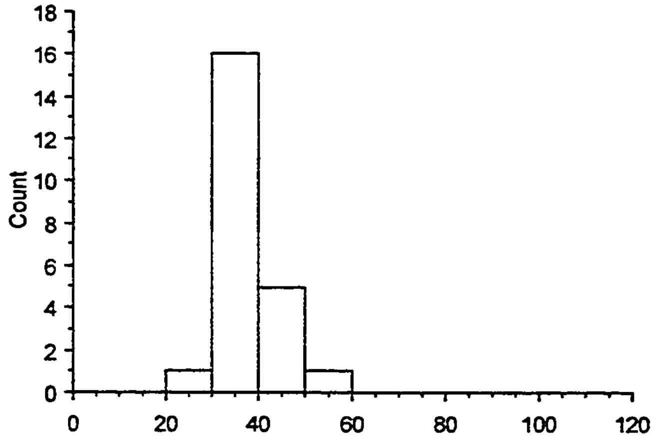


Appendix 4 (continued)
Standard length histograms (mm) of *Pseudopleuronectes americanus*
Interval includes lowest value.

June 10, 1999 Outgoing n = 25

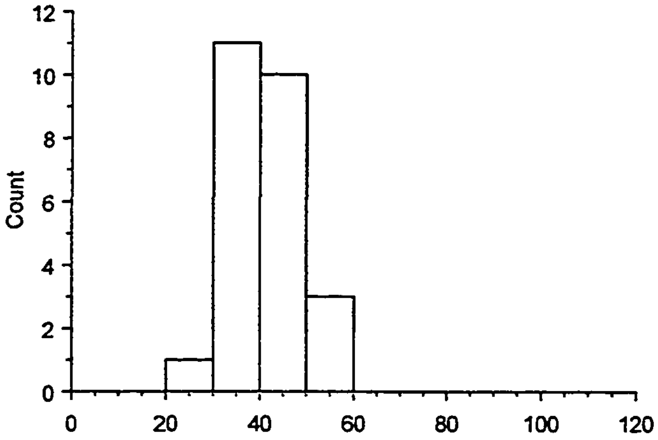


July 8, 1999 Outgoing n = 23

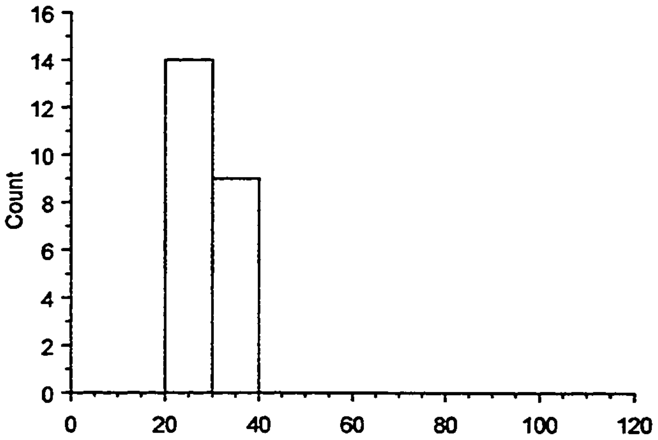


Appendix 4 (continued)
Standard length histograms (mm) of *Pseudopleuronectes americanus*
Interval includes lowest value.

August 6, 1999 n = 25

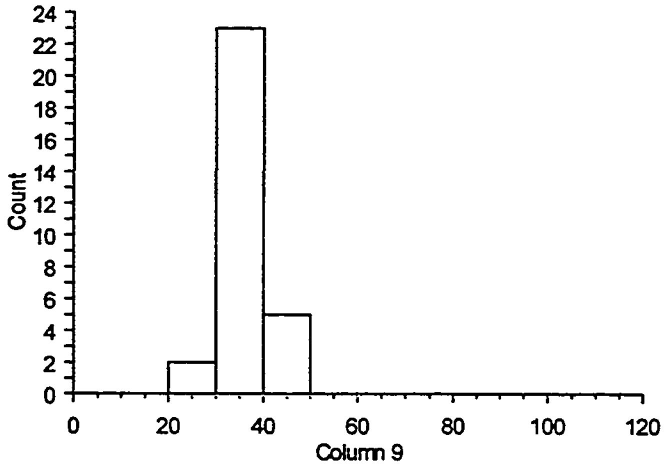


May 31, 2000 Outgoing n = 23



Appendix 4 (continued)
Standard length histograms (mm) of *Pseudopleuronectes americanus*
Interval includes lowest value.

June 19, 2000 Incoming n = 30

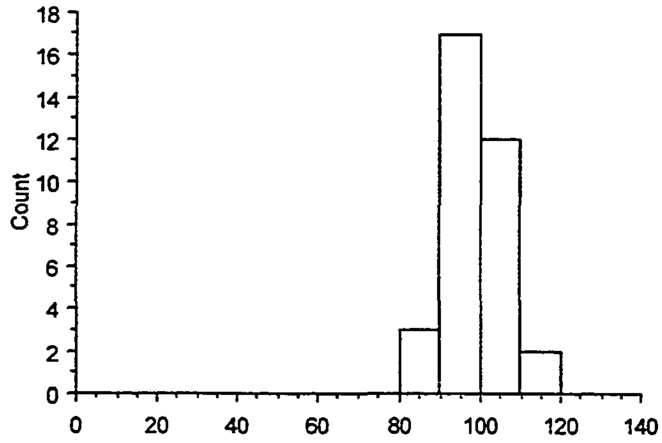


Appendix 5

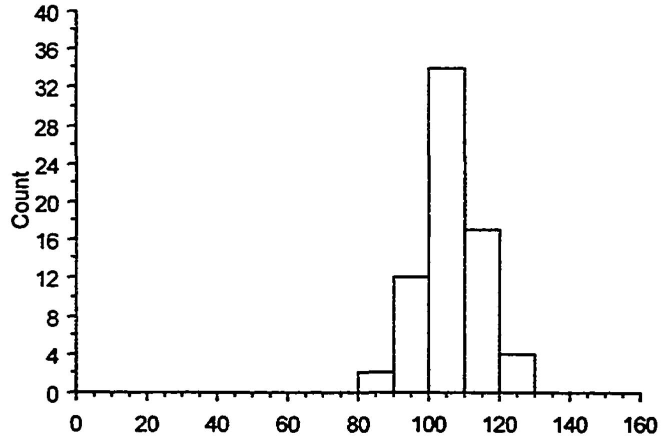
Standard length (mm) histograms of *Pomatomus saltatrix*

Interval includes lowest value.

July 27, 1998 Outgoing n = 34



August 3, 1998 Incoming n = 70

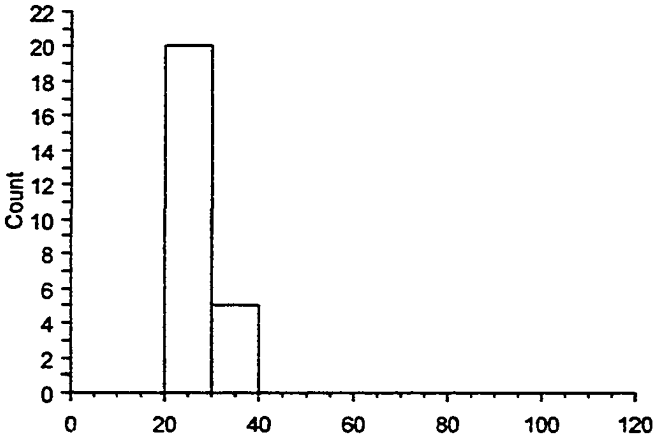


Appendix 6

Standard length histogram (mm) for *Cyprinodon variegatus*

Interval includes lowest value.

July 8, 1999 Incoming n = 25



Appendix 7

Prey taxa identifications

Taxa	**Marsh**	**Outer Estuary**
Cnidaria		
Actinaria	*Diadumene leucolena*	
	Metridium senile	
Mollusca		
Bivalvia	*Gemma gemma*	*Gemma gemma*
		Modiolus modiolus
Gastropoda	*Littorina obtusata*	*Littorina sp.*
	Littorina littorea	
	Melampus bidentaus	
	Skeneopsidae planorbis	*Skenenopsidae planorbis*
Annelida		
Polychaeta	*Neresis succinea*	*Neresis succinea*
	Neresis diversicolor	*Neresis diversicolor*
	Neresis virens	
	Eteone sp.	*Eteone sp.*
Arthropoda		
Cladocera	*Podon sp.*	
		Evadne sp.
Amphipoda	*Gammarus mucronatus*	*Gammarus mucronatus*
	Corophium sp.	*Corophium sp.*
	Microdeutopus gryllotalpa	*Microdeutopus gryllotalpa*
	Melita nitida	*Melita nitida*
	Microprotopus raneyi	
	Chelura sp.	
	Caprella sp.	
Isopoda	*Sphaeroma quadridentatum*	*Sphaeroma quadridentatum*
	Cyathura polita	
	Edotea montosa	*Edotea montosa*
	Gnathia cerina	
	Jaera marina	

Appendix 7

Prey taxa identifications (continued)

Decapoda	*Balanus improvisus*	*Balanus sp.*
	Neomysis americana	*Neomysis americana*
		Erythrops erythropthalma
		Palaeomonetes pugio
	Crangon septemspinosa	*Crangon septemspinosa*
		Panopeus herbstii
	Pagurus longicarpus	*Pagurus longicarpus*
	Uca sp.	
	Limulus polyphemus	*Limulus polyphemus*
Chordata	*Menidia menidia*	*Menidia menidia*
	Fundulus heteroclitus	*Fundulus heteroclitus*

Appendix 8

Keys and Source of Long Island Map

Abbott, R.T. and P.A. Morris. 1995. *Peterson Field Guide Series: Shells of the Atlantic & Gulf Coasts & The West Indies.* Boston: Houghton Mifflin. xxxiii + 350 pages.

Bousfield, E.L.1973. *Shallow Water Marine Amphipoda.* Ithaca: Cornell University Press. i – xii + 312 pages.

ESRI. *ESRI Data and Maps for ArcView 3.3.* Redlands, California.

Fauchald, K. 1977. *The Polychaete Worms Definition and Keys to the Orders, Families and Genera.* Los Angelus: Natural History Museum Science Series 28. i – x + 188 pages.

Gosner, K. 1978. *Peterson Field Guide Series: A Field Guide to the Atlantic Seashore.* Boston:Houghton Mifflin. i – xvi + 329 pages.

Murdy, E.O., Birdsong, R.S. and J.A. Musick. 1997. *Fishes of Chesapeake Bay.* Washington:Smithsonian Institution Press. i – xi + 324 pages.

Pettibone, M.H. 1963. *Marine Polychaete Worms of the New England Region: 1.Aphroditidaethrough Trochochaetidae.* Washington: Smithsonian Institution U.S. National Museum Bulletin 227 Part 1. i – v + 356 pages.

Pollock, L.W. 1998. *A Practical Guide to the Marine Animals of Northeastern North America.* New Brunswick: Rutgers University Press. i – vii + 367 pages.

Smith, C.L. 1985. *The Inland Fishes New York State.* Albany: NYS Dept. of Environmental Conservation. i – xi + 522 pages.

Smith, D.L. and K.B. Johnson. 1996. *Guide to Marine Coastal Plankton and Marine Invertebrate Larvae. 2nd edit.* Dubuque: Kendall/Hunt. i – xv + 221 pages.

Literature Cited

Allen, D. M., W. S. Johnson, and V.Ogburn-Matthews. 1995. Trophic relationships and seasonal utilization of salt-marsh creeks by zooplanktivorous fishes. Environmental Biology of Fishes **42**:37-50.

Allen, E. A., P. E. Fell, M. A. Peck, J. A. Gieg, C. R. Guthke, and M. D. Newkirk. 1994. Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural marshes. Estuaries **17**:462-471.

Baker-Dittus, A. M. 1978. Foraging patterns of three sympatric killifish. Copeia:383-389.

Buckel, J. A., and D. O. Conover. 1997. Movements, feeding periods, and ration of piscivorus young-of-the-year bluefish, *Pomatomus saltatrix,* in the Hudson River estuary. Fishery Bulletin, U.S. **95**:665-679.

Buckel, J. A., and A. W. Stoner. 2000. Functional response and switching behavior of young-of-year piscivorus bluefish. Journal of Experimental Marine Biology and Ecology **245**:25-41.

Cadigan, K. M., and P. E. Fell. 1985. Reproductive, growth and feeding habits of *Menidia menidia* (Atherinidae) in a tidal marsh-esturarine ecosystem in southern New England. Copeia:21-26.

Cross, R.E. and A.E. Stiven. 1997. Experimental studies of competition in salt marsh juvenile fish (*Fundulus heteroclitus* Linnaeus) and shrimp (*Palaemonetes pugis*) in laboratory microcosms. Journal of Experimental Marine Biology and Ecology **212**:133-146.

Crawford, R. 1990. Winter flounder in Rhode Island Coastal Ponds. Rhode Island Sea Grant RI 02882-1197. 24 pages.

Franz, D. R., and J. T. Tancredi. 1992. Secondary production of the amphipod *Ampelisca abdita* Mills and its importance in the diet of juvenile winter flounder *(Pseudopleuronectes americanus)*: prey availability and diversity. Transactions of the American Fisheries Society **103**:261-269.

Freidland, K. D., G. C. Garman, A. J. Bejda, A. L. Studholme, and B. Olla. 1988. Interannual variation in diet and condition in juvenile bluefish during estuarine residence. Transactions of the American Fisheries Society **117**:474-479.

Grover, J.J. 1997. Feeding habits of pelagic summer flounder, *Paralichthys dentatus,* larvae in oceanic and estuarine habitats. Fishery Bulletin, U.S. **96**:248-257

Halpin, P. M. 1997. Habitat use patterns of the mummichog, *Fundulus heteroclitus*, in New England. I. Intramarsh Variations. Estuaries **20**:618-625.

Hartmann, K. J., and S. B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society **124**:520-537.

Harvey, C.J. 1998 Use of sandy beach habitat by *Fundulus majalis*, a surf zone fish. Marine Ecology Progress Series. **164**:307-310

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist **100**:419-424

Houser, D. S., and D. M. Allen. 1996. Zooplankton dynamics in an intertidal salt-marsh basin. Estuaries **19**:659-673.

Howell, P. T., D. R. Molnar, and R. B. Harris. 1999. Juvenile winter flounder distribution by habitat type. Estuaries **22**:1090-1095.

Juanes, F., R. E. Marks, K. A. McKown, and D. C. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. Transactions of the American Fisheries Society **122**:348-356.

Kneib, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. American Zoologist **26**:259-269.

Kneib, R. T. 1987. Seasonal abundance, distribution and growth of postlarval and juvenile grass shrimp *(Palaemonetes pugio)* in a Georgia, USA, salt marsh. Marine Biology **96**:215-223.

Kneib, R. T. 1997a. Early life stages of resident nekton in intertidal marshes. Estuaries **20**:214-230.

Kneib, R. T. 1997b. The role of tidal marshes in the ecology of estuarine nekton. p.163-220 *in* A. D. Ansell, R. N. Gibson, and M. Barnes, editors. Oceanography and Marine Biology An annual Review. UCL Press, London.

Krebs, C. J. 1999. Ecological Methodology, 2nd edition. Addison Wesley Longman, Menlo Park, CA. p.470-471

Labropoulou, M. , Athanasios, M and N. Tsimenides. 1999. Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus 1758). Fishery Bulletin. **97**:495-507

Laffaille, P. Lefeurvre, J-C, Schricke, M-T, and E. Feunteun. 2001. Feeding ecology of 0-group sea bass *(Dicentrachus labrax)* in salt marshes of Mont Saint Michel Bay (France). Estuaries **24**:116-125.

Lotrich, V. A. 1975. Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. Ecology **56**:191-198.

Mallin, and H.W. Pearl. 1994 . Planktonic trophic transfer in a estuary: seasonal, diel, and community structure effects. Ecology **75**:2168-2184

Manderson, J. P., B. A. Phelan, A. W. Stoner, and J. Hilbert. 2000. Predator-prey relations between age-1+ flounder *(Paralichthys dentatus*, Linnaeus*)* and age-0 winter flounder *(Pseudopleuronectes americanus*, Walbaum*)*: predatory diets, prey selection, and effects of sediments and macrophytes. Journal of Experimental Marine Biology and Ecology **251**:17-39.

McIvor, C. C., and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology **69**:1341-1351.

Meise, C., J. S. Collie, J. Widman, and P. Howell. 1999. Growth and mortality of juvenile winter flounder in two New England estuaries. Estuaries **22**:297-303.

Meng, L., and J. C. Powell. 1999. Linking juvenile fish and their habitats: an example from Narragansett Bay Rhode Island. Estuaries **22**:905-916.

Middaugh, D. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Copeia: 766-776.

Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington. i - x + 324 pages.

Nixon, S. W., and C. A. Oviatt. 1973. Ecology of a New England Salt Marsh. Ecological Monographs **43**:463-498.

Pearcy, W. G. 1962. Ecology of an esturarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum) Parts I-IV. Bulletin of the Bingham Oceanographic Collection **18**:1-78.

Phelan, B. A., R. Goldberg, A. J. Bejda, S. Pereira, S. Hagan, P. Clark, A. L. Studholme, A. Calabrese, and K. W. Able. 2000. Estuarine and habitat-related differences in growth rates of young-of-year winter flounder *(Pseudopleuronectes americanus)* amd tautog *(Tautoga onitis)* in three northeastern US estuaries. Journal of Experimental Marine Biology and Ecology **247**:1-28.

Poole, J. C. 1966 The use of salt-water coves as winter flounder as winter flounder nursery grounds. New York Fish and Game Journal **13**:221-225.

Richards, S. W. 1976. Age, growth, and food of bluefish *(Pomatomus saltatrix)* from east-central Long Island Sound from July through November 1975. Transactions of the American Fisheries Society **105**:523-525.

Roundtree, R. A., and K. W. Able. 1992a. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance, and biomass. Estuaries **15**:171-185.

Roundtree, R. A., and K. W. Able. 1992b. Foraging habits, growth, and temporal patterns of salt marsh creek habitat use by young-of-year summer flounder in New Jersey. Transactions of the American Fisheries Society **121**:765-776.

Rozas, L.P. , McIvor, C.C. and W.E. Odum 1988. Intertidal rivulets and creekbanks: corridors between tidal creeks and marshes. Marine Ecology Progress Series **47**:303-397

Rozas, L. P., and M. W. LaSalle. 1990. A comparison of the diets of the gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. Estuaries **13**:332-336.

Rozas, L. P., and R. J. Zimmerman. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). Marine Ecology Progress Series **193**:217-239.

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

Shreffler, D. K., C. A. Simenstad, and R. M. Thom. 1992. Foraging by juvenile salmon in a restored estuarine wetland. Estuaries **15**:204-213.

Stehlik, L. L., and C.J.Meise. 2000. Diet of winter flounder in a New Jersey: ontogenetic change and spatial variation. Estuaries **23**:381-391.

Swenson, R. O., and A. T. McCray. 1996. Feeding ecology of the tidewater goby. Transactions of the American Fisheries Society **125**:956-970.

Vince, S., I. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. Journal of Experimental Marine Biology and Ecology **23**:255-266.

Warkentine, B.E. and J.W. Rachlin. 1989. Winter offshore diet of Atlantic silverside, *Menidia menidia*. Copeia:195-198.

Weinstein, M. P., S. Y. Lytvin, K. L. Bosley, C. M. Fuller, and S. C. Wainwright. 2000. The role of tidal salt marsh as an energy source for marine transient and resident finfish: a stable isotope approach. Transactions of the American Fisheries Society **129**:797-810.

Weisberg, S. B., and V. A. Lotrich. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog, *Fundulus heteroclitus:* an experimental approach. Marine Biology **66**:307-310.

Weisberg, S. B., R. Whalen, and V. A. Lotrich. 1981. Tidal and diurnal influence on food consumption of a salt marsh killifish *Fundulus heteroclitus*. Marine Biology **61**:243-246.

Weisberg, S.B. 1986. Competition and co-existence among f0ur estuarine species of *Fundulus*. American Zoologist **26**: 249-257

Weiss, H. M. 1995. Marine Animals of Southern New England and New York Bulletin 115. DEP, Hartford.

Werme, C. E. 1981. Resource partitioning in a salt marsh fish community. Dissertation. Tufts, Boston. i - xvi + 131 pages.

West, J.M. and J.B. Zedler 2000. Marsh -creek connectivity: fish use of a tidal salt marsh in southern California. Estuaries **23:**699-710

Wolda , H. 1981. Similarity indices, sample size and diversity. Oecologia. **50**:296-302.

Zaret, T. M. and A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principal. Ecology **52**:337-342