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Habitat use, secondary production, and trophic export by salt marsh nekton in shallow waters

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HABITAT USE, SECONDARY PRODUCTION, AND TROPHIC EXPORT BY SALT MARSH NEKTON IN SHALLOW WATERS

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

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by
Giancarlo Cicchetti
1998

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

Giancarlo Cicchetti

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DEDICATION

This dissertation is dedicated to my family and friends.

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ACKNOWLEDGMENTS

I would like to acknowledge the help of the many people who assisted me with this project. My wife Jennifer was very supportive from the very beginning of my program at VIMS. My mother Audrey Cicchetti and my sister Giulia Shlimak were also very helpful, and my sons Nicholas and Paul each contributed in their own way. Bob Diaz, my major professor, provided encouragement as well as excellent advice on a great diversity of topics. The marsh infaunal study which added insight to this project was courtesy of Bob Diaz, Dave Yozzo, Beth Hinchey, Janet Nestlerode, and Eric Wooden. Eric, Janet, and Beth also deserve special recognition for their many, many hours of help in the field and for their friendship. Funding was provided by the Chesapeake Bay National Estuarine Research Reserve in Virginia, The College of William and Mary, The John and Marilyn Zeigler Award, the William J. Hargis Award, and by VIMS Graduate Student Association minigrants. My Dissertation Committee - - Bob Diaz, Linda Schaffner, Jim Bauer, Jacques van Montfrans, and Ken Able - - were helpful, constructive, and very knowledgeable. Field crews and other valuable individuals included Marty Cavalluzzi, Janet Nestlerode, Beth Hinchey, Eric Wooden, Dave Yozzo, Randy Cutter, Treda Smith, Sandra Brooke, Linda Schaffner, William Reay, Carolyn Gardner, Mo Lynch, April Bahen, Dave Niebuhr, Aaron Bartholomew, Scott Lerberg, Lawrence Rozas, Tom Minello, Robyn Draheim, Dave Yozzo, Marilyn Zeigler, John Milliman, Jay Petersen, Andrea Alfaro, Lisa Ayers, Jeff Brust, Vince Buonaccorsi, Gina Burrell, Chris Buzzelli, Mike Campana, Pat Crewe, Shirley Crossley, Colleen Cunningham, Brenda Flores, Anamarija Frankic-Bandula, Raymond Forrest, Chuck Gerdes, Sarah Gaichas, Juli Harding, Rich Kraus, Mike Land, Tripp MacDonald, Kirt Moody, Jen Newton, Tom Orrell, John Parker, Brian Pearson, Chris Perle, VIMS Publications, Sue Presson, Paul Purves, John Rhoads, Susan Rollins, Alessandra Sagasti, Jamie Samuelson, Holly Simpkins, VIMS Sponsored Research, Mark Terwilliger, Alice Lee Tillage, VIMS Vessel Operations, John Walton, and Geoff White. These and many other people made my project possible, but also made my stay at VIMS much more enjoyable and rewarding.

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ABSTRACT

I present a quantitative study of habitat use, secondary production, and trophic export by intertidal nekton. I used 1.75 m^2 drop rings and throw rings to sample communities of shallow water nekton at high and low tides in salt marshes, intertidal flats, and seagrass beds (*Ruppia maritima*). Thirty-two species of nekton were captured between June and October 1995, with a mean overall abundance of 28.6 inds m^{-2} and a mean biomass of 3.8 g m^{-2} (dry weight). The blue crab, *Callinectes sapidus*, was the biomass dominant species. Seagrass and marsh edge habitats were extensively used by all sizes of blue crab, from recruiting juvenile to adult. Year-to-year variation was seen between 1995 and 1996 in blue crab recruitment. *Palaemonetes* shrimp were the most abundant nekton in the study, and interesting patterns of allopatry and apparent sympatry were found among the three species inhabiting this area. *Fundulus heteroclitus*, *F. majalis*, and *Lucania parva* were the dominant marsh resident fishes, while *Gobiosoma bosc* was the most abundant fish in seagrass habitats. Certain sciaenids used marsh habitats in a transient or opportunistic manner, as did *Menidia menidia*. The marsh surface was apparently used as a night-time refuge by *M. menidia*. Behavioral patterns for five marsh residents (*F. heteroclitus*, *F. majalis*, *L. parva*, *G. bosc*, and *P. intermedius*) differed from patterns reported elsewhere. This is taken as evidence of behavioral flexibility in habitat use between regions.

On the community level, each sampled habitat saw a unique pattern of use. Seagrass and marsh edge areas both supported a large biomass of nekton at high tide, but seagrass habitats held greater densities of nekton. Fundulids, blue crabs, *Palaemonetes pugio* and transient fishes used marsh surface habitats at high tide and took low-tide refuge in adjacent habitats. Secondary production in marsh habitats was estimated at approximately 7.4 - 8.0 gdw m^{-2} 150 d^{-1} (28.4 - 30.7 gww m^{-2} 150 d^{-1}) for the entire salt marsh nekton community between June and October, 1995 (150 days) if corrected for poorly sampled small size classes and for the removal efficiency of the gear. Gut contents of nekton were examined, and a mathematical model was constructed to estimate consumption by nekton in marsh and unvegetated habitats. The model also estimates export of animal tissue as predation by transient species. Predation on invertebrates was highest in marsh edge areas, at 44.2 gdw m^{-2} 150 d^{-1} of animal prey removed; predation at the edge by transients (export) was 28.0 gdw m^{-2} 150 d^{-1}. The value of marsh edge was clearly linked to both the vegetated and the unvegetated sides of the interface as refuge and feeding. Predation in the entire marsh area flooded at mean high tide was approximately 13 gdw m^{-2} 150 d^{-1}, and transient export was 5.6 gdw m^{-2} 150 d^{-1}. The major path for export from marsh interior habitats into deeper waters was blue crab predation on the marsh resident crabs *Uca* and *Sesarma*. Predation in unvegetated areas was 13.3 - 17.0 gdw m^{-2} 150 d^{-1} and export was 8.0 - 11.7 gdw m^{-2} 150 d^{-1}. The unvegetated intertidal was an important resource for nekton due to long periods of inundation and abundant polychaete prey. The largest part of the intertidal nekton community used all three habitat types (marsh, unvegetated, and seagrass), and the trophic contribution of each habitat was significant. Marsh, unvegetated, and seagrass habitats function together in this area to provide trophic support for intertidal nekton.

HABITAT USE, SECONDARY PRODUCTION, AND TROPHIC EXPORT BY SALT MARSH NEKTON IN SHALLOW WATERS

CHAPTER I. PROJECT OVERVIEW, SITE DESCRIPTION, AND SAMPLING METHODS

ABSTRACT

Marshes, seagrass beds, and unvegetated intertidal areas are critical to the trophic organization of most estuaries. The role of intertidal nekton as they move between these and other habitats is an important aspect of estuarine function. This study investigates habitat use, secondary production, and trophic export by intertidal nekton using quantitative 1.75 m^2 drop rings and throw rings. Five habitats were sampled at high tide: the marsh interior; the area of marsh within 3 m of the edge; the marsh edge itself; the unvegetated intertidal; and a patchy bed of *Ruppia maritima*. Three habitats were sampled at low tide: the shallow unvegetated intertidal (0 - 10 cm); the deep unvegetated intertidal (10 - 30 cm); and the bed of *Ruppia maritima*. Gut content studies were done on all groups of intertidal nekton. Patterns of habitat use were linked to feeding and export using a habitat-specific mathematical model. The model applies feeding information to sampled population sizes, and estimates consumption and predation in each habitat. The model results were used to evaluate links between shallow water habitats as nekton move from one area to another at each tidal cycle.

PROJECT OVERVIEW AND INTRODUCTION

Intertidal and shallow water estuarine areas are typically characterized by a complex and interconnected network of different habitats. These habitats grade from the marsh interior through the marsh edge, the unvegetated intertidal, marsh creeks, SAV beds, and into deeper unvegetated open water habitats. Water, mobilized by the twice-daily action of the tides, continuously floods and drains these areas. Mobile aquatic animals follow the tidal pulses into and out of each habitat. In this way, the various shallow water habitats are connected by the moving water and by the associated organisms. Kneib (1997a) states that "with regard to the influence of hydrodynamic processes on ecosystem function, it is difficult to imagine a more dynamic system than a tidal marsh". The major goals of this project are to quantitatively examine tidally-driven patterns of habitat use by nekton in shallow waters, to examine production of these nekton on the salt marsh, and to estimate the flows of biomass and trophic energy that connect habitats.

This dissertation is divided into four chapters. Chapter 1 is an introduction to the study and contains a project overview, a justification for the study, a description of the sampling area, and details on the drop trap sampling methods used to gather data for the remaining three chapters of the dissertation. Chapter 2 describes patterns of nekton use of shallow water areas based on the sampled abundances and size distributions of each species at high and low tide in each habitat. Use can be evaluated in many ways based on the spatial and temporal scales of interest; the first section of this chapter introduces these different ways to consider nekton. The second half of the chapter considers the use patterns of each major species, then attempts to synthesize a community-wide summary of use patterns. Chapter 3 moves beyond abundance and biomass, and examines secondary production of dominant salt marsh nekton to give another view of energetic processes in these habitats. Chapter 4 describes a mathematical model constructed to evaluate the trophic links between nekton and their invertebrate prey in salt marshes and adjacent habitats. The model is also used to

estimate the export of biomass from the salt marsh into adjacent waters as a connection between intertidal habitats and the deeper waters of the estuary. The last section of this dissertation, as synthesis and conclusion, provides a summary discussion of the investigated processes on the salt marsh surface and in adjacent waters.

BACKGROUND, JUSTIFICATION AND OBJECTIVES OF THE PROJECT

Marshes are important ecosystems in the overall functioning of the coastal ocean. John Clark (1974) identified marshes as "paramount among the vital areas of many coastal ecosystems". Yet the important trophic energy transfer processes within marshes, and those that connect marshes to other waters are poorly understood and have never been directly quantified on an ecosystem scale. This project contributes to a better understanding of the larger scale ecological processes involved in between-habitat energy transfer. The project also adds to our knowledge of habitat use by shallow water nekton. These are important goals towards an improved understanding of marsh and estuarine function.

Many aspects of predator - prey interactions in estuarine ecosystems are well described in the scientific literature. Trophic energy transfer between marshes, shallow waters, and deeper waters is less well studied, however, and many important questions remain unanswered (Kneib 1997a). Thayer *et al.* (1978) suggested that the actual boundary of salt marsh habitat is not the edge of the wetland, since materials and living biomass move extensively over this edge. The contribution of marshes to deeper waters has long been a subject of controversy in wetland ecology (Weinstein 1984) and is an important aspect of our understanding of estuarine structure and function.

This project attempts to address three gaps that exist in marsh habitat and energy flow research. First, most studies are reductionist and do not consider the entire community (Mattila 1992). Many insightful papers (Kneib and Stiven 1982, Quammen 1984, Wiltse *et al.* 1984, McIvor and Odum 1988) concentrate on one or a few predator-prey relationships. Other projects have focused on one area along a marsh-to-open water gradient: Teal (1962) primarily investigated lower trophic levels on the marsh surface, Nixon and Oviatt (1973) focused on a shallow subtidal embayment, while Weinstein and Walters (1981) looked at fish in subtidal marsh creeks. Second, several marsh energy transfer studies (Rountree and Able 1992a, 1992b) do not quantify the described flows of energy on a per square meter basis. Third, most of the

studies that are quantitative examine biomass, but do not investigate production. Production characterizes energy flow, growth, and yield (Diaz and Schaffner 1990). Each of the problems mentioned above can be solved by the use of easily deployable gear that samples effectively along an entire estuarine depth gradient. My project uses sampling gear that is quantitative in the habitats of concern and give results that allow valid comparisons between habitats.

This dissertation includes habitat use determinations and secondary production work with the abundant marsh-dependent nekton as well as consumption calculations and determination of feeding habits. The analysis of habitat use patterns in contiguous marsh, SAV, and unvegetated areas provides an important background for the trophic exchange work. Laboratory studies on the energetics of marsh nekton are widely available, but have not been satisfactorily linked to field data on an ecosystem scale. I attempt to do this by constructing an ecosystem-level dynamic energy flow model. The combination of published lab energetic studies with field quantifications of nekton abundance, biomass, diet, and production contributes to this synthesis of salt marsh trophic dynamics.

A practical objective of my study is to help coastal managers develop and implement more realistic habitat protection and restoration plans. Both land use managers and fisheries scientists benefit from a better understanding of marsh trophic dynamics. Houde and Rutherford (1993) mention that "an incomplete knowledge of trophic dependencies and transfer efficiencies limits the ability to predict estuarine fishery production and yields"; this is an area that needs research. A more detailed knowledge of interdependencies between estuarine habitats is vital to managing and protecting overall estuarine function. The case for protecting shallow water ecosystems is stronger if those ecosystems can be trophically and economically linked to deeper waters and to fisheries species. Boesch and Turner (1984) state that "In addition to the inherent scientific importance of the food and refuge issues, understanding the functional relationships between fishery production and coastal wetlands is of great practical importance." I hope to address some of these issues through the analysis of trophic transfer from shallow waters to deeper waters via predation.

Objectives Summary

(1) Describe and quantify spatial and temporal patterns of salt marsh use by nekton.

(2) Estimate the secondary production of dominant salt marsh nekton species.

(3) Estimate the flow of trophic energy from marsh surface invertebrates to nekton with a quantitative determination of consumption rates and feeding habits.

(4) Estimate the export of trophic energy from marsh surface to shallow subtidal via nekton migration and predation.

(5) Construct a habitat model to provide an energetic synthesis of trophic stocks and flows within this intertidal system.

DESCRIPTION OF SAMPLING AREA

The Goodwin Islands NERR

All research was conducted at the Goodwin Islands, a series of uninhabited islands at the mouth of the York River, Chesapeake Bay, Virginia (Figure 1). These islands are managed by the Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA) and are owned by the College of William and Mary. The total area of the islands is 154.5 hectares (Perry and Atkinson 1997), 85 hectares of which is intertidal marsh (Buzzelli 1996). Certain areas on the largest island are composed of forest and upland vegetation, but many of the smaller islands are entirely vegetated by marsh plants. The island is surrounded by extensive shoal areas, which Buzzelli (1996) reported as including approximately 100 hectares of unvegetated intertidal habitat and 120 hectares of subtidal seagrass habitat, primarily *Zostera marina* with some *Ruppia maritima* in the shallower areas.

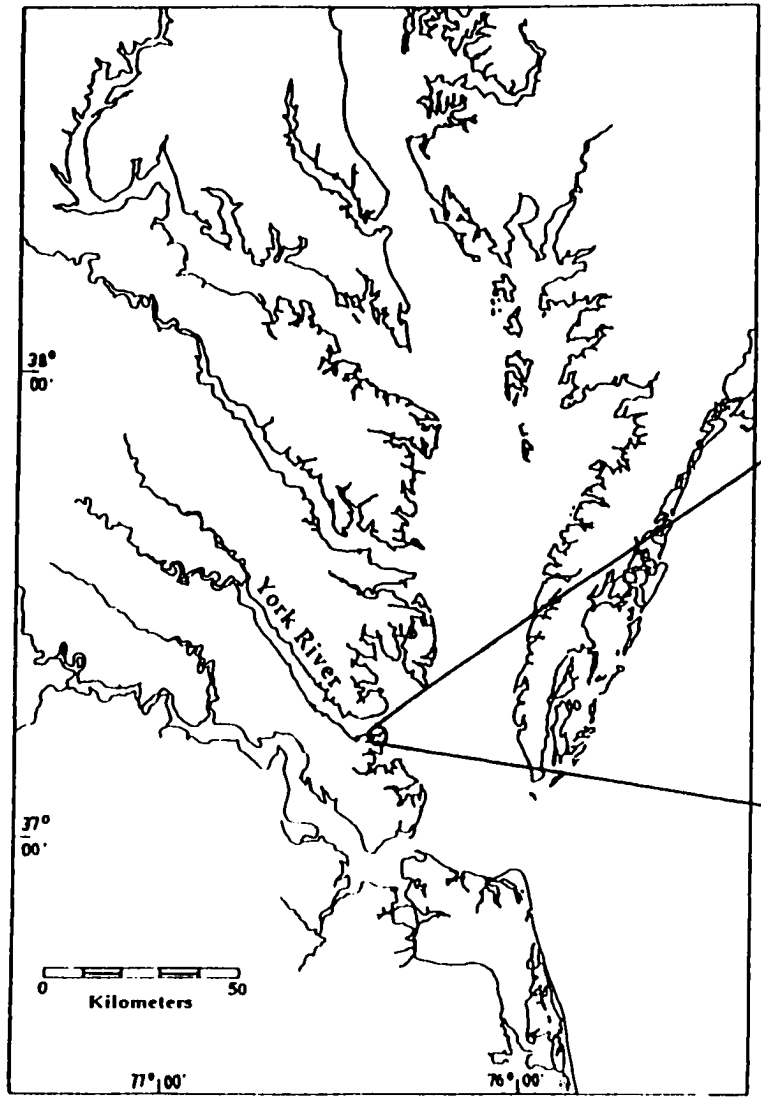
Within the Goodwin Islands marsh system, one smaller marsh area was chosen as a primary sampling area. The specific location used as a primary research area was the southern side of a small embayment in the center of the south-eastern face of the islands, arrow 1 on Figure 1. This embayment has also been used in other studies of the Goodwin Islands (Buzzelli 1996, K. Moore unpublished data, W. Reay unpublished data).

Physical description of the sampled habitats

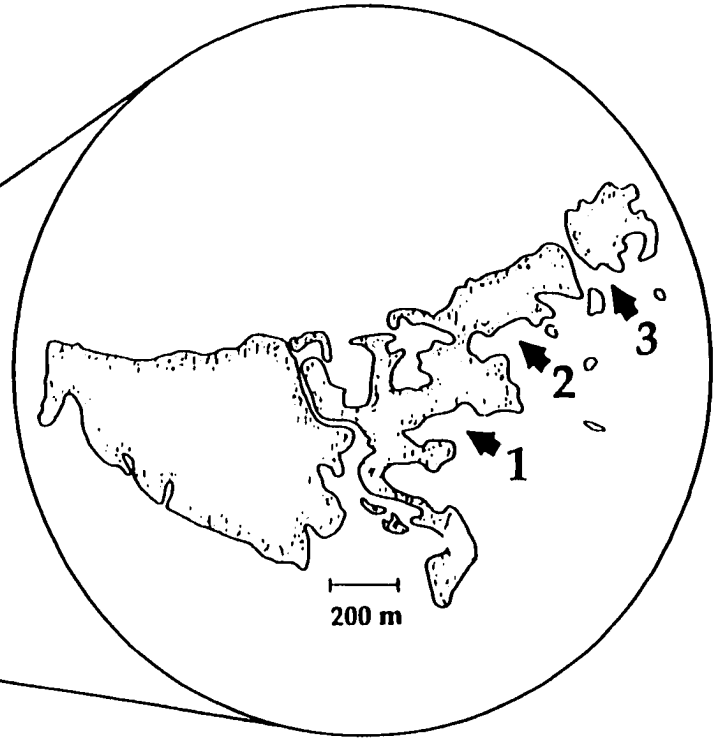
The sampling area is characterized by narrow fringing marshes bordering an open embayment, and is exposed to moderate wave energy. Most of the area investigated features a depositional marsh edge, though areas with an erosional margin up to 20 cm high also exist at the sampling area. A marsh elevation study coupled to tidal data showed that the sampling area experienced a mean horizontal flooding distance of 16 m during the time period of the study, and a mean spring tide horizontal flooding distance of 23 m. Vegetation at the marsh

Figure 1. Sampling Area

A map of Chesapeake Bay is shown with an enlargement of the Goodwin Islands National Estuarine Research Reserve. Sampling Area 1 (primary area), and Sampling Areas 2 and 3 (comparison areas) are indicated with arrows.



Chesapeake Bay



The Goodwin Islands

37° 12′ 46″ N, 76° 23′ 46″ W

edge was tall form or (to a lesser extent) short form *Spartina alterniflora* grading into short form *S. alterniflora* within three meters of the marsh edge. Short form *S. alterniflora*, in some areas mixed with *Distichlis spicata*, made up the marsh interior areas. No raised levee was present at the marsh edge. Elevation of the marsh surface changed most rapidly within the first few meters of the marsh edge, and interior areas were considerably more flat. The area in which sampling took place was a fringing marsh without creeks. One small tidal creek was present outside of the sampled area at the rear of the small embayment, and another was located on the opposite side of the embayment. The marsh faces a gently sloping unvegetated intertidal area with a grade of 2% - 4% (W. Reay, unpublished data). Sediments in the unvegetated intertidal near the marsh edge vary from the sandier exposed end of the embayment (4% gravel, 32% coarse sand, 55% fine sand, 8% silt, 1% clay, W. Reay, unpublished 1998 data) to the softer sediments in the protected end (< 1% gravel, 6% coarse sand, 54% fine sand, 37% silt, 3% clay, W. Reay, unpublished 1998 data). The gradual incline of the unvegetated intertidal continues into a bed of *Ruppia maritima* in the shallow subtidal; this submersed vegetation occupies a large part of the small shallow embayment (1 - 2 m deep at high tide) that abuts the area. The gross morphology of this marsh is a type that is fairly common on these islands and in this region; fringing marshes made up 38% of the marsh shoreline (by linear measure) in the York River system in the mid 1970's (Anderson *et al.* 1975, Hobbs *et al.* 1975, Anderson *et al.* 1976).

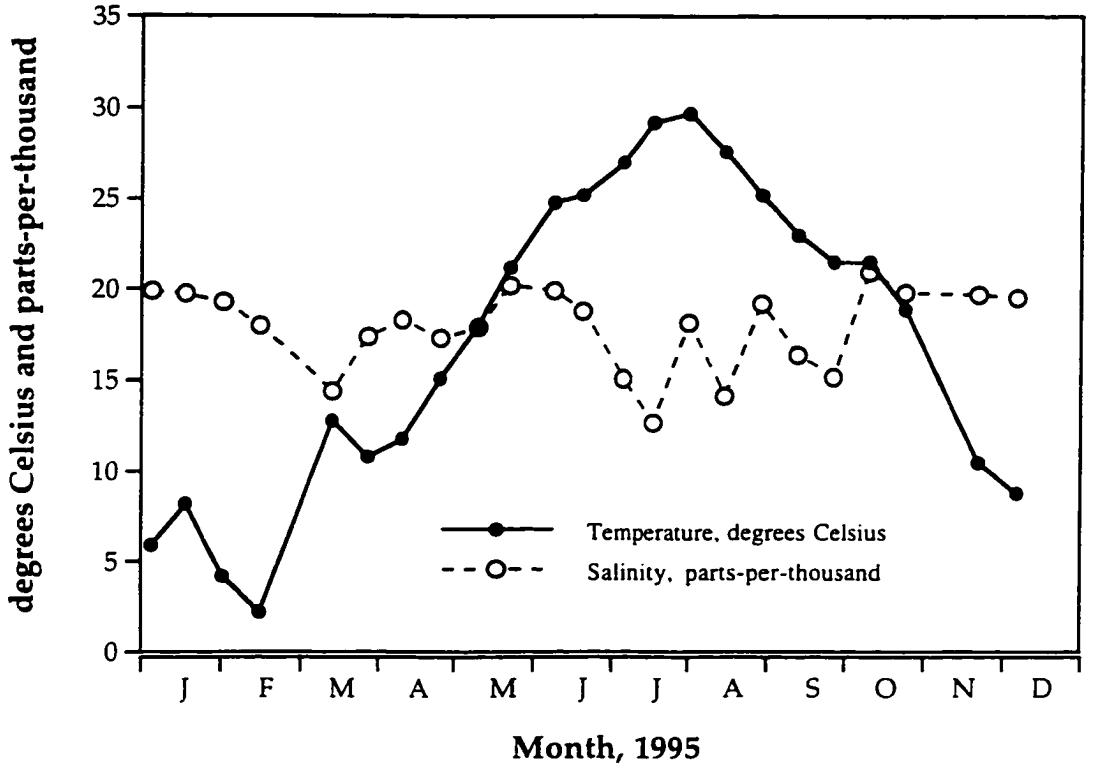
Water column characteristics

The Goodwin Islands have been described as polyhaline, with a characteristic salinity range of 18.0 - 22.0 ppt (Perry and Atkinson 1997). Salinities during the time period of my study ranged from 13 to 22 parts per thousand, with a mean of 18 parts per thousand (K. A. Moore, unpublished data). Summertime temperatures in the adjacent embayment reach 30° C. (K. A. Moore, unpublished data), and the shallow areas sampled in this project experienced even higher temperatures. Figure 2 shows salinity and temperature during the time period of

Figure 2. Temperature and Salinity, The Goodwin Islands, 1995

Data were collected at the entrance to the small embayment at arrow 1, Figure 1. Data are courtesy of K. A. Moore and B. Berry-Neikirk.

Temperature and Salinity, Goodwin Islands
(K. A. Moore, unpublished data)



the study (K. A. Moore, unpublished data). Tides are astronomically forced, and the marsh floods regularly. During the 5 month time period of this study, the mean tidal amplitude was 0.69 m, the mean horizontal flooding distance onto the marsh surface was 16 m, and the marsh flooded to a horizontal distance of at least 2 m on all days except one (NOAA tide data for Gloucester Point, VA, correlated to the sampling area, see below).

Biological characteristics

Standing stocks of autotrophs and primary production were examined by Buzzelli (1996) in 1995 (the year of this study) on the northern side of the small embayment described above. Buzzelli's area was 100 - 200 meters away from the primary area used in this study. Aboveground live biomass of *Spartina alterniflora* in Buzzelli's low marsh habitats (the elevations where my nekton samples were collected) varied seasonally from 512 gdw m^{-2} in May 1995 to 1176 gdw m^{-2} in September 1995 to 115 gdw m^{-2} in December. Shoot and root-rhizome biomass of *Spartina alterniflora* at low marsh areas of the Goodwin Islands site were within the range of values reported for other estuarine marshes of the Atlantic coast (Buzzelli 1996). Primary production of *S. alterniflora* on the marsh surface was 830 gC m^{-2} yr^{-1} (Buzzelli 1996).

Buzzelli (1996) also quantified sediment microalgal biomass in four habitats: the salt marsh surface, the unvegetated intertidal, SAV beds, and the unvegetated subtidal. Sediment chlorophyll *a* concentration ranged from 24.9 mg Chl *a* m^{-2} for the unvegetated subtidal to 85.3 mg Chl *a* m^{-2} for the vegetated subtidal (SAV) habitat in February. No statistical differences were found among the four habitats within each season. Primary production of sediment microalgae was estimated as 127.6 gC m^{-2} yr^{-1} on the salt marsh surface, 169.0 gC m^{-2} yr^{-1} in the unvegetated intertidal, 101.2 gC m^{-2} yr^{-1} in the SAV beds, and 127.6 gC m^{-2} yr^{-1} in the unvegetated subtidal.

Additional sampling areas

Two additional areas within the larger system were examined for comparison purposes (Figure 1). Area 2 (arrow 2 on Figure 1) is a small embayment that is just north of the primary research area (Area 1). This embayment is morphologically similar to the primary research area, except that the mean depth of the embayment is approximately 10 cm shallower than at the primary site. Area 2 is also more protected from wave energy than Area 1; several small islands and shallow sand bars lie between Area 2 and the open water of Chesapeake Bay. The other area (arrow 3 on Figure 1) is a high energy tidal cut between several small marsh islands at the north-east corner of the Goodwin Islands. The marsh edge at these three areas also differs. The edge at the primary site (arrow 1) is vegetated with a mix of tall and short form *S. alterniflora*. At the low energy site (arrow 2), the marsh edge is almost entirely vegetated with short form *Spartina alterniflora*. At the high-energy site (arrow 3) the edge vegetation consists almost entirely of tall form *S. alterniflora*, which is generally of a greater height than at the primary site. These comparison marshes are used to provide an assessment of the variability of marsh utilization by nekton between areas. No elevation or tidal data specific to either of these additional areas were taken.

SAMPLING METHODS

Selection of drop traps as sampling gear

Drop traps were chosen as the primary quantitative sampling device for this study. This gear can be similarly deployed both on the marsh surface and in subtidal habitats to minimize gear comparability artifacts (Rozas and Minello 1997). Drop traps have a high catch efficiency and are among the most quantitative sampling devices available. Drop traps are generally recommended for quantifications of small nekton in shallow water (Kushlan 1974, Adams 1976a, Rozas and Minello 1997). Zimmerman *et al.* (1984) compared estimates of gear effectiveness in quantifying brown shrimp, *Penaeus aztecus*. They found in unvegetated water that a 1 m beam trawl, a 5.5 m wide bag seine, and a 3.7 m wide otter trawl reported densities that were 82%, 33% and 17% of densities from drop sampling, respectively. Of this gear, only the beam trawl was operable in marsh surface *Spartina* habitats, where it reported densities that were 23% of those reported from drop sampling. Kushlan (1974) states that "The most precise data on shallow water fish communities are obtained by use of bottomless drop traps which are moved to new sites for each sample." Since precise quantification per square meter of habitat was a primary goal of this study, drop traps were selected as the primary sampling gear.

Adverse effects of drop trap gear on quality of collected data

Rountree and Able (1992) comment that drop traps are highly biased toward small epibenthic forms; it is my belief that this is in part due to an edge effect of the trap, and in part due to fleeing of the approaching trap by mobile forms. Both of these problems are exacerbated when smaller diameter (1 m) drop traps are used. Ruiz *et al.* (1993) found that an upper asymptote in density estimates of *Callinectes sapidus* and *Apeltes quadracus* (the two dominant species) was reached with a cylinder diameter of 1.51 m. Ruiz *et al.* (1993) found that rings with diameters of 0.92 m and 0.61 m underestimated density of these species with

reference to the 1.51 m diameter ring, but that increasing diameter to 2.43 m did not increase density estimates relative to the 1.51 m ring. Both *C. sapidus* and *A. quadracus* are epibenthic species; nonetheless this example serves to illustrate scaling effects of trap size. Based on Ruiz *et al.* and on construction limitations imposed by the availability of galvanized metal in 4 foot by 8 foot sheets, a ring size of 1.48 m diameter was used in my study. This size of drop trap serves to lessen bias in sampling, at least in comparison to data obtained by smaller traps.

Even at a diameter of 1.48 m or more, drop traps do not sample a very large area. They are only effective at estimating abundances of common species. Five drop samples were taken in this study as a standard replication per habitat per month (see below), and this sampled an area of 8.75 m^2. Fishes with densities of 0.1 inds/m^2 , for example, are clearly not well sampled by this procedure since total area sampled is less than the mean area occupied by one individual. Moreover, very little work has been done to quantitatively address the problems of larger mobile species avoiding approaching fishing gear or leaving an area altogether. This remains a concern for this study as well as for all studies employing any type of active fishing gear. The escape reaction of benthic species to a person walking through unvegetated habitat may be triggered at 0 - 1.5 m, and at 3.2 m for a larger adult goby species during calm sunny conditions with good water visibility and no wind (Pihl and Rosenberg 1982). Enclosure traps tend to underestimate densities of all fishes by a factor of 0.81 for a 1 m^2 drop trap, and in particular to underestimate densities of large fishes (Jacobsen and Kushlan 1987). These limitations of the sampling gear must be considered in evaluating reported fish densities.

Mitigating factors in the particular case of my dissertation are the generally turbid waters of Chesapeake Bay and the focus of this project on vegetated habitats. Both of these factors help to visually obscure the approaching gear; in addition, the vegetation may provide a perceived refuge for nekton and may decrease the inclination to flee. Samples taken from unvegetated habitats and, particularly, low tide (shallow) unvegetated habitats should be interpreted with these issues in mind. The water in the low tide unvegetated habitats was

shallow enough that turbidity in general did not obscure view of the gear by nekton; this will be discussed in more detail below.

In spite of the above mentioned concerns with drop trap gear, it is difficult to envision an easily employed method that would avoid these problems and provide as much sampling precision over the marsh, unvegetated, and SAV habitats investigated in this project. All existing sampling gears are subject to some form of bias (Rozas and Minello 1997). Drop traps are no exception, but at this point in the science no better options may exist for shallow water fish capture and quantification in different habitats. In fact, drop samplers are the only gear type recommended highly for all shallow water habitats I sampled (Rozas and Minello 1997).

Deployment of drop trap and throw trap gear

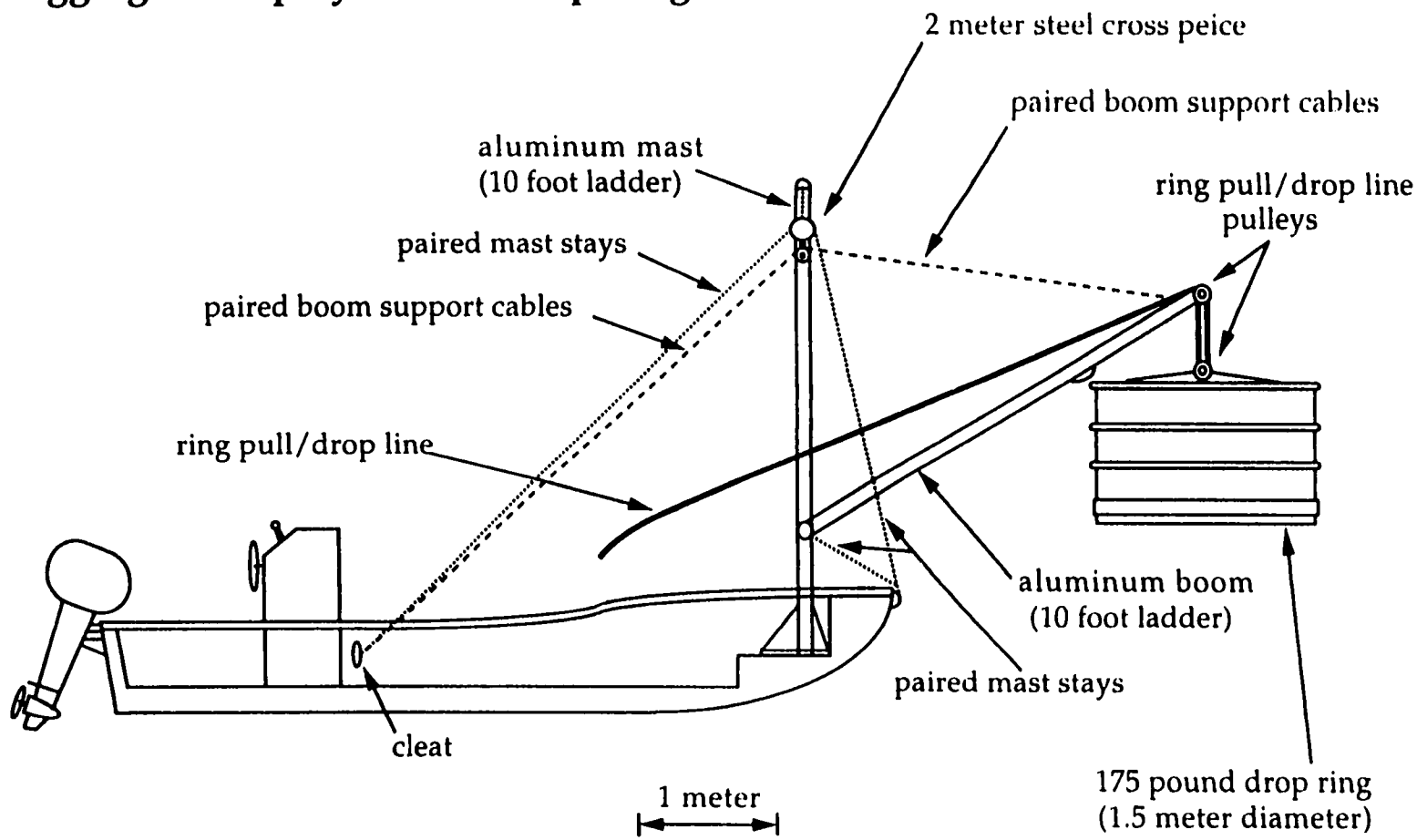
A 1.48 m diameter circular galvanized sheet metal drop trap was deployed from 3 m boom mounted on a small boat (Figure 3). The trap was sufficiently heavy (80 kg or 175 pounds) to cut through thick marsh vegetation and form an effective seal with the sediment. A lighter (24 kg or 52 pounds) shallow-water model of this was used as a throw trap where water depths precluded sampling from a boat; it also had a diameter of 1.48 m but was effective only in short form *Spartina alterniflora*, in SAV beds, and in unvegetated habitats because it lacked the weight to cut through the heavy vegetation of tall form *S. alterniflora*. These cylinders were pounded into the sediment as necessary by jumping on a plank laid across the top of the ring to ensure an effective lower seal. The ring was dropped or thrown in a different location each time. A random numbers table was used to select a 5 m x 5 m area for sampling; the exact placement of the ring within this area was then haphazard. The order in which habitats were sampled was selected with a random numbers table.

Wind force on the drop cylinder frequently caused steering problems in field use with a vessel. This was due to the large lever arm created by the extending boom. One person poling the boat or pushing from the stern (as in Minello *et al.* 1994) was unable to control the boat at 15 or more knots of wind. Rather than adopt two procedures for differing wind speeds, a single

Figure 3. Rigging for Deployment of Drop Ring

This figure shows the aluminum ladders, supports, cables, and lines used to rig a 5.5 m Privateer boat for deployment of drop rings. The drawing is close to scale.

Rigging for Deployment of Drop Ring



procedure was developed to allow consistent deployments by two people at all wind speeds between 0 and 20 knots. The boat was rigged with mast and boom several hundred meters from the deployment area and the motor was never intentionally raised above idle speed (900 rpm) once in the sampling area. The boat was powered by a up-tilted outboard motor at idling speed to typically within 10 - 30 meters (depending on wind strength) of the randomly selected site. At this point the motor was shut off and the boat allowed to glide the remaining distance to the site. Once the drop ring was over the proper habitat stratum (see below) the ring was allowed to free fall. The 2.5 cm diameter pull line moved over large polyurethane rollers on greased stainless steel shafts so that silence was maintained until the device struck the water. Silence was maintained in the boat as much as possible during the entire period of sampling, and especially in the moments approaching a sampling site. Nonetheless, the dropping of the ring itself and the procedure of removing organisms from the ring did constitute a disturbance of the sampling area, and potentially affected subsequent samples. The interval between samples was always greater than 20 minutes, and no samples were taken closer than 50 meters from the previous sample. Avoidance is of particular concern in the sampling of large transient predators such as seatrout (*Cynoscion nebulosus*), striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) that have the mobility to leave a sampling area entirely.

A somewhat different procedure was developed for deployment of throw rings. The ring used for this procedure was supported by an internal crosspiece made of wood, aluminum, stainless steel, and epoxy. The crosspiece supported one handle for managing the ring and was connected to the ring at five points with removable fasteners. Another handle was affixed to the outside of the ring itself. For sampling on the marsh surface, the ring and the plank used for jumping on the ring were carried to within 10 meters of where the operator would stand to throw the ring. The operator would then wait for several minutes to allow any fish disturbed by the approach to return to the area, then walk the ring at a predesignated time to the predesignated spot and throw. The throw was initiated with the ring in a vertical position, facing the site to be sampled. A good throw would place the ring almost 3 meters above the

water surface at the apex and at least 4 meters from the operator upon landing, measured from the center of the ring.

In order to seal properly, the ring must fall straight down at the end of its trajectory and land horizontally so that the cutting edge of the ring strikes the sediment at the same instant around the entire circumference. In throwing, it was necessary to attain as much altitude with the ring as possible to allow sufficient hang time that forward motion of the ring was nearly arrested by air resistance by the time the ring landed. This produced the necessary straight vertical fall. The flat horizontal landing of the ring was achieved by placing a very slight forward spin on the ring from the initial vertical position so that the ring had rotated exactly 90 degrees at the instant of landing. Given that the ring weighed 24 kg (over fifty pounds) and was awkward to handle, this procedure required a fair amount of practice.

After throwing, the operator would run the plank to the ring, place the plank on top of the ring, and jump up and down to create a good seal with the substrate. In practice, the ring typically sealed around 90 - 95% of the circumference upon initially landing, and the jumping procedure was used to seal any remaining gaps caused by irregular topography of the marsh surface. Even after much practice with the ring, it was still necessary to redo many samples because of inadequate sealing to the marsh surface caused by pits in the marsh, shell clumps of *Geukensia demissa* under the edge of the ring, or poor throwing procedure.

The decision to redo a sample was always made before emptying the ring so as to avoid scientist bias. The ring was always checked completely for a satisfactorily seal prior to emptying; if the ring was emptied, then the collected sample was retained for analysis. In unvegetated and SAV habitats it was never necessary to jump on the ring with a plank; the ring typically sealed completely if thrown properly. Both the drop ring and the throw ring were emptied in the same manner using the device described below.

Removal of organisms from drop traps

To empty these traps, a hinged rotating clearing device (Figure 4) was folded up on itself and inserted into the drop ring after the internal support/crosspiece of the drop or throw ring was removed. This clearing device consisted of two halves connected at a vertical hinge. Each half had a width equal to the radius of the drop ring. One half acted as a stationary bag-like cod end (2 mm mesh) that sealed to both the drop ring and the substrate, and provided a perceived refuge for nekton to enter. A large rubber flap was used to seal the side of the stationary half against the drop ring, and an attached stainless steel blade was pounded down into the sediment to seal against the substrate. The other half of the clearing device rotated on the vertical hinge in the center of the drop ring, traveling around the entire inner sidewall of the ring. This rotating section pressed a rubber seal against the inside of the drop ring, and scraped the substrate with rake teeth spaced 8 mm apart. The rotating section raked the entire area of the drop ring, scraping mobile creatures into the stationary bag-like cod end until the movable half was pressed tightly against the stationary half, trapping all creatures in the mesh bag. The entire clearing device was then lifted from the drop ring in this closed position, and all organisms were removed from the mesh cod end. The device was swept around the ring only once. In use on the marsh surface, it was necessary to apply considerable force to the rotating rake section in order to force it through the *Spartina*, and to force the rake teeth down into the sediment so as to compensate for irregularities of the marsh surface. The sampled marsh featured a generally flat surface, which was very helpful. Considerably less exertion was required to work this gear in SAV and unvegetated habitats.

Gear removal efficiency

This ring clearing device performed well in both unvegetated and vegetated habitats, removed samples rapidly, collected clean samples without excessive amounts of detritus, and could be worked through all the types of vegetation encountered at these sites. Removal efficiency gear testing (Table 1) showed a catch efficiency of 84 - 99% for *Fundulus*

Figure 4. Device for Clearing Drop Ring

The device used to extract nekton from drop rings is shown. This device is folded up like a closed book, inserted into the deployed drop ring, and the stationary half is pounded into the substrate. A stainless steel blade prevents escape by digging. The blade seal at the sediment, and the rubber seal of the stationary side against the drop ring side wall are examined for proper closure. To work the gear, one person holds the stationary side. A second person forces the rotating side in a complete circle around the drop ring, raking through vegetation at the top of the root mass. The mesh bag cod end is supported by a rigid hinged frame, and folds down to provide a perceived refuge for nekton. Nekton are raked, scraped, and scared into the cod end. In soft unvegetated habitats, the raking teeth are below the sediment surface and the top layer of mud is also scraped into the cod end. The rotating side is pressed into the cod end to seal nekton into the mesh bag, and the entire device is lifted out of the drop ring. The device is laid down horizontally, opened, and nekton are removed from the cod end. If necessary, excess sediment is sieved through the 2 mm mesh of the cod end in open water before nekton are removed.

Device for Clearing Drop Ring

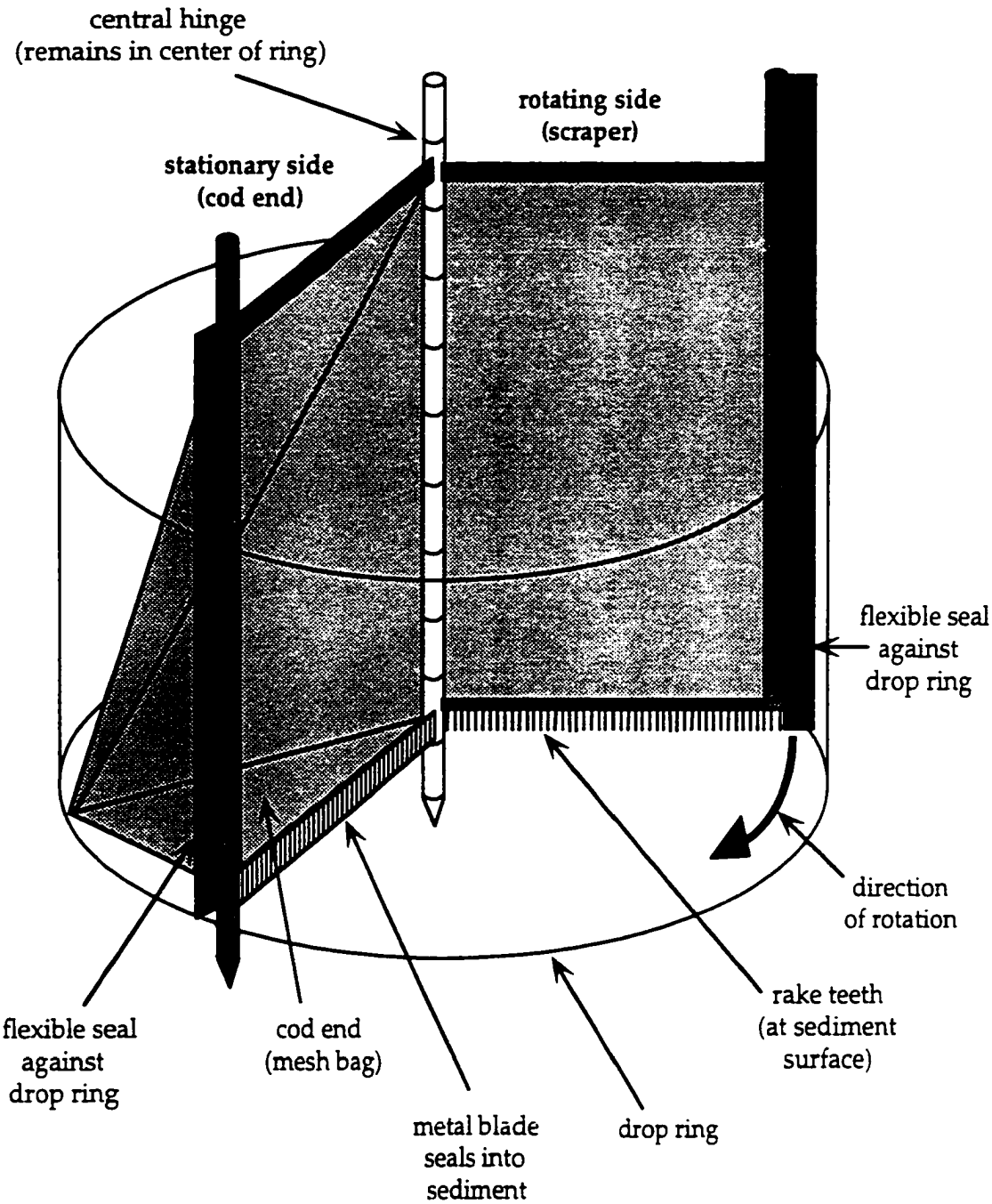


Table 1. Clearing Device Recovery Efficiencies

Recovery efficiencies (Rozas and Minello 1997) were estimated for the clearing device shown in Figure 4. This was done using mark-recapture techniques for fishes and crabs. Fishes used in the tests were *Fundulus heteroclitus, Cyprinodon variegatus,* and *Fundulus majalis.* Removal efficiencies for palaemonids were estimated using a serial recapture technique: at least 100 palaemonids were added to the ring, which was cleared three times. The Moran-Zippin method to determine closed populations in repeated sampling without replacement (Youngs and Robson 1987) was used to estimate the total number of shrimp in the drop ring. The number of shrimp removed in each clearing event was compared to the number estimated to have been in the ring at that time to calculate removal efficiency. This statistical method assumes that recovery efficiency does not change between sequential trials; the data suggested that this assumption was met. *Palaemonetes* spp used in this test were not identified to species.

Clearing Device Recovery Efficiencies

Group	Size	Habitat	Trials	Inds	Estimate	95% C.I.	Method
fundulids and cyprinodontids	28 - 102 mm TL	*S. alterniflora*	8	106	84%	72 - 97%	mark-recapture
fundulids and cyprinodontids	28 - 102 mm TL	SAV	5	80	93%	83 - 100%	mark-recapture
fundulids and cyprinodontids	28 - 102 mm TL	unvegetated	4	80	99%	95 - 100%	mark-recapture
Callinectes sapidus	50-100 mm CW	*S. alterniflora*	7	9	86%	63 - 100%	mark-recapture
Callinectes sapidus	3 - 30 mm CW	*S. alterniflora*	6	52	16%	4 - 29%	mark-recapture
Callinectes sapidus	3 - 30 mm CW	SAV	4	31	39%	24 - 54%	mark-recapture
palaemonids	15 - 45 mm TL	*S. alterniflora*	3 x 3	2703	78%	63 - 93%	Moran-Zippin*
palaemonids	15 - 45 mm TL	unvegetated	3 x 3	428	72%	53 - 92%	Moran-Zippin*

* The Moran-Zippin method for estimating closed populations in repeated sampling without replacement was used, as described in Youngs and Robson 1987.

heteroclitus, *F. majalis*, and *Cyprinodon variegatus* > 20 mm total length and for blue crabs (*Callinectes sapidus*) > 50 mm carapace width in the habitats of concern. Removal efficiencies for small blue crabs from 5 to 30 mm carapace width were much lower, between 16% and 39%. Low removal efficiency for small crabs was expected; this gear is less effective in capturing small less-mobile nekton that hide in the substrate. Removal efficiencies for palaemonid shrimp was 72 - 78%. The gear has worked well for the purposes of this study in all sampled habitats in the study area.

This clearing device required at least 5 cm of water depth in marsh surface habitats in order to function properly. The unsampled very shallow vegetated habitat may be extensively used by larval and early juvenile marsh resident fishes (Kneib 1997b). Few larval and early juvenile fishes (< 15 - 20 mm TL) were captured in my study on the marsh surface in 1995 using this gear. This may well have been caused by the elimination of very shallow marsh surface habitats. If these larval fishes selected water 5 cm deep or less on the marsh surface, they would be unavailable to the sampling gear. The raking device was effective at capturing larval fishes in deeper water, evidenced by high catches of larval *Menidia menidia* in the spring of 1996 (G. Cicchetti, unpublished data). The raking device also is effective at sampling soft-bottomed unvegetated habitats in water as shallow as 1 cm, because the rake is used to shovel the entire top layer (3 - 5 cm) of sediment into the cod end. The mud is then sieved through the cod end for processing. It remains true, however, that this study cannot provide good information on larval and early juvenile fish use of the marsh surface. Since the habitats which were sampled may not have been prime microhabitat for these very small fishes, the study concentrates on use by fishes and crustaceans greater than 15 - 20 mm TL.

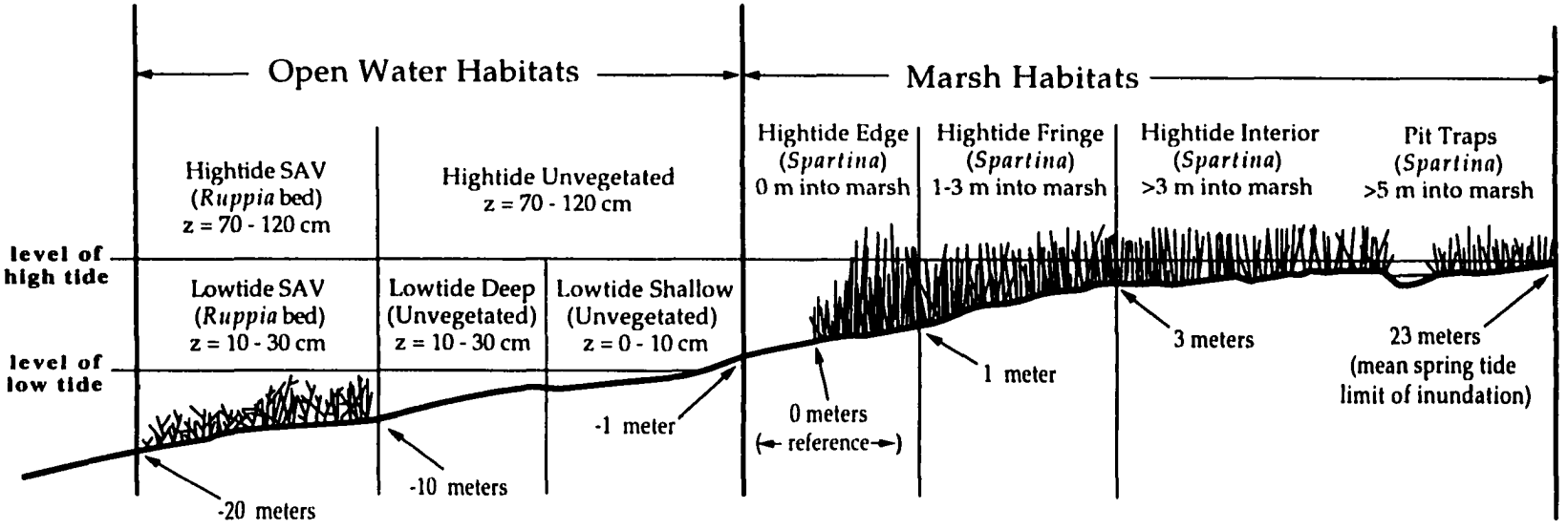
Sampling design for the primary habitat/trophic study

Sampling for the main part of this project was carried out from June through October 1995 using the devices described above (Figure 5). Those habitats sampled at high tide included the marsh interior (3 - 20 m from the marsh edge), the band of marsh from 1 m to 3 m

Figure 5. Sampled Habitats

The eight habitats sampled in the primary study are shown. Five habitats were sampled at high tide, three at low tide. Distances are indicated as meters from the marsh/unvegetated edge. The figure is not drawn to scale, but the horizontal distance numbers are accurate.

Sampled Habitats



(Figure not drawn to any vertical or horizontal scale)

from the edge (henceforth referred to as the "Marsh Fringe" habitat), the depositional marsh edge itself (with the drop ring half on the marsh and half in the unvegetated area), the unvegetated sand/mud area within 10 m of the marsh, and the shallow *Ruppia maritima* habitat within approximately 20 meters of the marsh. Sampling took place within 1 to 2 hours of slack high tide based on the finding of Kneib and Wagner (1994) that nekton abundance and species richness was greatest on the marsh surface at slack high tide. Low tide habitats included the 0 to 10 cm deep unvegetated shallows within 3 meters of the water's edge, the slightly deeper (10 to 30 cm of water) unvegetated shallows within 10 m of the water's edge, and the shallow *Ruppia maritima* habitat within 20 meters of the marsh.

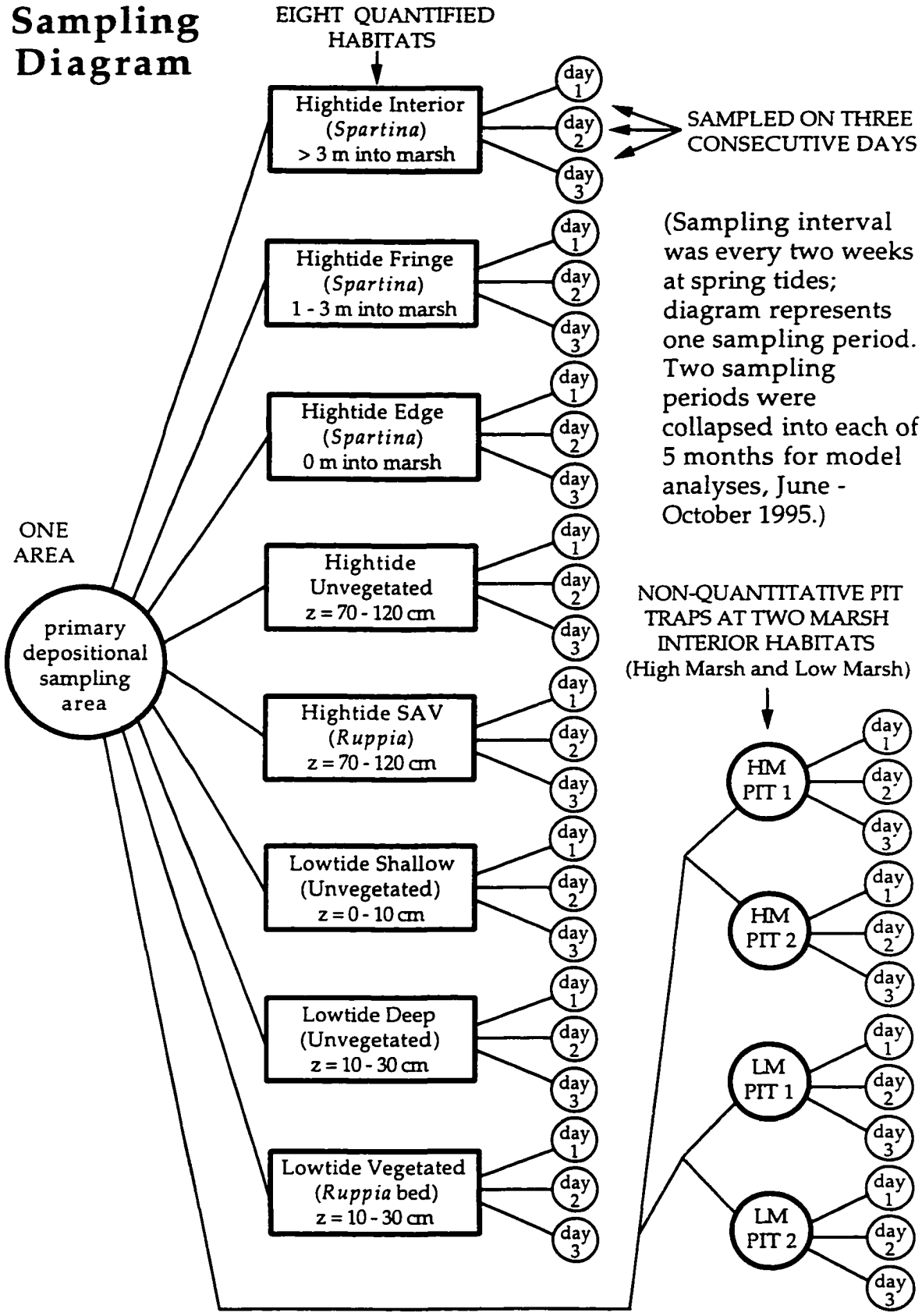
The statistical design of drop sampling for the habitat use and trophic linkage projects considered one depositional marsh as a sampling area and eight habitats. A stratified random sampling design was applied with habitats as strata (Figure 6). The sampling design was randomized spatially within each marsh habitat as much as possible using a random numbers table and the constraint of not sampling adjacent areas consecutively. The order in which habitats were sampled within each tide was also determined using a random numbers table. Replication was carried out on 3 separate days, with each of the 8 habitats (5 at high tide and 3 at low tide) sampled each day. Sampling on consecutive days is recommended by Varnell *et al.* (1995) as a means to account for day-to-day variability and to increase accuracy. Pertinent information was recorded on a data sheet with each drop sample: time, tide, habitat, location of drop, water depth, description of vegetation in ring, presence of structure in ring, etc. Sampling took place during daylight, and was repeated every two weeks at spring tides. The Marsh Fringe and Lowtide SAV habitats were not sampled in the month of June, and Hightide SAV habitat was not sampled in the months of June or July.

Four pit traps of the type described in Yozzo *et al.* (1994a) were installed on the marsh surface in September 1995. The traps were plastic bins measuring 23 cm x 33 cm, with a depth of 18 cm. A 1 mm mesh liner was used to facilitate removal of organisms, as suggested in Yozzo *et al.* (1994a). Two of these traps were located in the infrequently flooded high marsh and

Figure 6. Sampling Diagram

This figure shows a diagram of the sampling design for the primary habitat study. Habitats are as depicted in Figure 5. Samples were collected on three separate (usually consecutive) days biweekly at every spring tide. The two biweekly collection periods were collapsed into monthly estimates of populations from June through October, 1995. Five replicates in each habitat were used to characterize nekton populations each month. Replication for some habitat/month combinations is less than five; this is indicated in Figure 3, Chapter 2. The SAV and Hightide Fringe habitats were not sampled in June, and in addition the Hightide SAV habitat was not sampled in July. Pit traps were not installed on the marsh until September, and pit trap data was collected from September through November, 1995.

Sampling Diagram



(Sampling interval was every two weeks at spring tides; diagram represents one sampling period. Two sampling periods were collapsed into each of 5 months for model analyses, June - October 1995.)

very rarely caught nekton. The other two traps were located within the regularly flooded marsh. Nekton were collected from each trap at low tide on the 12 sampling dates between September and November 1995.

All biweekly data collected were collapsed so that data are reported by month. Each month is ideally represented by a total of five drop samples per habitat, taken from both of the biweekly sampling periods of that month. Due to bad weather and other adverse factors, five replicates were not taken in every habitat of every month (see Figure 3 in Chapter 2).

The results from the primary sampling project described above were applied to the habitat study (Chapter 2), the production study (Chapter 3), and the trophic study (Chapter 4). Other investigations included a marsh area comparison, a year-to-year variability study, and a day-night comparison; sampling details for these studies will be discussed in Chapter 2.

Treatment of captured organisms

Captured fishes and crustaceans were immediately preserved in the field using liquid nitrogen. On shore, they were transferred to an ultracold freezer for storage. In the lab, all collected nekton were identified, enumerated, and measured. Lengths were recorded for all captured macrofaunal organisms. Weights for *Palaemonetes* shrimp and blue crabs ≤ 30 mm were estimated with length-weight regressions (Chapter 2, Table 2); all other captured individuals were weighed directly as wet weight, which was converted mathematically to dry weight using information from Cummins and Wuycheck (1971) and other sources. Gut contents were examined quantitatively for all captured fishes > 20 mm and for all blue crabs > 30 mm. Gut studies were done on subsamples of collected *Palaemonetes* shrimp, for subsamples of collected fishes ≤ 20 mm, and for subsamples of collected blue crabs ≤ 30 mm. Percent composition by volume of dietary items in the guts was estimated indirectly (Hyslop 1980) using a grid on the stage of a dissecting microscope (Odum 1970). Percent volumes were converted directly into estimates of percent composition by weight using the assumption that

volumes of items in the gut are directly proportional to weights (Swedberg and Walburg 1970). The gut content study is described in further detail in Chapter 4.

Determination of marsh elevation and tidal heights.

A survey of the marsh surface was conducted to determined elevation in July 1996 at 133 sites (total) on 11 transects at the sampling area. This was done with a hydraulic level, hand bearing compass, marking stakes, the use of a vertically marked piling and the embayment water as an initial referenced horizontal surface, and other primitive surveying equipment. Despite the relatively crude approach, tests of precision (repeatability) showed 95 to 98% similarity for each measurement when the procedure was repeated (blind) on different days.

Tidal heights were recorded on each sampling day between June and October 1995 on a fixed marked piling at the sampling area. NOAA tide gauge data collected at Gloucester Point, VA (10 km distant) was then correlated to the tidal heights recorded at the sampling area, and the correlated values were used to describe the tidal signal at the sampled marsh. The regression line calculated for the correlation had an r-squared value of 0.95, n = 58. The results of this correlation agreed well with tidal information reported in Buzzelli (1996) for the Goodwin Islands. This correlated tidal signal was also referenced to the marsh elevation survey and was used to generate mean inundation times for the sampled habitats. These patterns of inundation are described in Chapter 4.

SUMMARY

This project was designed to quantitatively evaluate 8 different habitats, with the goals of examining habitat use by nekton and estimating trophic connections between habitats. The choice of drop rings and throw rings as sampling gear was based in large part on the requirement of sampling comparably in different habitats. The basic methodology for sampling, described in this chapter, applies to the following three chapters, and it is in these next chapters that results of the study are presented and discussed.

CHAPTER II. SPATIAL AND TEMPORAL PATTERNS OF NEKTON USE OF SHALLOW WATER HABITATS

ABSTRACT

Shallow water communities of nekton were quantitatively sampled from June through October, 1995, in a contiguous marsh-unvegetated-SAV system at the Goodwin Islands National Estuarine Research Reserve, York River, Virginia. Drop traps (1.75 m^2) were used to sample five habitat strata at high tide and three at low tide for a total of eight habitats. Species abundance and diversity was high in these habitats; 32 species were captured and the overall mean abundance was 28.6 inds m^{-2} with a mean biomass of 3.8 gdw m^{-2}. *Callinectes sapidus* was the biomass dominant and *Palaemonetes* shrimp were the numeric dominants. Fishes made up 75% of the number of species captured. *Fundulus heteroclitus* was the most abundant fish in marsh habitats; *Gobiosoma bosc* was the most abundant in SAV habitats.

Species that migrated on and off the marsh with each tide were *Fundulus heteroclitus, Lucania parva, F. majalis, Callinectes sapidus,* and *Palaemonetes pugio.* In contrast, *Gobiosoma bosc, P. vulgaris,* and *P. intermedius* remained in SAV habitats at all tides. For many of these species, habitat use differed from reports for other marsh areas. This suggests behavioral flexibility between regions. Recruitment to the marsh edge by juvenile *C. sapidus* was documented, and this habitat is hypothesized to be an important blue crab nursery. Significant year-to-year variation was found in crab recruitment between 1995 and 1996, however. Transient marsh fish species were most abundant at the marsh edge in August and September (mean 1.3 inds m^{-2}) but were less common in other months and in other marsh habitats. *Menidia menidia* was significantly more abundant on the marsh surface during night high tides than during day high tides. Interesting examples of spatial partitioning were seen between palaemonid shrimp. *P. vulgaris* and *P. intermedius* appeared to be sympatric inhabitants of SAV habitat, whereas *P. pugio* was found in marsh habitats as well as SAV habitats. Nekton use of intertidal habitats was found to be very complex.

Communities of nekton in marsh habitats differed between the marsh edge and the marsh interior, with edge habitats containing more species, higher biomass, and greater numbers of many species, though these trends were not always statistically significant. Marsh interior habitats contained greater numbers of *Fundulus heteroclitus* and *F. majalis.* In general, SAV habitats were characterized by greater numbers and by more species than were marsh habitats, but biomass of nekton was statistically similar between SAV and marsh edge habitats. At high tide, SAV and marsh habitats were used significantly more by most species and groups than were unvegetated habitats. At low tide the unvegetated - - and in particular the shallow (0 - 10 cm) unvegetated - - saw extensive use by marsh residents as a refuge. Animal-habitat relationships were complex, and significant exchanges between marsh, SAV, and unvegetated habitats took place. Most individuals (65%) and biomass (86%) of nekton were of species found in all three habitat types at different tidal stages, and were regularly redistributed between habitats with the twice-daily tides of Chesapeake Bay.

INTRODUCTION

Nekton use of the salt marsh surface and of adjacent habitats can be analyzed in several ways along different spatial and temporal scales. This chapter explains variability in patterns of nekton use along gradients of scale. Understanding these causes of variability is vital to evaluating the results of a marsh study. Spatial processes that affect nekton use of salt marshes and adjacent habitats are discussed from larger spatial scales to smaller scales. Temporal processes are described on a continuum ranging from variability between years to variability within a tidal cycle.

SPATIAL PATTERNS OF NEKTON USE

Spatial patterns between marshes: differences due to geographic location

Differences in geographic location play a major role in use of the marsh surface by nekton. Rozas (1993), in a review of published quantitative studies, concluded that densities of nekton using Atlantic coast marshes were at least an order of magnitude lower than those reported from Gulf coast marshes. Ayvazian *et al.* (1992) found that values of summer biomass in unvegetated areas adjacent to marshes in southern Maine (the Acadian zoogeographic province) were an order of magnitude lower than were values for similar habitat in southern Massachusetts (the Virginian zoogeographic province). It is difficult to draw general latitudinal conclusions based on this information despite the fact that, in each of these comparisons, abundance of nekton is higher in the south. The higher abundances of Gulf coast vs. Atlantic coast marshes may be due more to hydrologic and geomorphologic factors than directly to latitude (Thomas *et al.* 1990, Zimmerman *et al.* 1991, Rozas 1993). Most of the Atlantic marshes used by Rozas (1993) in his comparison were in the Carolinian province, and I could find no direct comparison studies between marsh nekton from the Virginian and Carolinian provinces. West coast marshes of the United States also exhibit their own unique

set of geographic patterns. This discussion, however, will concentrate on marshes located on the east and Gulf coasts of the United States, in part because of the much greater body of literature available for these areas (Kneib 1997a).

One major aspect of geographic location that plays a central role in nekton use of marshes is the difference in flooding regimes found in each area. Odum (1980) discusses the hypothesis of tidal subsidy, wherein (within limits) increased tidal range leads to increased primary production on the marsh surface. Zimmerman *et al.* (1991) suggest that the trend towards greater secondary production of Gulf coast marshes relative to Atlantic coast marshes may be due to differences in tidal regimes, inundation patterns, and marsh morphology between the two coasts. Submergence marshes in the central and western Gulf of Mexico are characterized by longer inundation times and greater amounts of productive marsh edge habitat (Zimmerman *et al.* 1991). The southern Atlantic coast marshes in Georgia have a high tidal amplitude, which can result in the formation of raised levees at the marsh edge (Wiegert and Freeman 1990). This also affects nekton use of marshes (Peterson and Turner 1994). Deegan and Garritt (1997) also suggest that the connection between marshes and aquatic estuarine food webs is dependent on tidal range, and on the extent that the marsh floods at high tide. Tides are a central force in the dynamics of marshes (Teal 1962, Kneib 1997a), and any comparison between nekton use of different marshes must account for the tidal signal.

Temperature is also an important factor dividing biogeographical provinces. Temperature may drive latitudinal patterns of species composition, but secondary production is also linked to temperature. Secondary production is generally thought to increase with higher temperatures for invertebrates (Diaz and Schaffner 1990, Edgar 1990, Tumbiolo and Downing 1994) and for fishes (Edgar *et al.* 1995a), at least up to a certain point. Tumbiolo and Downing (1994) suggest that this might be due to Q_{10} effects of increased physiological rates at warmer temperatures. A longer growing season is coupled with higher temperatures in southern latitudes. This may in part explain a general trend of increasing nekton biomass in the southern direction, if a trend in fact exists.

Many of the factors potentially driving differences in marsh use between zoogeographic provinces are linked, and are difficult to separate. Whatever the reasons for geographic trends in marsh use by nekton, the end result is that marshes, and the communities of nekton that inhabit them, differ significantly with geographic location. This result should be considered in any comparison between marshes from different geographic locations.

Spatial patterns between marshes: differences within one estuary

Within one estuary, the difference in salinity along the estuarine gradient is clearly a very important factor in structuring nekton use of salt marshes. Rakocinski *et al.* (1992) found that salinity was the major determinant of community structure for marsh-edge fish species. Weinstein (1979) found that higher salinity (polyhaline) marshes were characterized by a lower standing crop but greater species richness than were lower salinity marshes. Sheridan (1983) found similar trends in a study of the Galveston Bay system that did not directly consider marshes. In his study, numbers of fishes were higher in the upper part of the estuary while diversity was greatest at the mouth of the Bay. Weinstein *et al.* (1980) comments that many marine stenohaline fishes are restricted to salinities greater than 16 parts per thousand; the absence of these fishes in areas of lower salinity tends to decrease species diversity. Deegan and Garritt (1997) used isotopic analyses to show that utilized sources of primary production varied along an estuarine gradient from oligohaline areas to the lower estuary, and that consumers used organic matter produced in the location they inhabited. Salinity has been shown to have important structuring effects on communities of estuarine nekton, including marsh nekton.

Stream order within marshes (the ranking of aquatic pathways on a scale from small tidal creeks to large bodies of water, Odum 1984) also plays an important role in determining marsh use. Rozas and Odum (1987) showed that total numbers of fishes in tidal freshwater marshes (salinity 0 - 1.8 parts per thousand) was greater at headwater (Order 2) and main creek (Order 3) stations than at river (order 4+) stations, though they suggested that this

result may in part have been due to the presence of SAV in lower order streams. Ayers (1995) conducted a flume weir comparison of a bay-exposed fringing marsh (high stream order) and a sheltered creek channel marsh (low stream order) at the Goodwin Islands, York River, Virginia. Though salinities were similar at her two sites, the creek marsh was characterized by considerably higher fish densities and biomass, mostly of marsh residents. Species composition in the exposed marsh was less dominated by marsh residents, and was more variable over the sampling season than it was in the protected marsh. Hettler (1989a) used block nets to compare nekton use of channel marshes (Stream Order 3) to rivulet (Stream Order 1) marshes near Beaufort, North Carolina. Both sites experienced similar salinities, but in addition to stream order differences, channel marshes differed from rivulet marshes in having a steep bank, higher energy, and in the proximity of deeper water. Hettler found that rivulet marshes contained fewer species, but higher numbers and biomass than channel marshes (except during winter). Channel marshes contained more blue crabs and greater numbers and biomass of all fishes except killifishes, white mullet, and spotfin mojarra. The general trend in these studies is towards higher abundances (especially of marsh residents) at low stream order areas and towards higher diversity at high stream order areas. This trend parallels the salinity-driven patterns seen in the larger estuary (see previous section).

Sediment type also may play an important role in determining nekton use of shallow water habitat, though sediment type is generally associated with stream order as well. Weinstein *et al.* (1980) found that distribution patterns for several species of nekton were significantly correlated with sediment type. Diaz and Schaffner, in a 1990 review of estuarine benthos, concluded that mixed sediments supported higher secondary production of invertebrates, though their study did not directly evaluate secondary production specific to marshes.

Many of the factors which structure living communities along an estuarine gradient do not exist in isolation. High-energy, high stream order marshes tend to abut deeper waters, have coarser substrates and tend to provide more erosional edge due to the higher energy

regimes involved. Low stream order marshes in general may be shallower, muddier and may feature more depositional edges. Low stream order marshes can experience generally lower salinities as well, if located further from open estuarine areas more influenced by oceanic waters. In many cases it is difficult to analyze one factor in isolation without considering other inextricably linked factors that determine nekton use of an area. Indeed, many of the studies cited above, which primarily compare one aspect of marshes, are actually comparing several aspects. This is often noted by the authors of those studies. It is perhaps more accurate to consider stream order, sediment type, salinity, edge type, water depth, energy regime, and proximity to deeper water as linked factors that affect nekton distributions.

Spatial patterns within marshes: differences between edge and interior

Marsh edge habitats often support higher densities of estuarine nekton than do marsh interior habitat (Minello and Zimmerman 1992, Baltz *et al.* 1993, Minello *et al.* 1994, Peterson and Turner 1994). This may have implications for the use of marsh systems by nekton; within an area of marsh, the edge in plan view can be reticulated with small islands, channels, and marsh creeks, or it may be straight and relatively featureless. Reticulated marshes with extensive edge may support higher numbers and biomass of nekton per hectare than do featureless marshes. In fact, it is recommended that mitigation marshes be constructed to maximize available edge for this purpose (Minello and Zimmerman 1992, Peterson and Turner 1994, but see Fonseca *et al.* 1994). Rozas (1993) concluded in a review paper that estuarine transient species selected for marsh edge over interior areas. The extent of marsh edge relative to interior area may be an important factor in determining abundance and composition of the nekton community frequenting a marsh system.

Spatial patterns within marshes: differences between types of edge

Marsh edge can vary considerably in profile. In high energy areas, erosional processes can remove peat so as to leave a sheer overhang (Figure 1, erosional edge). Where water

velocities slow down in low energy areas, sediments may fall out of suspended load and accrete to form a gradually inclined surface leading to marsh vegetation (Figure 1, depositional edge). High energy areas with erosional edges in marsh systems typically include open bay sites exposed to wave energy, and the outsides of bends in tidal creeks where greater current velocities occur. Low energy areas with depositional edges include marsh sites that are protected from wave energy by land formations or by extensive shoal areas, and the insides of bends in tidal creeks where currents may slow down.

Erosional and depositional marsh edges are used differently by nekton. McIvor and Odum (1988) used flume nets to show that, in tidal freshwater creeks, depositional marsh edges were characterized by higher abundances of small fishes than were erosional marsh edges. While SAV may also have played a role in these processes, experimentation showed greater infaunal food availability at depositional sites and higher levels of piscivorous predation at erosional sites. Hettler (1989a) used flume nets in a polyhaline creek system and found similar results, though the focus of this work was primarily a stream order comparison (see discussion of stream order above). Gradually sloping depositional rivulet marshes offer a shallow water refuge from predation for small fishes (Hettler 1989a). Furthermore, greater numbers and biomass of most transient marine species and piscivores occurred in deeper channel marshes that were adjacent to a steep bank (Hettler 1989a). Hettler (1989a) suggested that piscivores forage more effectively in these deeper areas. Both of these studies indicate different patterns of fish use between erosional and depositional edges in marsh creeks, linked also to stream order in Hettler's study. Note, however, that Rozas (1992) found no significant differences in predation on tethered *Fundulus grandis* along different types of edge in Louisiana salt marsh channels. Rozas suggested that the difference in edge profile between sites might not have been sufficient (due to subsequent edge slumping) to cause significant differences in predation. In general, nekton use of marsh edge habitat is linked to edge type.

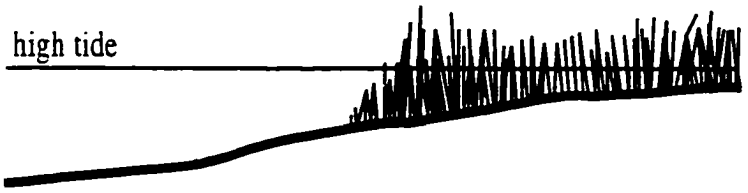
Even along a depositional edge marsh area, nekton do not use the entire edge uniformly to access the marsh surface. Rivulets are lower-elevation sites along a depositional creekbank

Figure 1. Depositional vs. Erosional Marsh Edge

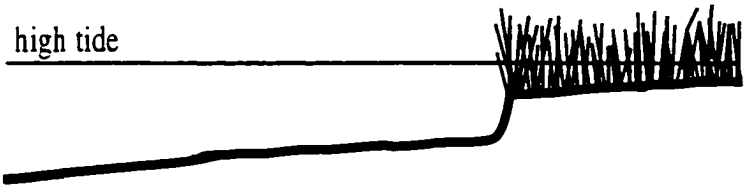
Depositional and erosional marsh edge profiles are shown. The figures are not drawn to scale.

Depositional vs. Erosional Marsh Edge

Depositional Marsh Edge



Erosional Marsh Edge



that act as channels for water movement during flooding and ebbing tides. Rozas *et al.* (1988) found significantly greater abundances of nekton accessing the marsh surface at creekbank rivulets compared to at the surrounding depositional creekbanks. Rozas concluded, however, that more fishes accessed the marsh surface along depositional creekbanks due to the very small relative area of rivulets. The extent of available edge influences use of a marsh by nekton, but the type of edge (erosional or depositional or rivulet) does as well. Marshes contain large amounts of distinct edge that natant macrofauna cross each tidal cycle; this physical structure is an important aspect in the dynamics of marsh nekton.

Spatial patterns within marshes: nekton use of tidal creeks

Although tidal creeks are not investigated in this project, they are very important in the function of marshes that feature them, and serve as major conduits of organisms into marsh habitats (Kneib 1997a). In addition, these creeks are probably the best-studied marsh environment with regard to non-resident nekton. In fact, many of the studies referenced above were conducted in tidal creeks or in marshes adjacent to creeks (Weinstein 1979, Weinstein *et al.* 1980, Rozas and Odum 1987, McIvor and Odum 1988, Rozas *et al.* 1988, Hettler 1989a, Rountree and Able 1992a). Creeks also provide a great deal of marsh edge habitat and often include both erosional and depositional areas. Several studies have documented considerable use of tidal creeks by commercially valuable fishes and crabs (Shenker and Dean 1979, Weinstein 1979, Weinstein *et al.* 1984, Rulifson 1991, Rountree and Able 1992). Creeks are important pathways for commercially and ecologically valuable fishes and crustaceans; this is generally recognized by marsh ecologists and is incorporated into hydrogeomorphic models of marsh function. Use of marsh edge that faces open water and is not adjacent to a creek is relatively unstudied, however; this provides impetus for my study.

Spatial patterns within marshes: differences across the marsh surface

Spatial differences in marsh surface use are primarily driven by tidal regimes and by marsh elevation in an area (Zimmerman and Minello 1984, Yozzo *et al.* 1994b). This is because nekton use of the marsh surface depends ultimately on inundation (Kneib and Wagner 1994). Rozas (1993) suggests that two factors are of particular importance in nekton selection of marsh surface habitats: submergence time, and proximity to subtidal habitat. Kneib (1997a) points out that frequency and duration of flooding varies between marshes, and can constitute a major factor in determining nekton use of the various habitats on the marsh surface in any marsh system. Although different factors may structure communities of different marsh surface systems, many studies have concluded that a major division in nekton use of the marsh surface seems to be between a marsh edge community and a marsh interior community (Rakocinski *et al.* 1992, Peterson and Turner 1994, Minello *et al.* 1994).

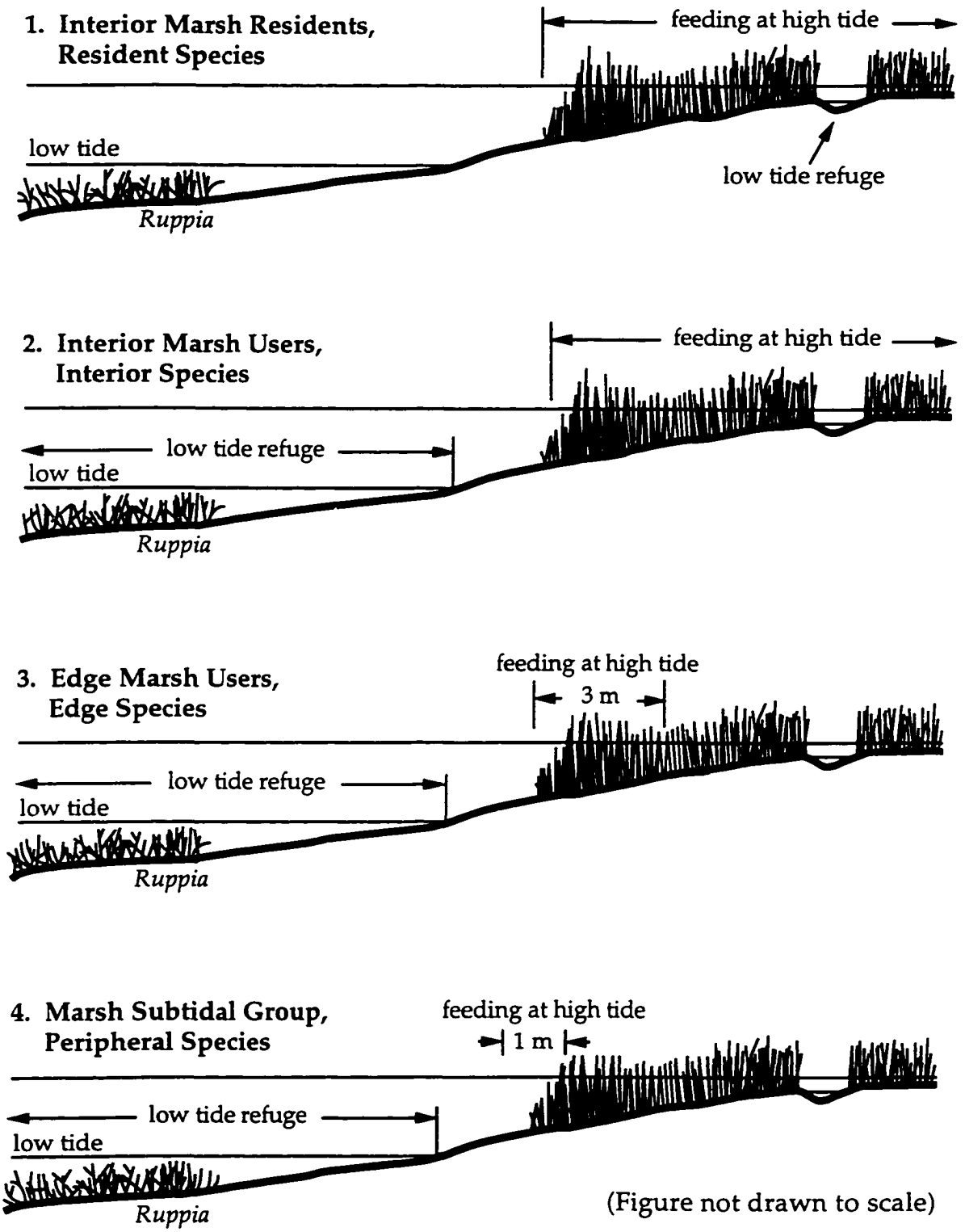
Rozas (1993) and Peterson and Turner (1994) described four general patterns of marsh surface use. Peterson and Turner (1994) studied a Louisiana marsh using flumes of different lengths. These authors found that densities of most captured species were greatest within three meters of the marsh edge, and that marsh interior areas were primarily used by marsh-resident fishes. These patterns characterize nekton use of the marsh surface and are depicted in Figure 2. First, "interior marsh residents" (Peterson and Turner 1994) or "resident species" (Rozas 1993) are generally juvenile fishes and crabs that stay on the marsh surface through the entire tidal cycle (Figure 2). For example, mummichogs use marsh surface microhabitats as low tide refuge until they reach approximately 15 mm in size (Kneib 1997a) at which time they begin to migrate off of the marsh surface at low tide. Interior marsh residents may reach very high densities on the marsh surface: Kneib (1997b) found average mean densities of 11.7 individuals per m^2, of which 7.2 individuals per m^2 were juvenile *Fundulus heteroclitus*.

Second, marsh "interior species" (Rozas 1993) or "interior marsh users" (Peterson and Turner 1994) are creatures such as adult *Palaemonetes*, mummichogs, and striped killifish that use the entire marsh surface at high tide, but move into the subtidal at low tide (Figure 2).

Figure 2. Four Hypothesized Pathways of Marsh Use

This figure shows hypothesized patterns of migration between marsh surface habitats and low tide refuge habitats. These patterns are taken from Rozas (1993) and Peterson and Turner (1994); the terminology of each author is used.

Four hypothesized pathways of marsh use, after Rozas 1993 and Peterson and Turner 1994



(Figure not drawn to scale)

These organisms are thought to be very important vectors of energy (Kneib 1997a) due to their relatively small individual size, large numbers, and continuous movement between habitats with each tidal cycle.

Third, "edge species" (Rozas 1993) or "edge marsh users" (Peterson and Turner 1994) are relatively larger organisms that feed on the marsh surface, but stay within 3 meters of the vegetated marsh edge (Figure 2). Fourth, "peripheral species" (Rozas 1993) or the "marsh subtidal group" (Peterson and Turner 1994) are generally larger organisms that feed on the open-water side of the marsh edge at high tide, but do not venture onto the marsh surface itself (Figure 2). Seatrout and flatfish are examples of peripheral species. Nekton use the various parts of the marsh surface in different ways, which contributes to the complexity of these systems.

This spatial means of categorizing marsh nekton seems particularly useful in defining the importance of various marsh surface habitats towards maintaining populations of nekton. Peterson and Turner (1994) caution, however, that using a spatial division of marsh into habitats for the purpose of assigning value of marsh habitats to fisheries production would be premature. They point out the complexity of wetland-open water couplings and suggest that the interactions between these habitats need better investigation before conclusions of relative value can be drawn.

Spatial patterns within marshes: relationships to unvegetated areas

High tide comparisons of nekton between the marsh surface and the unvegetated adjacent areas show different communities in each habitat, as one might expect. In general, abundance of small fishes is lower in the unvegetated than in marsh surface habitats. Baltz *et al.* (1993) in a Gulf of Mexico drop ring study found that fish abundance decreased with distance into open water from the marsh edge. Rakocinski *et al.* (1992), based on much of the same data as Baltz *et al.* (1993), reported that the marsh edge fish community was substantially different from the open-water community. Zimmerman and Minello (1984) in a

paired drop ring study of vegetated marsh vs. unvegetated adjacent areas found significantly higher densities of *Palaemonetes pugio, Penaeus aztecus,* and *Callinectes sapidus* in marsh areas. Similarly, densities of *Gobiosoma bosc, Lagodon rhomboides,* and *Fundulus similis* were greater in marsh habitats, while densities of *Leiostomus xanthurus* and *Micropogonias undulatus* were greater in unvegetated habitats. Rozas and Minello (1998 in press) conducted a drop ring comparison between the marsh surface, SAV, and unvegetated areas. Of the abundant species collected, only *Anchoa mitchelli* was found to have higher densities in unvegetated habitats compared to either vegetated habitat. Exceptions exist, but in general the literature suggests that unvegetated areas at high tide are inhabited by lower abundances of nekton than is the marsh surface. Marsh surface habitats support different - and usually denser - communities of nekton than do adjacent unvegetated habitats at high tide.

Spatial patterns within marshes: relationships to adjacent SAV beds

Few comparisons between nekton use of the marsh surface and adjacent SAV habitats exist in the literature (Rozas and Minello 1998 in press). In most cases, these habitats have been compared so as to evaluate their relative value in supporting communities of nekton. Patterns of differences between these two vegetated habitats are also of considerable interest in understanding the role of structure in providing food and refuge to aquatic organisms.

Weinstein and Brooks (1983) compared tidal creek and SAV communities at night high tides using trawls and 2.4 m diameter Wegener rings. Species richness and diversity were greater in seagrass habitats. Spot (*Leiostomus xanthurus*) were the most abundant fish, and were present in higher densities in marsh creek habitats. Spot abundance peaked in April and May, when spot < 50 mm SL dominated fish collections (5.35 - 34.47 per square meter in marsh creek habitat, 1.44 - 22.11 per square meter in SAV habitat, Wegener ring samples). Blue crabs (*Callinectes sapidus*) and summer flounder (*Paralichthys dentatus*) were more abundant in grassbeds than in marsh creeks, but were present in both systems.

Rozas and Minello (1998 in press) conducted a drop ring comparison between the marsh surface, SAV (mixed stands of *Ruppia maritima* and *Halodule wrightii*) and unvegetated areas. Rozas and Minello found no statistical difference in density between marsh and SAV habitats for *Gobiosoma bosc* or *Lucania parva*, although a higher mean density of *L. parva* was found in marsh surface habitats. Densities of *Palaemonetes pugio*, *P. intermedius*, and *Callinectes sapidus* were greatest on the marsh surface, while densities of *Penaeus aztecus* were greatest in SAV habitats (Rozas and Minello 1998 in press). Most species for which a significant difference in size occurred between SAV and marsh habitats, were larger in marsh habitats. These results were obtained during a time period where both SAV and marsh habitats were almost continuously inundated; in my sampling site only SAV habitat was continuously inundated, and marsh habitat was completely exposed with almost every tide. For several species, use of marsh and SAV habitats at my sampling area differed from use seen in Rozas and Minello (1998 in press); this is discussed below. Variation in tidal regime no doubt plays a role in the differences between Atlantic coast marshes and Gulf coast marshes, as is suggested by Rozas and Minello (1998 in press).

Orth and van Montfrans (1987) found that early juvenile blue crabs (*Callinectes sapidus*) were an order of magnitude more abundant in SAV habitats than in marsh creek habitats during the peak recruitment season of late summer and fall. Densities of larger (>25 mm carapace width) crabs in both habitats were much lower than for early juveniles, with mean seasonal values between 0.6 and 0.9 per square meter in SAV habitats.

Differences exist between species composition and size distributions of seagrass and marsh nekton communities. These habitats are characterized by very different assemblages of invertebrates and nekton. Despite differences, however, both SAV and marsh habitats support important components of estuarine nekton.

Studies which seek to demonstrate active links between salt marshes and adjacent seagrass habitat are rare, but a few papers describing these connections have been recently published. Fonseca *et al.* (1994) compared planted salt marshes with and without seagrass

adjacent to the marsh. The marsh surface was sampled with flumes nets, and the seagrass habitats were sampled with drop nets. Fonseca *et al.* (1994) found that only two species (*Callinectes sapidus* and *Fundulus heteroclitus*) were present on the marsh surface in higher numbers when SAV was present versus when SAV was not present. These differences existed only in June sampling and in each case only during one of the two years that the marshes were sampled; Fonseca *et al.* (1994) did not detect a strong linkage between the salt marsh surface during inundation and the nearby seagrass refuge. Irlandi and Crawford (1997), however, did find a linkage between SAV and marsh habitats for the omnivorous fish species *Lagodon rhomboides* (pinfish), which moved from one habitat to the other to some extent and transferred energy between the systems. Marsh-SAV links seem to be dependent on the particular systems and species that are involved.

Spatial patterns in marshes: summary

The spatial organization of marsh systems is very complex. Physical structure provided by the vegetated marsh surface, the marsh edge, tidal creeks, adjacent unvegetated and SAV areas play a major role in defining each marsh. Superimposed on this physical organization are the very important effects of tidal inundation. Marsh systems can be examined on many different scales, with each scale adding another layer of complexity.

TEMPORAL PATTERNS OF NEKTON USE

Temporal patterns: year-to-year variability in use of shallow water habitats

Year-to-year variability in species composition is a common feature of communities of shallow water nekton in areas of Chesapeake Bay and elsewhere, though many studies are completed in a single year and do not report this variation. Sheridan (1983) analyzed trawl data collected in 1963 and 1964 in Galveston Bay, Texas, and found that patterns of abundance for dominant species *Stellifer lanceolatus* (star drum) and *Anchoa mitchelli* varied significantly between years, while patterns for other dominant species *Micropogonias*

undulatus, *Leiostomus xanthurus*, and *Cynoscion arenius* did not. Sheridan also found spatial differences between years in fish use of the different parts of the estuary, but noted that mean fish biomass was relatively stable between years. Rulifson (1991) in a four year study of marsh creeks, found significant variation due to year for many of the abundant species examined. In a suction-sampling study of lower Chesapeake Bay between 1982 and 1986, Orth and van Montfrans (1987) report significant yearly variability in recruitment of blue crabs up to 11 mm in size in seagrass meadows and tidal creeks, but no significant variability between years for individuals larger than this. Rountree and Able (1992a), in a weir study of tidal marsh creeks in 1988 and 1989, found significant yearly differences for two (*Callinectes sapidus* and *Pomatomus saltatrix*) of the nine most abundant species in both years.

Year-to-year variation seems very common for subtidal residents of habitats associated with salt marshes, but is less well documented for dominant fish species of the salt marsh surface itself. This may in part be due to the typically local development of marsh resident fish larvae, while many other estuarine species have a wide-ranging planktonic larval phase. *Fundulus heteroclitus*, which lays eggs in marsh habitats (Able 1984), is generally very abundant every year in multiple year studies. Even so, year-to-year variation exists. The data of Yozzo and Smith (1998) show almost a doubling in numbers of this species collected from one year to the next, but in both years this species was still by far the numerically dominant fish. Yozzo and Smith (1998) also found markedly different abundances of *Fundulus luciae* between two sampling years. Werme (1981) noted the absence of *Cyprinodon variegatus* in one year of her study, while it was present (albeit in low numbers relative to other marsh residents) the next. Year-to-year year variability in marsh surface fish populations is important, but the same few species tend to remain as dominants every year in most long term studies of the marsh surface.

Temporal patterns: seasonal differences in marsh use

Ayvazian *et al.* (1992) describe seasonal movements of species in the Virginian zoogeographic province from deeper inshore water to shallow nearshore habitats as water temperature increases in the spring, followed by the reverse migration as temperature declines in the early fall. Rountree and Able (1992a) found a strong seasonal pattern that repeated itself over two years in a marsh creek weir study conducted in New Jersey. Biomass peaks were present in May and August, and species composition differed between seasons. Allen *et al.* (1995) also found strong seasonal patterns in a multi-year study of marsh creek zooplanktivores; Atlantic silversides were most abundant in winter, while the three other species studied were most abundant at the other times of year. Ayers (1995) reports a strong seasonal signal at the Goodwin Islands as well. These and other works show that studies of shallow water nekton must recognize seasonal patterns of faunal abundance.

Temporal patterns: differences in marsh use due to life history strategy

Several schemes have been developed to categorize estuarine fishes based on their life history strategies. A common approach, used by Peterson and Turner (1994) and by other workers, is to divide fishes into estuarine transients and estuarine residents. In this scheme, estuarine transients spend only a portion of their life cycle within an estuary, while residents spend their entire lives within the estuary. McHugh (1967), Day *et al.* (1989), and Ayvazian *et al.* (1992) presented more explicit schemes to divide fishes based on their dependence on estuaries into residents, nursery species, marine species, and adventitious visitors. This essentially subdivides the estuarine transient category into nursery species, marine species, and adventitious visitors. All of the categorizations used above, however, apply to the entire estuary, and not specifically to marshes. These schemes are valuable in evaluating the importance of estuaries in relation to the coastal ocean, but are less directed to marshes.

In the case of this dissertation, it is more central to evaluate the importance of marshes in relation to the larger estuary. The estuarine categorizations above can easily be shifted to

describe marsh dependence rather than estuarine dependence. Certain marsh workers have adopted this approach as well, notably Kneib (1997a). Peterson and Turner (1994) also distinguish between resident species, in the sense of estuarine residents, and marsh-residents as well. A life-history approach to the categorization of marsh nekton recognizes permanent marsh residents (Kneib and Wagner 1994, Kneib 1997a) and transient marsh nekton (*sensu* Kneib 1997a). Permanent marsh residents such as *Fundulus* spp and *P. pugio* are trophically tied to the marsh for essentially their entire lives (although *P. pugio* has a planktonic larval stage). Marsh transients use marsh habitats only for a portion of their life cycle (Kneib 1997a). The marsh transient nekton category can be further broken into marsh nursery species and opportunistic marsh visitors, similar to the approach of McHugh (1967), Day *et al.* (1989), and Ayvazian *et al.* (1992). Marsh nursery species are those that frequent marshes as juveniles, but not as adults, and regularly use marshes as food or refuge support for their maturation. Opportunistic marsh users are those species who utilize marshes sporadically during various parts of their life history, but also use other habitats extensively and would not be considered dependent on marsh habitat. For the purposes of this dissertation the most valuable divisions are between permanent marsh residents and marsh transients, which is further broken into marsh nursery species and opportunistic marsh visitors.

The degree to which a community of marsh nekton consists of permanent marsh residents, marsh nursery species, and opportunistic marsh visitors is of great interest in defining a marsh system. Zimmerman and Minello (1984) found that residents (*Palaemonetes pugio, Gobiosoma bosc,* and *Fundulus similis*) were the most abundant macrofauna in a drop ring study of a Texas marsh. After these species, most macrofauna were transient juveniles of estuarine dependent species. Life history strategies of estuarine nekton can be examined in many ways. Export of energy from marsh habitats in particular is linked to life history strategy; these processes are discussed further in Chapter 4.

Temporal patterns: day-to-day differences in marsh use

Varnell *et al.* (1995) showed considerable day-to-day variability in nekton use of two Virginia pocket marshes, and suggest that this day-to-day variability is an important aspect of marsh population dynamics. These authors point out that studies which replicate on consecutive days may produce more accurate results than those which do not.

Temporal patterns: diel differences in marsh use

On shorter time scales, diel patterns of marsh use are also of great importance. Certain species are more active or abundant in marsh habitats at night. Silver perch (*Bairdiella chrysoura*) may move into marsh creeks and feed on *Palaemonetes* shrimp in intertidal areas at night (Kleypas and Dean 1983). Studies in seagrass habitats have also found silver perch to be a nocturnal predator (Adams 1976b, Brooks 1985). Day-night differences in use of different habitats are particularly well documented in the Atlantic silverside, *Menidia menidia*. Schmelz (1964) remarked on the evening invasions of *Menidia menidia* into drainage ditches in a Delaware marsh. Silversides may be more abundant in marsh creeks during night flood tides compared with day flood tides (Rountree and Able 1993). In other situations, fishes are more active or abundant in marsh habitats during the day. Rountree and Able (1993) documented a migration of larger adult *M. menidia* into the creeks during the day in early summer, and attributed this to a reproductive movement. Silversides feed in the daytime, and those taken at night in seagrass beds have very little food in their guts (Adams 1976c). Mummichogs also are visual feeders that primarily feed at daytime high tides on the marsh surface (Weisberg *et al.* 1981). Because of these differences on the diel cycle, night studies are of great value in understanding how nekton use marsh habitat.

Temporal patterns: differences in marsh use within a tidal cycle

Differences in nekton use of marshes due to tidal regimes are discussed above in the geographic location section. This section discusses smaller-scale differences within one daily cycle of inundation.

At low tide, the primary refuges for marsh nekton greater than 15 or 20 mm are the unvegetated subtidal areas adjacent to the marsh (Kneib 1997a). These areas may provide a refuge from predation if water depth is shallow (Ruiz *et al.* 1992, Dittel *et al.* 1995). Small species, including *Fundulus heteroclitus, F. majalis, Palaemonetes pugio,* and *Gobiosoma bosc* were more abundant in water less than 70 cm deep in a Chesapeake Bay drop ring study (Ruiz *et al.* 1992). In the same study, larger predatory species were most abundant in waters deeper that 70 cm, and mortality of tethered *P. pugio* 30 - 35 mm, *F. heteroclitus* 40 - 50 mm, and *Callinectes sapidus* 30 - 70 mm increased significantly with depth (Ruiz *et al.* 1992). Shallow water depth offers a refuge from predation to small fishes and crustaceans. Miltner *et al.* (1995) found, however, that the shallow depth distribution of spot in tidal creeks was more influenced by food availability than by risk of predation. By migrating between the marsh surface at high tide and the shallow unvegetated at low tide, marsh resident nekton may lower their chances of capture by larger aquatic predators; they may also continue to feed in these unvegetated areas.

PATTERNS OF NEKTON USE BASED ON TAXONOMY

Patterns based on taxonomy: marsh resident fishes

Many cyprinodontids and fundulids are permanent marsh residents and are trophically tied to the marsh for essentially their entire lives (note that the term "fundulid" is used throughout this dissertation to refer to *Fundulus* and *Lucania* while "cyprinidontid" is used to refer to *Cyprinodon variegatus).* The most abundant fundulid at my marsh was *F. heteroclitus,* which deposits eggs in marsh habitats (Taylor and DiMichele 1983, Able 1984) and has been suggested to maintain a small home range for an entire season (Lotrich 1975). Fundulids may

exit the marsh at low tide to take refuge in the adjacent unvegetated, but seem to exhibit a strong preference for the marsh surface at high tide. These species spend the entire growth season if not their entire lives in the marsh area.

Mummichogs follow the advancing and receding tides onto the marsh surface, and occupy intermediate and high marsh areas more so than low marsh areas at slack high tide (Kneib 1984a). In some expansive marsh systems, larger size classes of nekton penetrate deeper into the marsh interior at spring tides than do smaller size classes (Kneib and Wagner 1984). High marsh areas may nonetheless be extensively utilized by larval and juvenile nekton (Talbot and Able 1984).

Mummichogs require access to the marsh surface in order to obtain enough energy for growth (Weisberg and Lotrich 1982b). However, mummichogs restricted to adjacent unvegetated areas may be able to obtain enough food to maintain their body weight, and the unvegetated can provide up to 75% of the energy uptake of the natural population of these fishes (Weisberg and Lotrich 1982b). Other studies (Butner and Brattstrom 1960, Rozas and LaSalle 1990) have found killifish guts to be significantly more full when the fishes were leaving the marsh surface on an ebbing tide compared to when they were entering the marsh on a flooding tide. Marsh habitat is clearly very important to many fundulids.

Patterns based on taxonomy: marsh transient fishes

Several taxa of fishes use the marsh surface in a transient or opportunistic way. Rozas (1993) reports selection for marsh edge versus marsh interior by these transient species. Peterson and Turner (1994) report greater catches of marine transients at high tide in seine samples than at low tide, suggesting that these species migrate from deeper water areas at low tide into marshes at high tide. In a North Carolina marsh, transient fishes were more abundant in channel marsh sites facing deeper water than in rivulet sites abutting shallow waters at the heads of small creeks (Hettler 1989a). A general conclusion can be drawn that

transient fishes utilize marshes which provide access to deeper water, and migrate tidally from the deeper water into marsh habitat to forage.

Atlantic silversides (*Menidia menidia)* are an example of a marsh transient species. These fish are dependent on marshes for reproduction and early development (Fay *et al.* 1983) and are seasonal users of the marsh surface. Atlantic silversides are also abundant in marsh creeks and derive significant nutrition from this habitat (Allen *et al.* 1995). Adult silversides migrate out of the estuary in winter and spend several months offshore, when they experience very high mortality (Fay *et al.* 1983). Through this migration, silversides export energy from marsh areas into offshore waters.

Patterns based on taxonomy: *Callinectes sapidus*

Blue crabs are abundant in submerged habitats of Chesapeake Bay (Orth and van Montfrans 1987, Ryer 1987, Mansour 1992); many studies have also found blue crabs to be abundant in marsh surface habitats of Chesapeake Bay and elsewhere (Ryer 1987, Thomas *et al.* 1990, Peterson and Turner 1994, Minello *et al.* 1994). Densities of blue crabs < 40 mm CW ranged from 1.3 to 22.1 inds m^{-2} in marsh habitats of two Texas bays (Thomas *et al.* 1990). Densities reported for crabs in marsh habitats along the Atlantic coast are generally lower than this (Orth and van Montfrans 1987, Mense and Wenner 1989, Wilson *et al.* 1990).

Blue crabs are found over the entire marsh surface. In a Texas marsh system, *Callinectes sapidus* was distributed evenly among inner marsh habitats regardless of distance to a channel (Minello *et al.* 1994). In a Louisiana marsh, crabs were collected from the marsh interior but may have utilized edge habitats to an even greater degree (Peterson and Turner 1984). Use of the marsh surface by juvenile blue crabs is also documented in Atlantic coast marshes (Kneib 1997b, Yozzo and Smith 1998).

Blue crabs have shown a strong preference for marsh habitat over unvegetated habitat in the Gulf of Mexico (Zimmerman and Minello 1984, Thomas *et al.* 1990). In Atlantic coast marshes, this preference does not always occur (Wilson *et al.* 1990). In fact, crabs were more

abundant in unvegetated areas than on the marsh surface in South Carolina, though densities of crabs were very low in every habitat sampled (Mense and Wenner 1989). Crab use of the marsh surface, though well documented in some regions, may not be universal throughout the range of this species.

Patterns based on taxonomy: palaemonids

Palaemonetes pugio can occur in high densities in marsh habitats. Zimmerman and Minello (1984) found peak densities of *P. pugio* of 70 inds m^{-2} in Galveston Bay (Texas) in the summer. Nixon and Oviatt (1973) reported that a fall peak of *P. pugio* in a shallow cove reached 250 - 800 inds m^{-2} and 15.3 g m^{-2} (dry weight), though estimates for other seasons were considerably lower. In part because of these large abundances, *P. pugio* is considered a very important species in the dynamics of marsh nekton (Sikora 1977).

SUMMARY

Variability in nekton use of marshes in relation to the sampled marsh

Marshes are complicated systems that differ on various spatial and temporal scales. Although the resident marsh fauna is generally composed of only a few species, use of marshes by nekton is complex due to the highly varied and dynamic marsh landscape and energy regime. Because of this complexity, and because every marsh is unique, it can be misleading to simply apply results from one marsh to another. Nekton use of a marsh is satisfactorily explained only in the context of the numerous factors that characterize the sampled marsh. If this is done, then productive comparisons between marshes can be made, because the various factors which are thought to drive differences in nekton use are also accounted for. The marsh sampled in this project is described thoroughly in Chapter 1. To highlight features discussed in the previous sections, this area is a narrow fringing marsh that directly faces an open embayment at the mouth of the York River subestuary (Chesapeake Bay, Virginia). The primary sampling area (arrow 1, Figure 1, Chapter 1) made up one side of a small embayment

with a maximum flooded area of about 4000 square meters and about 170 meters of marsh edge. This marsh edge was primarily depositional (Figure 1), but erosional edge with a small embankment of up to 20 cm did exist within the area. Wave energy was high relative to other depositional edge intertidal marshes in the region. Tides are astronomically driven and regular, with a mean range of 0.7 m and a maximum range of 1.2 m during the time period of the study. The sampled area flooded a mean distance of 16 meters from the open water interface at high tide during this time, and a mean distance of 23 meters on spring high tides. The sampling area contained no tidal creeks. Sediments in the sampled unvegetated habitat ranged from primarily coarse and fine sands at the exposed end of the embayment to primarily fine sand and silt at the protected end (W. Reay, unpublished 1998 data). Salinity was on the low end of the polyhaline range (Figure 2, Chapter 1). The marsh faced an adjacent gradually sloping intertidal flat (2 - 4% grade, W. Reay unpublished data) which led into a shallow patchy bed of *Ruppia maritima* about 5 - 15 m from the marsh edge. It is intended that the discussion and description above be used to help explain use of the sampled marsh by natant macrofauna. The next sections of this chapter detail these patterns of use for each of the major taxonomic and ecological groups of nekton as the results of this study.

METHODS SUMMARY

General analytical approach

Drop ring sampling was carried out as described in Chapter 1. Five habitats were sampled at high tide, and 3 habitats were sampled at low tide (Figure 5, Chapter 1). Sampling took place between June and October, 1995.

Data obtained from drop ring sampling were not normally distributed, and were analyzed using non-parametric statistics. The Kruskal-Wallace, Wilcoxon-Mann-Whitney, and Dunn analyses were used to test for significant differences in species use based on numbers of individuals per sample. Tests on total nekton are based on grams dry weight per sample to avoid problems of inflated alpha (significance) with regrouping species that have already been tested on numbers of individuals. An analysis of total nekton by grams dry weight per sample may be thought to be heavily influenced by large blue crabs. In every case, the total nekton analysis was also run on total nekton excluding blue crabs to test for this influence. In each pair of tests, results from tests excluding blue crabs led to the same conclusions as tests which included them. Results obtained by Kruskal-Wallace and Wilcoxon-Mann-Whitney tests on total grams dry weight of nekton are robust indicators of the entire community, and do not seem to be unduly influenced by large blue crabs.

Throughout this discussion, mean values ($\pm$ standard error) of abundance and biomass are provided to describe habitat use. These values are always means of all samples collected for the time period, and not grand means of the monthly means. Mean values provided in the text are not intended to be connected to the statistical test results in any way, since the analyses used do not examine means. Mean values are provided for informative purposes only; they are the standard used in other studies, and are given here to facilitate comparisons to other work.

Table 1. Length-Weight Regressions for Common Species

Length-weight regressions calculated for the common species are listed. The regression equations provide grams wet weight for a known length of individual (in mm) within the size range given. N and R-squared values for each regression are also provided.

Length-Weight Regressions for Common Species, Goodwin Islands 1995

Species	Size range (mm)	Measurement	N	Regression	R sq
Callinectes sapidus	5 - 30	point to point	42	gww = 0.00008794 * mm ^ 3.0201	0.93
Callinectes sapidus	33 - 119	point to point	115	gww = 0.0001152 * mm ^ 2.9338	0.95
Cyprinidon variegatus	22 - 50	total length	31	gww = 0.000005082 * mm ^ 3.4098	0.95
Fundulus heteroclitus	7 - 20	total length	70	gww = 0.000009856 * mm ^ 2.9634	0.73
Fundulus heteroclitus	21 - 100	total length	452	gww = 0.000004796 * mm ^ 3.2718	0.97
Fundulus majalis	24 - 111	total length	87	gww = 0.000004453 * mm ^ 3.2385	0.98
Gobiosoma bosc	9 - 19	total length	28	gww = 0.000007826 * mm ^ 3.0951	0.88
Gobiosoma bosc	20 - 52	total length	94	gww = 0.000005168 * mm ^ 3.2397	0.96
Lucania parva	9 - 19	total length	22	gww = 0.000008027 * mm ^ 3.0855	0.88
Lucania parva	20 - 48	total length	128	gww = 0.00001583 * mm ^ 2.9169	0.87
Menidia menidia	12 - 21	fork length	26	gww = 0.00000007046 * mm ^ 4.5147	0.75
Menidia menidia	22 - 92	fork length	196	gww = 0.00001455 * mm ^ 2.8501	0.95
Palaemonetes pugio	12 - 42	rostrum - telson	204	gww = 0.000004064 * mm ^ 3.2651	0.93
Symphurus plagiusa	27 - 80	total length	37	gww = 0.00001030 * mm ^ 2.9775	0.98

Wet weights obtained from common species were used to construct length-weight regressions (Table 1). Except in unusual situations such as when specimens were incomplete, all nekton > 20 mm were weighed individually throughout this study, however. All individuals of species for which regressions are not presented in Table 1 were also individually weighed.

Data are not corrected for gear efficiency in this chapter. Removal efficiencies of the clearing device (Table 1 of Chapter 1) are referred to within the text, but all numbers reported in this chapter represent creatures that were actually captured. Removal efficiency was high in general, with the exception of small blue crabs in vegetated habitats. Note that Chapters 3 and 4 do include corrections for removal efficiency based on Table 1 of Chapter 1.

Habitat use study

The habitat study was carried out to examine utilization of marsh, SAV, and unvegetated areas by shallow water nekton. Drop samples were taken in Area 1 (arrow 1, Figure 1, Chapter 1) between June and October 1995 using the methods and sampling design described in Chapter 1 of this dissertation. Figure 5 in Chapter 1 shows the habitats that were sampled. As mentioned in Chapter 1, Marsh Fringe and SAV habitats were not sampled in June, and the Hightide SAV habitat was not sampled in July.

Mean abundance and biomass per square meter are reported for each species (in alphabetical order) for each habitat (Table 3). Totals for crustaceans, fishes, and nekton are provided at the end of Table 3. Habitats in which species were never captured are not included. Note that in this table the mean habitat value for all months (the last column) represents the grand mean of all monthly means for which the habitat was sampled; it is not the mean of all drop samples taken. Unequal numbers of replicates were taken in certain month/habitat combinations, and columns in Table 3 were developed to provide better comparisons through time. Similarly, the means of all sampled habitats (the last rows for each species) are calculated as the average of all habitats in which sampling took place. These rows provide a mean value per square meter that includes all sampled habitats, even

when the species in question was never captured in a habitat. This "mean of all sampled habitats" row therefore reports a low value per square meter, but one that allows for comparisons between months for each species. The grand total box for each species (lower right corner of each species block) gives the average of all habitat means in the last column of the table. This total is not equivalent to the average of all monthly means, again because sampling effort was not uniform in each habitat. The grand total cannot be multiplied by the area sampled to obtain the total numbers captured in the study. Totals in Table 3 are designed for comparative purposes, to examine difference between months and between habitats. These totals should not be used for absolute quantifications. However, the values presented with standard errors in each species/habitat box of Table 3 are means of the samples taken and can be taken as quantifications per square meter. Also, Figure 4 provides totals over the sampling period based on the means of the collected samples in each habitat. Totals from Figure 4 are therefore used as quantifications when these statistics are desired.

Figures 3 and 4 display essentially the same information as does Table 3, however Figures 3 and 4 are arranged by habitat instead of by species and provide a better community-level view of shallow water nekton. Mean values for all months are shown in Figure 4. As mentioned above, these mean values are calculated as means of all samples taken in each habitat and include standard errors. This figure provides an overview of general trends in community composition.

Four pit traps were installed on the marsh surface and were sampled between September and November of 1995 as described in Chapter 1. Data represent 12 samples from each trap (Figure 5). These traps were not quantitative. It should be noted that two of the pit traps were placed in the infrequently flooded high marsh and rarely captured any organisms. Almost all of the individuals reported in Figure 5 were captured in the 2 low marsh traps, i.e. in the 12 samples taken from each of these traps.

In order to statistically compare habitat use, only drop trap data from August through September were analyzed, when all habitats were sampled. Data were not normally

distributed, and were evaluated for significant differences among habitats using the non-parametric Kruskal-Wallace test as calculated by SAS (SAS Institute). Where differences were found, the Dunn multiple comparison test described in Zar (1996) was used to identify the sources responsible for these differences (Table 4). The most abundant species were tested for differences on numbers of individuals per sample (Table 4 A - F). Totals for crustaceans, marsh resident fishes, fishes, and all nekton are also tested statistically (Table 4 G - J) but were tested on grams dry weight per sample to avoid issues of inflated alpha (significance) with the individual species tests. Note, however, that some data were reused in testing marsh resident fishes, fishes, and all nekton, as well as in testing crustaceans and all nekton. Because p values were always less than 0.0005 for the Kruskal-Wallace tests, inflated alpha is not thought to be a problem here.

Sampling area study

A separate study was conducted in 1996 to examine differences in nekton use of three different areas on the Goodwin Islands and to better evaluate the results of the habitat study with reference to other local marshes. Eight replicate drop samples were taken in each of three marsh areas of the Goodwin Islands (Chapter 1, Figure 1). These areas are described in Chapter 1 and differences are emphasized again in the discussion section of this chapter. Sampling took place only in the Hightide Fringe habitat to minimize variability due to habitat differences within each site. Sampling took place on July 23 and 24 and on August 2 and 5, 1996. The design of the project was to collect two drop samples at high tide in each sampling area each day. The order in which areas were visited was determined using a random numbers table, as was the location of each drop within each area. One site was not sampled on one of the sampling dates. An extra sample from this site was taken in each of two subsequent sampling days. A total of 24 drop samples were collected. The Kruskal-Wallace test was used to examine differences among sampled areas.

Day-night study

Day-night patterns of marsh surface use at high tide were examined in August and September of 1996. Four paired day and night spring high tides were selected so that predicted maximum tidal height would be similar at day and at night. Two of these tides occurred on the full moon, two on the new moon; all nights were relatively cloudless. The ambient nighttime illumination was very different between new moon and full moon sampling dates, as might be expected. Marsh edge, marsh fringe, and marsh interior habitats were sampled on each date during daylight, and again at the next high tide, which was always well after sundown. The order in which habitats were sampled was determined using a random numbers table, as was the location of each drop. A total of 24 samples were collected (12 day, 12 night, replicated on four day-night cycles). The non-parametric Wilcoxon-Mann-Whitney analysis was used to test for significant differences between day and night use by those species sufficiently abundant to analyze. The Wilcoxon-Mann-Whitney test is the two-group version of the Kruskal-Wallace test used to examine differences between three or more groups in the previously described studies.

Year-to-year variability study

The day time samples from the 1996 day-night study described above were compared to samples collected on the corresponding dates in 1995. Most of these 1995 samples were collected in the 1995 habitat study described above, but that was not always the case. Sampling methods were identical for all 1995 and 1996 samples, however. Paired dates were: 8-29-95 and 8-29-96; 8-30-95 and 8-30-96; 9-12-95 and 9-12-96; and 9-13-95 and 9-13-96. The marsh interior habitat was not sampled on 8-30-95. Data from a sample taken on 9-11-95 (the unused sample closest in time to 8-30-95) were substituted for this missing sample instead. Other than this, one sample in each of the marsh high tide habitats (Edge, Fringe, Interior;

Figure 5, Chapter 1) was taken on each of the 8 sampling dates. The difference in mean salinity during this time period was less than 1 part-per-thousand between years; the difference in mean temperature was less than 2 degrees Celsius between years (K. A. Moore, unpublished data). The ranges in salinity and temperature between years were also similar. As above, the non-parametric Wilcoxon-Mann-Whitney analysis was used to test for significant differences between years for those species sufficiently abundant to analyze.

Table 2. Total Catch

The total numbers and biomasses of all species captured in the primary habitat study (June through October 1995) are provided in order of decreasing abundance. Data represent totals of 166 drop samples, equivalent to 290.5 square meters sampled in all habitats combined. Since sampling effort was not identical for all habitats, this table should not be considered an even depiction of relative abundances in the entire shallow water community.

Total Catch (166 drop samples, June - October 1995)		
Species	**No. Inds.**	**Grams d.w.**
Palaemonetes pugio	3478	104.90
Palaemonetes vulgaris	1590	42.14
Callinectes sapidus	1173	726.75
Unidentifiable palaemonids	560	10.98
Hippolyte spp	315	1.13
Fundulus heteroclitus	300	83.03
Lucania parva	204	15.38
Gobiosoma bosc	199	14.38
Palaemonetes intermedius	177	3.30
Fundulus majalis	63	28.77
Crangon septemspinosa	39	0.76
Menidia menidia	35	9.32
Symphurus plagiusa	34	8.36
Syngnathus fuscus	26	1.46
Gobiesox strumosus	13	3.17
Penaeus duorarum	13	3.00
Syngnathus floridae	11	1.37
Leiostomus xanthurus	10	1.23
Unidentifiable penaeids	10	0.86
Penaeus aztecus	9	2.60
Cyprinodon variegatus	8	1.01
Bairdiella chrysoura	5	6.03
Cynoscion nebulosus	5	4.75
Opsanus tau	5	0.86
Anguilla rostrata	4	17.80
Mugil cephalus	4	6.65
Sciaenops ocellatus	3	0.31
Microgobius thalassinus	3	0.24
Anchoa mitchelli	3	0.04
Chaetodipterus faber	2	0.32
Hypsoblennius hentzi	2	0.17
Chasmodes bosquianus	1	1.00
Fundulus luciae	1	0.10
Apeltes quadracus	1	0.09
Total	8305 inds	1102.25 gdw

Table 3. Abundance and Biomass of Nekton

This table provides population data per square meter for each species captured in the primary habitat study, June through October 1995. Species are arranged alphabetically; totals for crustaceans, fishes, and total nekton are provided at the end of the table. Data are not provided for habitats in which species were never captured. Data for each habitat/month are identical to Figure 3; however the seasonal totals provided in Table 3 are calculated differently from Figure 4. Table 3 (this table) calculates seasonal totals (the last column of the table) as grand means of the monthly sampling estimates, not as means for all the collected samples. Habitat totals (the last row for each species) are for all habitats sampled in that time period, regardless of whether the species was present in that habitat or not. The grand total box for each species (the lower right box of the species cluster) is the average of all values in the last column. In the text of this dissertation, all numbers provided as totals are from Figure 4, and represent mean values for the samples taken, not grand means of monthly means.

Abundance and Biomass of Nekton, Goodwin Islands 1995

Habitats in which a species was not captured are not displayed
ns = not sampled SE = standard error

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
Anchoa	Hightide SAV	inds/m2	ns	ns	0.86	0	0	0.29
mitchelli		SE	ns	ns	0.61	0	0	
		gdw/m2	ns	ns	0.011	0	0	0.004
(bay anchovy)		SE	ns	ns	0.008	0	0	
	Mean of all	inds/m2	0	0	0.108	0	0	0.036
	sampled habitats	gdw/m2	0	0	0.0014	0	0	0.0005
Anguilla	Hightide SAV	inds/m2	ns	ns	0	0.46	0	0.15
rostrata		SE	ns	ns	0	0.13	0	
		gdw/m2	ns	ns	0	2.034	0	0.678
(American eel)		SE	ns	ns	0	0.557	0	
	Mean of all	inds/m2	0	0	0	0.058	0	0.019
	sampled habitats	gdw/m2	0	0	0	0.2543	0	0.0848
Apeltes	Lowtide SAV	inds/m2	ns	0	0.14	0	0	0.04
quadracus		SE	ns	0	0.07	0	0	
		gdw/m2	ns	0	0.013	0	0	0.003
(fourspine		SE	ns	0	0.007	0	0	
stickleback)	Mean of all	inds/m2	0	0	0.018	0	0	0.005
	sampled habitats	gdw/m2	0	0	0.0016	0	0	0.0004
Bairdiella	Hightide SAV	inds/m2	ns	ns	0.29	0	0	0.1
chrysoura		SE	ns	ns	0.2	0	0	
		gdw/m2	ns	ns	0.147	0	0	0.049
(silver perch)		SE	ns	ns	0.104	0	0	
	Hightide Edge	inds/m2	0	0	0.23	0	0	0.05
		SE	0	0	0.1	0	0	
		gdw/m2	0	0	0.339	0	0	0.068
		SE	0	0	0.151	0	0	
	Hightide Interior	inds/m2	0	0	0.11	0	0	0.02
		SE	0	0	0.05	0	0	
		gdw/m2	0	0	0.12	0	0	0.024
		SE	0	0	0.054	0	0	
	Lowtide SAV	inds/m2	ns	0	0	0.14	0	0.04
		SE	ns	0	0	0.07	0	
		gdw/m2	ns	0	0	0.214	0	0.054
		SE	ns	0	0	0.107	0	
	Mean of all	inds/m2	0	0	0.079	0.018	0	0.026
	sampled habitats	gdw/m2	0	0	0.0758	0.0268	0	0.0244
Callinectes	Hightide SAV	inds/m2	ns	ns	8.57	15.54	21.14	15.09
sapidus		SE	ns	ns	1.21	1.03	2.71	
		gdw/m2	ns	ns	1.807	7.926	1.027	3.586
(blue crab)		SE	ns	ns	1.077	3.192	0.106	
	Hightide Unveg.	inds/m2	0.76	0.11	0.34	6.51	3.2	2.19
		SE	0.29	0.05	0.06	0.75	0.56	
		gdw/m2	4.111	0.22	2.284	0.428	1.173	1.643
(continued)		SE	1.648	0.098	0.484	0.074	0.406	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(C. sapidus)	Hightide Edge	inds/m2	0.38	0.23	0.69	11.43	5.37	3.62
		SE	0.11	0.1	0.25	1.29	0.57	
		gdw/m2	1.541	3.675	1.973	7.193	4.914	3.859
		SE	0.858	1.644	0.746	2.39	1.56	
	Hightide Fringe	inds/m2	ns	0.11	0.11	1.83	2.51	1.14
		SE	ns	0.05	0.05	0.3	0.4	
		gdw/m2	ns	0.22	1.422	1.319	3.075	1.509
		SE	ns	0.098	0.636	0.274	0.78	
	Hightide Interior	inds/m2	0	0.11	0	1.03	1.43	0.51
		SE	0	0.05	0	0.28	0.43	
		gdw/m2	0	0.142	0	3.274	0.537	0.79
		SE	0	0.063	0	1.448	0.156	
	Lowtide SAV	inds/m2	ns	0.38	3.86	12.57	16.11	8.23
		SE	ns	0.22	0.62	2.04	1.36	
		gdw/m2	ns	3.946	25.448	3.258	1.66	8.578
		SE	ns	2.278	8.077	1.173	0.403	
	Lowtide Deep	inds/m2	1.03	0.11	0.46	9.71	7.29	3.72
		SE	0.19	0.05	0.15	1.03	0.49	
		gdw/m2	0.979	0.18	1.501	5.316	1.499	1.895
		SE	0.285	0.081	0.412	0.479	0.179	
	Lowtide Shallow	inds/m2	0.34	0.23	0.69	5.71	4.91	2.38
		SE	0.1	0.06	0.31	0.52	0.97	
		gdw/m2	0.268	0.986	0.025	0.424	0.381	0.417
		SE	0.114	0.293	0.011	0.066	0.059	
	Mean of all	inds/m2	0.502	0.213	1.84	8.041	7.745	4.61
	sampled habitats	gdw/m2	1.3798	1.5615	4.3075	3.6423	1.7833	2.7846
Chaetodipterus faber	Lowtide Deep	inds/m2	0	0	0.23	0	0	0.05
		SE	0	0	0.06	0	0	
		gdw/m2	0	0	0.036	0	0	0.007
(spadefish)		SE	0	0	0.011	0	0	
	Mean of all	inds/m2	0	0	0.029	0	0	0.006
	sampled habitats	gdw/m2	0	0	0.0045	0	0	0.0009
Chasmodes bosquianus	Hightide Edge	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
		gdw/m2	0	0	0	0.114	0	0.023
(striped blenny)		SE	0	0	0	0.051	0	
	Mean of all	inds/m2	0	0	0	0.014	0	0.003
	sampled habitats	gdw/m2	0	0	0	0.0143	0	0.0029
Crangon septemspinosa	Hightide SAV	inds/m2	ns	ns	0	0.34	0.46	0.27
		SE	ns	ns	0	0.1	0.1	
		gdw/m2	ns	ns	0	0.005	0.018	0.008
(sand shrimp)		SE	ns	ns	0	0.001	0.006	
	Lowtide SAV	inds/m2	ns	0	0	0.14	0.57	0.18
		SE	ns	0	0	0.07	0.14	
		gdw/m2	ns	0	0	0.002	0.023	0.006
(continued)		SE	ns	0	0	0.001	0.006	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(C. septemspinosa)	Lowtide Deep	inds/m2	0	0	0	0.23	3.43	0.73
		SE	0	0	0	0.1	1.71	
		gdw/m2	0	0	0	0.003	0.045	0.009
		SE	0	0	0	0.001	0.022	
	Mean of all	inds/m2	0	0	0	0.089	0.558	0.148
	sampled habitats	gdw/m2	0	0	0	0.0013	0.0108	0.0029
Cynoscion	Hightide SAV	inds/m2	ns	ns	0	0.11	0	0.04
nebulosus		SE	ns	ns	0	0.05	0	
		gdw/m2	ns	ns	0	0.038	0	0.013
(spotted		SE	ns	ns	0	0.017	0	
seatrout)	Hightide Edge	inds/m2	0	0	0.11	0.11	0	0.05
		SE	0	0	0.05	0.05	0	
		gdw/m2	0	0	0.172	0.29	0	0.093
		SE	0	0	0.077	0.13	0	
	Lowtide SAV	inds/m2	ns	0	0.14	0.14	0	0.07
		SE	ns	0	0.07	0.07	0	
		gdw/m2	ns	0	0.039	0.014	0	0.013
		SE	ns	0	0.02	0.007	0	
	Mean of all	inds/m2	0	0	0.031	0.045	0	0.02
	sampled habitats	gdw/m2	0	0	0.0264	0.0428	0	0.0149
Cyprinodon	Hightide Fringe	inds/m2	ns	0.23	0	0	0	0.06
variegatus		SE	ns	0.06	0	0	0	
		gdw/m2	ns	0.039	0	0	0	0.01
(sheepshead		SE	ns	0.013	0	0	0	
minnow)	Hightide Interior	inds/m2	0.14	0	0	0	0	0.03
		SE	0.07	0	0	0	0	
		gdw/m2	0.027	0	0	0	0	0.005
		SE	0.013	0	0	0	0	
	Lowtide SAV	inds/m2	ns	0	0.14	0	0	0.04
		SE	ns	0	0.07	0	0	
		gdw/m2	ns	0	0.064	0	0	0.016
		SE	ns	0	0.032	0	0	
	Lowtide Shallow	inds/m2	0	0.11	0.34	0	0	0.09
		SE	0	0.05	0.15	0	0	
		gdw/m2	0	0.004	0.001	0	0	0.001
		SE	0	0.002	0	0	0	
	Mean of all	inds/m2	0.028	0.057	0.06	0	0	0.028
	sampled habitats	gdw/m2	0.0054	0.0072	0.0081	0	0	0.004
Fundulus	Hightide Unveg.	inds/m2	0	0.11	0	0	0	0.02
heteroclitus		SE	0	0.05	0	0	0	
		gdw/m2	0	0.02	0	0	0	0.004
(mummichog)		SE	0	0.009	0	0	0	
	Hightide Edge	inds/m2	0.76	0.34	1.14	0.34	0.23	0.56
		SE	0.29	0.1	0.35	0.1	0.06	
		gdw/m2	0.218	0.341	2.151	0.448	0.151	0.662
(continued)		SE	0.124	0.135	0.685	0.131	0.042	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(F. heteroclitus)	Hightide Fringe	inds/m2	ns	2.74	2.4	1.37	0.91	1.86
		SE	ns	0.55	0.59	0.29	0.24	
		gdw/m2	ns	0.437	0.739	0.475	0.363	0.504
		SE	ns	0.094	0.224	0.088	0.112	
	Hightide Interior	inds/m2	1.71	2.51	3.09	1.83	1	2.03
		SE	0.58	0.53	0.26	0.31	0.07	
		gdw/m2	0.175	0.128	0.396	1.31	0.318	0.465
		SE	0.056	0.031	0.086	0.284	0.058	
	Lowtide SAV	inds/m2	ns	0.95	3.14	0	0.11	1.05
		SE	ns	0.29	0.74	0	0.05	
		gdw/m2	ns	0.112	0.189	0	0.087	0.097
		SE	ns	0.039	0.088	0	0.039	
	Lowtide Deep	inds/m2	2.17	0.34	0.11	0.46	0	0.62
		SE	0.7	0.06	0.05	0.2	0	
		gdw/m2	0.016	0.033	0.053	0.503	0	0.121
		SE	0.005	0.006	0.024	0.225	0	
	Lowtide Shallow	inds/m2	1.26	3.09	0.34	0.34	3.31	1.67
		SE	0.33	0.78	0.15	0.15	1.17	
		gdw/m2	0.015	0.067	0.002	0.182	0.829	0.219
		SE	0.003	0.015	0.001	0.081	0.3	
	Mean of all	inds/m2	1.18	1.68	1.278	0.543	0.695	0.976
	sampled habitats	gdw/m2	0.0848	0.1897	0.4413	0.3648	0.2185	0.259
Fundulus	Hightide Interior	inds/m2	0	0	0	0	0.14	0.03
luciae		SE	0	0	0	0	0.07	
		gdw/m2	0	0	0	0	0.015	0.003
(spotfin		SE	0	0	0	0	0.007	
killifish)	Mean of all	inds/m2	0	0	0	0	0.018	0.004
	sampled habitats	gdw/m2	0	0	0	0	0.0019	0.0004
Fundulus	Hightide Edge	inds/m2	0	0	0.57	0	0.23	0.16
majalis		SE	0	0	0.26	0	0.1	
		gdw/m2	0	0	0.289	0	0.414	0.141
(striped		SE	0	0	0.129	0	0.185	
killifish)	Hightide Fringe	inds/m2	ns	0	0	0.23	0.23	0.11
		SE	ns	0	0	0.1	0.1	
		gdw/m2	ns	0	0	0.1	0.694	0.199
		SE	ns	0	0	0.045	0.311	
	Hightide Interior	inds/m2	0.29	0	0.46	0.91	0.71	0.47
		SE	0.14	0	0.2	0.35	0.27	
		gdw/m2	0.294	0	0.137	0.395	0.261	0.217
		SE	0.147	0	0.061	0.155	0.086	
	Lowtide Deep	inds/m2	0	0	0	0.11	0.14	0.05
		SE	0	0	0	0.05	0.07	
		gdw/m2	0	0	0	0.075	0.06	0.027
		SE	0	0	0	0.034	0.03	
	Lowtide Shallow	inds/m2	0	0	0.57	1.14	1.83	0.71
		SE	0	0	0.2	0.45	0.76	
		gdw/m2	0	0	0.062	0.211	0.419	0.138
(continued)		SE	0	0	0.017	0.091	0.174	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(F. majalis)	Mean of all	inds/m2	0.058	0	0.2	0.299	0.393	0.188
	sampled habitats	gdw/m2	0.0588	0	0.061	0.0976	0.231	0.0903
Gobiesox	Hightide SAV	inds/m2	ns	ns	0	0.23	0.11	0.11
strumosus		SE	ns	ns	0	0.06	0.05	
		gdw/m2	ns	ns	0	0.02	0.004	0.008
(skilletfish)		SE	ns	ns	0	0.007	0.002	
	Hightide Edge	inds/m2	0	0	0.11	0	0.11	0.05
		SE	0	0	0.05	0	0.05	
		gdw/m2	0	0	0.051	0	0.032	0.016
		SE	0	0	0.023	0	0.014	
	Lowtide SAV	inds/m2	ns	0	0	0.14	0.34	0.12
		SE	ns	0	0	0.07	0.1	
		gdw/m2	ns	0	0	0.032	0.098	0.033
		SE	ns	0	0	0.016	0.03	
	Lowtide Deep	inds/m2	0	0	0	0.11	0.14	0.05
		SE	0	0	0	0.05	0.07	
		gdw/m2	0	0	0	0.066	0.035	0.02
		SE	0	0	0	0.029	0.017	
	Lowtide Shallow	inds/m2	0	0	0	0.23	0	0.05
		SE	0	0	0	0.06	0	
		gdw/m2	0	0	0	0.038	0	0.008
		SE	0	0	0	0.011	0	
	Mean of all	inds/m2	0	0	0.014	0.089	0.088	0.048
	sampled habitats	gdw/m2	0	0	0.0064	0.0195	0.0211	0.0106
Gobiosoma	Hightide SAV	inds/m2	ns	ns	10	4.23	4.57	6.27
bosc		SE	ns	ns	0.61	0.45	0.37	
		gdw/m2	ns	ns	0.403	0.236	0.412	0.35
(naked goby)		SE	ns	ns	0.087	0.023	0.033	
	Hightide Unveg.	inds/m2	0	0	0	0.34	0.11	0.09
		SE	0	0	0	0.1	0.05	
		gdw/m2	0	0	0	0.014	0.025	0.008
		SE	0	0	0	0.004	0.011	
	Hightide Edge	inds/m2	0	0	0.11	0.11	0.11	0.07
		SE	0	0	0.05	0.05	0.05	
		gdw/m2	0	0	0.005	0.008	0.019	0.006
		SE	0	0	0.002	0.003	0.008	
	Lowtide SAV	inds/m2	ns	0	1.86	4.43	2.29	2.14
		SE	ns	0	0.61	0.27	0.28	
		gdw/m2	ns	0	0.124	0.288	0.279	0.173
		SE	ns	0	0.051	0.026	0.027	
	Lowtide Deep	inds/m2	0	0	0.11	0.91	0.57	0.32
		SE	0	0	0.05	0.13	0.12	
		gdw/m2	0	0	0.001	0.076	0.088	0.033
(continued)		SE	0	0	0	0.024	0.015	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(G. bosc)	Lowtide Shallow	inds/m2	0	0	0.34	0	0	0.07
		SE	0	0	0.1	0	0	
		gdw/m2	0	0	0.008	0	0	0.002
		SE	0	0	0.002	0	0	
	Mean of all	inds/m2	0	0	1.553	1.253	0.956	1.12
	sampled habitats	gdw/m2	0	0	0.0676	0.0778	0.1029	0.0715
Hippolyte spp	Hightide SAV	inds/m2	ns	ns	1.43	1.26	13.94	5.54
		SE	ns	ns	0.2	0.31	1.68	
(a small shrimp)		gdw/m2	ns	ns	0.005	0.005	0.05	0.02
		SE	ns	ns	0.001	0.001	0.006	
	Lowtide SAV	inds/m2	ns	0	2.86	2.71	14.86	5.11
		SE	ns	0	1.43	0.89	1.54	
		gdw/m2	ns	0	0.01	0.01	0.053	0.018
		SE	ns	0	0.005	0.003	0.006	
	Lowtide Shallow	inds/m2	0	0	0	0	0.91	0.18
		SE	0	0	0	0	0.41	
		gdw/m2	0	0	0	0	0.003	0.001
		SE	0	0	0	0	0.001	
	Mean of all	inds/m2	0	0	0.536	0.496	3.714	1.354
	sampled habitats	gdw/m2	0	0	0.0019	0.0019	0.0133	0.0049
Hypsoblennius	Hightide SAV	inds/m2	ns	ns	0	0.11	0	0.04
hentzi		SE	ns	ns	0	0.05	0	
		gdw/m2	ns	ns	0	0.019	0	0.006
(feather blenny)		SE	ns	ns	0	0.008	0	
	Lowtide Deep	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
		gdw/m2	0	0	0	0.001	0	0
		SE	0	0	0	0	0	
	Mean of all	inds/m2	0	0	0	0.028	0	0.008
	sampled habitats	gdw/m2	0	0	0	0.0025	0	75
Leiostomus	Hightide Unveg.	inds/m2	0.38	0	0	0.57	0	0.19
xanthurus		SE	0.11	0	0	0.2	0	
		gdw/m2	0.162	0	0	0.012	0	0.035
(spot)		SE	0.051	0	0	0.004	0	
	Hightide Edge	inds/m2	0	0	0	0.23	0	0.05
		SE	0	0	0	0.06	0	
		gdw/m2	0	0	0	0.016	0	0.003
		SE	0	0	0	0.005	0	
	Lowtide SAV	inds/m2	ns	0	0	0	0.11	0.03
		SE	ns	0	0	0	0.05	
		gdw/m2	ns	0	0	0	0.015	0.004
		SE	ns	0	0	0	0.007	
	Mean of all	inds/m2	0.076	0	0	0.1	0.014	0.034
	sampled habitats	gdw/m2	0.0324	0	0	0.0035	0.0019	0.0053
Lucania	Hightide SAV	inds/m2	ns	ns	0	0.11	0	0.04
parva		SE	ns	ns	0	0.05	0	
		gdw/m2	ns	ns	0	0.012	0	0.004
(continued)		SE	ns	ns	0	0.005	0	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(L. parva)	Hightide Unveg.	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
(rainwater		gdw/m2	0	0	0	0.011	0	0.002
killifish)		SE	0	0	0	0.005	0	
	Hightide Edge	inds/m2	0	0	2.63	1.14	0.57	0.87
		SE	0	0	0.94	0.29	0.2	
		gdw/m2	0	0	0.34	0.172	0.063	0.115
		SE	0	0	0.116	0.053	0.021	
	Hightide Fringe	inds/m2	ns	0.11	0	0.34	0.34	0.2
		SE	ns	0.05	0	0.15	0.1	
		gdw/m2	ns	0.098	0	0.05	0.048	0.049
		SE	ns	0.044	0	0.023	0.016	
	Hightide Interior	inds/m2	0	0	0.11	0.91	0.29	0.26
		SE	0	0	0.05	0.24	0.14	
		gdw/m2	0	0	0.017	0.107	0.033	0.031
		SE	0	0	0.008	0.028	0.016	
	Lowtide SAV	inds/m2	ns	4	14.71	0	2.17	5.22
		SE	ns	1.37	1.47	0	0.52	
		gdw/m2	ns	0.245	0.466	0	0.271	0.246
		SE	ns	0.087	0.062	0	0.072	
	Lowtide Deep	inds/m2	0	0	0	0.11	0.14	0.05
		SE	0	0	0	0.05	0.07	
		gdw/m2	0	0	0	0.013	0.009	0.005
		SE	0	0	0	0.006	0.005	
	Lowtide Shallow	inds/m2	0	0	0.11	0	0	0.02
		SE	0	0	0.05	0	0	
		gdw/m2	0	0	0.002	0	0	0
		SE	0	0	0.001	0	0	
	Mean of all	inds/m2	0	0.685	2.195	0.34	0.439	0.835
	sampled habitats	gdw/m2	0	0.0572	0.1031	0.0456	0.053	0.0565
Menidia	Hightide Unveg.	inds/m2	0	0.11	0.69	0	0	0.16
menidia		SE	0	0.05	0.15	0	0	
		gdw/m2	0	0.029	0.307	0	0	0.067
(Atlantic		SE	0	0.013	0.078	0	0	
silverside)	Hightide Edge	inds/m2	0.19	0.46	1.49	0	0	0.43
		SE	0.11	0.15	0.31	0	0	
		gdw/m2	0.06	0.065	0.362	0	0	0.097
		SE	0.035	0.023	0.096	0	0	
	Hightide Fringe	inds/m2	ns	0	0	0.8	0	0.2
		SE	ns	0	0	0.36	0	
		gdw/m2	ns	0	0	0.219	0	0.055
		SE	ns	0	0	0.098	0	
	Hightide Interior	inds/m2	0.14	0	0.11	0	0	0.05
		SE	0.07	0	0.05	0	0	
		gdw/m2	0.014	0	0.02	0	0	0.007
(continued)		SE	0.007	0	0.009	0	0	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(M. menidia)	Lowtide SAV	inds/m2	ns	0.19	0	0	0	0.05
		SE	ns	0.11	0	0	0	
		gdw/m2	ns	0.027	0	0	0	0.007
		SE	ns	0.016	0	0	0	
	Mean of all	inds/m2	0.066	0.127	0.286	0.1	0	0.111
	sampled habitats	gdw/m2	0.0148	0.0202	0.0861	0.0274	0	0.0291
Microgobius	Hightide Unveg.	inds/m2	0	0	0	0.23	0	0.05
thalassinus		SE	0	0	0	0.1	0	
		gdw/m2	0	0	0	0.015	0	0.003
(green goby)		SE	0	0	0	0.007	0	
	Lowtide SAV	inds/m2	ns	0	0	0.14	0	0.04
		SE	ns	0	0	0.07	0	
		gdw/m2	ns	0	0	0.016	0	0.004
		SE	ns	0	0	0.008	0	
	Mean of all	inds/m2	0	0	0	0.046	0	0.011
	sampled habitats	gdw/m2	0	0	0	0.0039	0	875
Mugil	Hightide Unveg.	inds/m2	0	0.34	0	0	0	0.07
cephalus		SE	0	0.15	0	0	0	
		gdw/m2	0	0.757	0	0	0	0.151
(striped mullet)		SE	0	0.338	0	0	0	
	Lowtide Shallow	inds/m2	0	0	0.11	0	0	0.02
		SE	0	0	0.05	0	0	
		gdw/m2	0	0	0.003	0	0	0.001
		SE	0	0	0.002	0	0	
	Mean of all	inds/m2	0	0.057	0.014	0	0	0.011
	sampled habitats	gdw/m2	0	0.1262	375	0	0	0.019
Opsanus	Hightide SAV	inds/m2	ns	ns	0.29	0	0	0.1
tau		SE	ns	ns	0.2	0	0	
		gdw/m2	ns	ns	0.072	0	0	0.024
(oyster toadfish)		SE	ns	ns	0.051	0	0	
	Lowtide SAV	inds/m2	ns	0.19	0.43	0	0	0.15
		SE	ns	0.11	0.21	0	0	
		gdw/m2	ns	0.006	0.082	0	0	0.022
		SE	ns	0.003	0.041	0	0	
	Mean of all	inds/m2	0	0.032	0.09	0	0	0.031
	sampled habitats	gdw/m2	0	0.001	0.0193	0	0	0.0058
Palaemonetes	Hightide SAV	inds/m2	ns	ns	0	0.75	9.57	3.44
intermedius		SE	ns	ns	0	0.28	2.71	
		gdw/m2	ns	ns	0	0.01	0.149	0.053
(grass shrimp)		SE	ns	ns	0	0.003	0.046	
	Lowtide SAV	inds/m2	ns	0	4.86	2.38	3.95	2.8
		SE	ns	0	2.43	1.19	0.67	
		gdw/m2	ns	0	0.136	0.024	0.088	0.062
		SE	ns	0	0.068	0.012	0.02	
	Lowtide Shallow	inds/m2	0	0	0	0	0.11	0.02
		SE	0	0	0	0	0.05	
		gdw/m2	0	0	0	0	0.003	0.001
(continued)		SE	0	0	0	0	0.001	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(P. intermedius)	Mean of all	inds/m2	0	0	0.608	0.391	1.704	0.783
	sampled habitats	gdw/m2	0	0	0.017	0.0043	0.03	0.0145
Palaemonetes	Hightide SAV	inds/m2	ns	ns	2.57	5.71	17.47	8.58
pugio		SE	ns	ns	0.61	1.49	2.5	
		gdw/m2	ns	ns	0.018	0.094	0.393	0.169
(grass shrimp)		SE	ns	ns	0.004	0.026	0.07	
	Hightide Unveg.	inds/m2	0	0	0	1.49	1.14	0.53
		SE	0	0	0	0.66	0.51	
		gdw/m2	0	0	0	0.008	0.011	0.004
		SE	0	0	0	0.004	0.005	
	Hightide Edge	inds/m2	0.76	13.37	5.6	32.91	8.8	12.29
		SE	0.22	3.33	1.39	8.87	1.48	
		gdw/m2	0.052	1.087	0.285	0.847	0.213	0.497
		SE	0.016	0.342	0.059	0.233	0.032	
	Hightide Fringe	inds/m2	ns	18.97	7.89	1.26	5.83	8.49
		SE	ns	6.59	1.92	0.34	0.6	
		gdw/m2	ns	0.914	0.261	0.015	0.168	0.34
		SE	ns	0.326	0.063	0.004	0.023	
	Hightide Interior	inds/m2	0.14	3.43	2.06	5.6	20.71	6.39
		SE	0.07	0.6	0.5	1.15	3.77	
		gdw/m2	0.016	0.11	0.056	0.145	0.469	0.159
		SE	0.008	0.017	0.017	0.034	0.086	
	Lowtide SAV	inds/m2	ns	7.05	43.57	1.9	8.21	15.18
		SE	ns	3.28	7.31	0.18	1.84	
		gdw/m2	ns	0.267	0.849	0.013	0.134	0.316
		SE	ns	0.125	0.129	0.002	0.041	
	Lowtide Deep	inds/m2	1.14	0.11	0.34	0.46	32.29	6.87
		SE	0.39	0.05	0.1	0.15	15.67	
		gdw/m2	0.107	0.003	0.006	0.004	1.893	0.403
		SE	0.042	0.001	0.003	0.001	0.941	
	Lowtide Shallow	inds/m2	0.46	8.8	37.49	41.76	82.56	34.21
		SE	0.15	1.88	10.84	16.29	23.15	
		gdw/m2	0.006	0.141	0.467	1.144	2.576	0.867
		SE	0.002	0.025	0.127	0.476	0.766	
	Mean of all	inds/m2	0.5	8.622	12.44	11.386	22.126	11.568
	sampled habitats	gdw/m2	0.0362	0.4203	0.2428	0.2838	0.7321	0.3444
Palaemonetes	Hightide SAV	inds/m2	ns	ns	10.29	22.29	60.99	31.19
vulgaris		SE	ns	ns	1.21	3.97	4.36	
		gdw/m2	ns	ns	0.275	0.404	1.325	0.668
(grass shrimp)		SE	ns	ns	0.075	0.077	0.087	
	Hightide Edge	inds/m2	0	0	0	0.11	0.11	0.05
		SE	0	0	0	0.05	0.05	
		gdw/m2	0	0	0	0.003	0.004	0.001
		SE	0	0	0	0.001	0.002	
	Hightide Fringe	inds/m2	ns	0	0	0	0.91	0.23
		SE	ns	0	0	0	0.41	
		gdw/m2	ns	0	0	0	0.069	0.017
(continued)		SE	ns	0	0	0	0.031	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(P. vulgaris)	Hightide Interior	inds/m2	0	0	0	0.23	0	0.05
		SE	0	0	0	0.1	0	
		gdw/m2	0	0	0	0.001	0	0
		SE	0	0	0	0.001	0	
	Lowtide SAV	inds/m2	ns	0	33.71	26.06	40.97	25.19
		SE	ns	0	16.86	8.84	6.93	
		gdw/m2	ns	0	2.067	0.357	0.928	0.838
		SE	ns	0	1.033	0.128	0.171	
	Lowtide Deep	inds/m2	0	0	0	3.89	0	0.78
		SE	0	0	0	1.67	0	
		gdw/m2	0	0	0	0.022	0	0.004
		SE	0	0	0	0.007	0	
	Lowtide Shallow	inds/m2	0	0	0	0.11	0.11	0.05
		SE	0	0	0	0.05	0.05	
		gdw/m2	0	0	0	0.008	0.002	0.002
		SE	0	0	0	0.004	0.001	
	Mean of all	inds/m2	0	0	5.5	6.586	12.886	7.193
	sampled habitats	gdw/m2	0	0	0.2928	0.0994	0.291	0.1913
Palaemonetes	Hightide SAV	inds/m2	ns	ns	0.57	3.36	8.59	4.18
spp		SE	ns	ns	0.4	0.88	1.46	
		gdw/m2	ns	ns	0.001	0.058	0.164	0.074
(unidentifiable		SE	ns	ns	0.001	0.017	0.027	
grass shrimp)	Hightide Edge	inds/m2	0	0	0.11	9.14	0.91	2.03
		SE	0	0	0.05	4.09	0.35	
		gdw/m2	0	0	0.006	0.171	0.032	0.042
		SE	0	0	0.003	0.076	0.014	
	Hightide Fringe	inds/m2	ns	0	0.23	0	0	0.06
		SE	ns	0	0.1	0	0	
		gdw/m2	ns	0	0.005	0	0	0.001
		SE	ns	0	0.002	0	0	
	Hightide Interior	inds/m2	0	0	0	0.11	0.57	0.14
		SE	0	0	0	0.05	0.2	
		gdw/m2	0	0	0	0.006	0.013	0.004
		SE	0	0	0	0.003	0.004	
	Lowtide SAV	inds/m2	ns	0	1.29	5.37	24.16	7.7
		SE	ns	0	0.64	1.65	9.61	
		gdw/m2	ns	0	0.006	0.083	0.519	0.152
		SE	ns	0	0.003	0.034	0.215	
	Lowtide Deep	inds/m2	0	0	0.11	0.69	0.57	0.27
		SE	0	0	0.05	0.31	0.29	
		gdw/m2	0	0	0.008	0.002	0.01	0.004
		SE	0	0	0.004	0.001	0.005	
	Lowtide Shallow	inds/m2	0	0	0.23	0.87	8.98	2.02
		SE	0	0	0.1	0.24	2.91	
		gdw/m2	0	0	0.003	0.021	0.172	0.039
		SE	0	0	0.001	0.007	0.054	
	Mean of all	inds/m2	0	0	0.318	2.443	5.473	2.05
	sampled habitats	gdw/m2	0	0	0.0036	0.0426	0.1138	0.0395

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
Penaeus spp	Hightide SAV	inds/m2	ns	ns	0.86	0.46	1.26	0.86
(P. aztecus		SE	ns	ns	0.61	0.15	0.22	
and		gdw/m2	ns	ns	0.056	0.076	0.281	0.137
P. duorarum)		SE	ns	ns	0.039	0.021	0.042	
	Hightide Unveg.	inds/m2	0	0	0	0.34	0	0.07
(brown shrimp,		SE	0	0	0	0.1	0	
pink shrimp)		gdw/m2	0	0	0	0.069	0	0.014
		SE	0	0	0	0.022	0	
	Lowtide SAV	inds/m2	ns	0	0	0.86	0.23	0.27
		SE	ns	0	0	0.25	0.06	
		gdw/m2	ns	0	0	0.104	0.115	0.055
		SE	ns	0	0	0.037	0.045	
	Lowtide Deep	inds/m2	0	0	0.11	0.23	0	0.07
		SE	0	0	0.05	0.1	0	
		gdw/m2	0	0	0.005	0.088	0	0.019
		SE	0	0	0.002	0.039	0	
	Mean of all	inds/m2	0	0	0.121	0.236	0.186	0.159
	sampled habitats	gdw/m2	0	0	0.0076	0.0421	0.0495	0.0281
Sciaenops	Lowtide SAV	inds/m2	ns	0	0	0	0.11	0.03
ocellatus		SE	ns	0	0	0	0.05	
		gdw/m2	ns	0	0	0	0.012	0.003
(red drum)		SE	ns	0	0	0	0.005	
	Lowtide Deep	inds/m2	0	0	0	0.11	0.14	0.05
		SE	0	0	0	0.05	0.07	
		gdw/m2	0	0	0	0	0.028	0.006
		SE	0	0	0	0	0.014	
	Mean of all	inds/m2	0	0	0	0.014	0.031	0.01
	sampled habitats	gdw/m2	0	0	0	0	0.005	0.0011
Symphurus	Hightide SAV	inds/m2	ns	ns	0.86	0.23	0.46	0.51
plagiusa		SE	ns	ns	0.2	0.06	0.1	
		gdw/m2	ns	ns	0.074	0.024	0.176	0.091
(blackcheek		SE	ns	ns	0.016	0.01	0.038	
tonguefish)	Hightide Unveg.	inds/m2	0	0	0.23	0.69	0	0.18
		SE	0	0	0.06	0.05	0	
		gdw/m2	0	0	0.011	0.157	0	0.034
		SE	0	0	0.003	0.019	0	
	Hightide Edge	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
		gdw/m2	0	0	0	0.037	0	0.007
		SE	0	0	0	0.017	0	
	Lowtide Deep	inds/m2	0.23	0	0.23	0.46	0.57	0.3
		SE	0.1	0	0.1	0.1	0.16	
		gdw/m2	0.14	0	0.005	0.128	0.213	0.097
		SE	0.063	0	0.002	0.032	0.062	
	Lowtide SAV	inds/m2	ns	0	0	0.29	0.23	0.13
		SE	ns	0	0	0.08	0.1	
		gdw/m2	ns	0	0	0.021	0.061	0.021
(continued)		SE	ns	0	0	0.01	0.027	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(S. plagiusa)	Mean of all	inds/m2	0.046	0	0.165	0.223	0.158	0.143
	sampled habitats	gdw/m2	0.028	0	0.0113	0.0459	0.0563	0.0313
Syngnathus	Hightide SAV	inds/m2	ns	ns	0.29	0.34	0.11	0.25
floridae		SE	ns	ns	0.2	0.1	0.05	
		gdw/m2	ns	ns	0.011	0.06	0.019	0.03
(dusky pipefish)		SE	ns	ns	0.008	0.025	0.009	
	Lowtide SAV	inds/m2	ns	0	0.14	0.14	0.34	0.16
		SE	ns	0	0.07	0.07	0.15	
		gdw/m2	ns	0	0.021	0.012	0.02	0.013
		SE	ns	0	0.01	0.006	0.009	
	Lowtide Deep	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
		gdw/m2	0	0	0	0.027	0	0.005
		SE	0	0	0	0.012	0	
	Mean of all	inds/m2	0	0	0.054	0.074	0.056	0.054
	sampled habitats	gdw/m2	0	0	0.004	0.0124	0.0049	0.006
Syngnathus	Hightide SAV	inds/m2	ns	ns	1.43	0.69	0.57	0.9
fuscus		SE	ns	ns	0.61	0.1	0.14	
		gdw/m2	ns	ns	0.063	0.029	0.026	0.039
(northern		SE	ns	ns	0.026	0.003	0.005	
pipefish)	Hightide Unveg.	inds/m2	0	0	0	0.11	0	0.02
		SE	0	0	0	0.05	0	
		gdw/m2	0	0	0	0.004	0	0.001
		SE	0	0	0	0.002	0	
	Lowtide SAV	inds/m2	ns	0	0.14	0.57	0.46	0.29
		SE	ns	0	0.07	0.12	0.1	
		gdw/m2	ns	0	0.049	0.029	0.02	0.024
		SE	ns	0	0.024	0.005	0.005	
	Mean of all	inds/m2	0	0	0.196	0.171	0.129	0.151
	sampled habitats	gdw/m2	0	0	0.014	0.0078	0.0058	0.008
Crustaceans	Hightide SAV	inds/m2	ns	ns	24.29	49.71	133.43	69.14
		SE	ns	ns	1.82	6.6	6.72	
(all natant		gdw/m2	ns	ns	2.161	8.577	3.408	4.715
crustaceans)		SE	ns	ns	1.108	3.135	0.179	
	Hightide Unveg.	inds/m2	0.76	0.11	0.34	8.34	4.34	2.78
		SE	0.29	0.05	0.06	1.27	1.06	
		gdw/m2	4.111	0.22	2.284	0.506	1.185	1.661
		SE	1.648	0.098	0.484	0.09	0.411	
	Hightide Edge	inds/m2	1.14	13.6	6.4	53.6	15.2	17.99
		SE	0.19	3.43	1.26	12	1.9	
		gdw/m2	1.593	4.763	2.263	8.214	5.163	4.399
		SE	0.842	1.982	0.709	2.505	1.58	
	Hightide Fringe	inds/m2	ns	19.09	8.23	3.09	9.26	9.91
		SE	ns	6.58	1.95	0.61	0.63	
		gdw/m2	ns	1.134	1.688	1.334	3.312	1.867
(continued)		SE	ns	0.321	0.694	0.275	0.805	

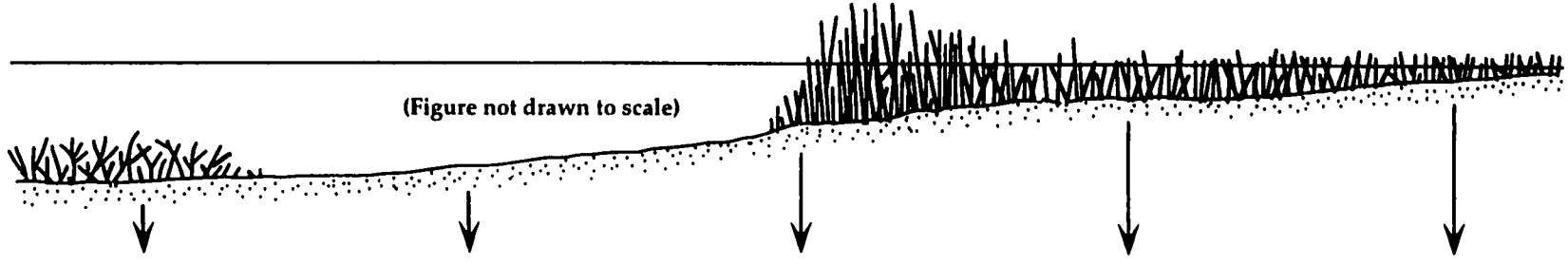
Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(Crustaceans)	Hightide Interior	inds/m2	0.14	3.54	2.06	6.97	22.71	7.09
		SE	0.07	0.61	0.5	1.13	4.23	
		gdw/m2	0.016	0.251	0.056	3.425	1.019	0.954
		SE	0.008	0.067	0.017	1.449	0.232	
	Lowtide SAV	inds/m2	ns	7.43	90.14	52	109.06	64.66
		SE	ns	3.5	26.93	14.67	6.89	
		gdw/m2	ns	4.213	28.516	3.851	3.521	10.025
		SE	ns	2.402	9.092	1.111	0.609	
	Lowtide Deep	inds/m2	2.17	0.23	1.03	15.2	43.57	12.44
		SE	0.49	0.06	0.22	2.5	15.51	
		gdw/m2	1.086	0.183	1.52	5.435	3.447	2.334
		SE	0.325	0.08	0.415	0.514	1.013	
	Lowtide Shallow	inds/m2	0.8	9.03	38.4	48.46	97.6	38.86
		SE	0.13	1.89	10.82	16.94	27.32	
		gdw/m2	0.274	1.127	0.495	1.597	3.137	1.326
		SE	0.114	0.299	0.124	0.547	0.856	
	Mean of all	inds/m2	1.002	8.838	21.361	29.671	54.396	27.859
	sampled habitats	gdw/m2	1.416	1.9818	4.8729	4.1174	3.024	3.4101
Fishes	Hightide SAV	inds/m2	ns	ns	14	6.51	5.83	8.78
		SE	ns	ns	1.41	0.51	0.37	
		gdw/m2	ns	ns	0.781	2.471	0.637	1.297
		SE	ns	ns	0.042	0.569	0.036	
	Hightide Unveg.	inds/m2	0.38	0.57	0.91	2.06	0.11	0.81
		SE	0.11	0.14	0.17	0.29	0.05	
		gdw/m2	0.162	0.806	0.319	0.212	0.025	0.305
		SE	0.051	0.333	0.078	0.023	0.011	
	Hightide Edge	inds/m2	0.95	0.8	6.4	2.17	1.26	2.32
		SE	0.4	0.24	1.1	0.28	0.26	
		gdw/m2	0.278	0.405	3.708	1.085	0.679	1.231
		SE	0.159	0.157	0.568	0.21	0.165	
	Hightide Fringe	inds/m2	ns	3.09	2.4	2.74	1.49	2.43
		SE	ns	0.59	0.59	0.42	0.39	
		gdw/m2	ns	0.573	0.739	0.845	1.106	0.816
		SE	ns	0.107	0.224	0.105	0.423	
	Hightide Interior	inds/m2	2.29	2.51	3.89	3.66	2.14	2.9
		SE	0.48	0.53	0.36	0.59	0.29	
		gdw/m2	0.509	0.128	0.691	1.813	0.626	0.753
		SE	0.12	0.031	0.105	0.383	0.07	
	Lowtide Deep	inds/m2	2.4	0.34	0.69	2.51	1.71	1.53
		SE	0.67	0.06	0.2	0.33	0.2	
		gdw/m2	0.156	0.033	0.095	0.889	0.433	0.321
		SE	0.061	0.006	0.036	0.266	0.076	
	Lowtide Shallow	inds/m2	1.26	3.2	1.83	1.71	5.14	2.63
		SE	0.33	0.83	0.37	0.42	1.24	
		gdw/m2	0.015	0.07	0.078	0.43	1.248	0.368
(continued)		SE	0.003	0.016	0.018	0.105	0.31	

Species	Habitat	Data	June	July	Aug.	Sept.	Oct.	Mn Mo
(Fishes)	Lowtide SAV	inds/m2	ns	5.33	20.86	6	6.17	9.59
		SE	ns	1.44	1.73	0.47	0.66	
		gdw/m2	ns	0.39	1.047	0.626	0.864	0.732
		SE	ns	0.112	0.132	0.119	0.221	
	Mean of all	inds/m2	1.456	2.64	6.373	3.42	2.981	3.874
	sampled habitats	gdw/m2	0.224	0.4008	0.9323	1.0464	0.7023	0.7279
Total Nekton	Hightide SAV	inds/m2	ns	ns	38.29	56.23	139.26	77.92
		SE	ns	ns	3.23	6.66	7	
(all natant		gdw/m2	ns	ns	2.942	11.049	4.045	6.012
macrofauna)		SE	ns	ns	1.149	3.517	0.195	
	Hightide Unveg.	inds/m2	1.14	0.69	1.26	10.4	4.46	3.59
		SE	0.38	0.13	0.2	1.4	1.05	
		gdw/m2	4.273	1.026	2.602	0.718	1.21	1.966
		SE	1.668	0.321	0.536	0.109	0.408	
	Hightide Edge	inds/m2	2.1	14.4	12.8	55.77	16.46	20.3
		SE	0.29	3.67	2.1	11.98	2.04	
		gdw/m2	1.871	5.168	5.971	9.299	5.842	5.63
		SE	1.001	2.139	0.851	2.693	1.518	
	Hightide Fringe	inds/m2	ns	22.17	10.63	5.83	10.74	12.34
		SE	ns	6.65	1.78	0.94	1	
		gdw/m2	ns	1.707	2.427	2.179	4.418	2.683
		SE	ns	0.377	0.678	0.334	1.009	
	Hightide Interior	inds/m2	2.43	6.06	5.94	10.63	24.86	9.98
		SE	0.46	0.87	0.67	1.17	4.5	
		gdw/m2	0.525	0.379	0.746	5.238	1.645	1.707
		SE	0.127	0.087	0.108	1.74	0.247	
	Lowtide SAV	inds/m2	ns	12.76	111	58	115.23	74.25
		SE	ns	4.94	28.58	14.75	7.44	
		gdw/m2	ns	4.603	29.563	4.477	4.384	10.757
		SE	ns	2.513	9.204	1.098	0.698	
	Lowtide Deep	inds/m2	4.57	0.57	1.71	17.71	45.29	13.97
		SE	0.76	0.08	0.37	2.63	15.69	
		gdw/m2	1.242	0.216	1.615	6.324	3.879	2.655
		SE	0.307	0.077	0.405	0.375	1.079	
	Lowtide Shallow	inds/m2	2.06	12.23	40.23	50.17	102.74	41.49
		SE	0.31	1.42	11.13	17	27.98	
		gdw/m2	0.289	1.197	0.573	2.027	4.385	1.694
		SE	0.114	0.291	0.129	0.613	1.021	
	Mean of all	inds/m2	2.46	11.48	27.733	33.093	57.38	31.73
	sampled habitats	gdw/m2	1.64	2.3827	5.8049	5.1639	3.726	4.138

Figure 3. Community Composition of Habitats by Month

Figures are provided to quantitatively describe community composition per square meter for all species captured in each high tide and low tide habitat sampled each month. Habitats are as shown in Figure 5, Chapter 1 and as described in the text. Species are arranged in each habitat column in order of decreasing biomass. Totals for crustaceans, fishes, and for all nekton are also shown in each habitat column. The number of samples used to compile each estimate is given (N). Standard errors (SE) are provided for abundance estimates; biomass estimates are given as percents of the total biomass in the habitat that month. The total biomass sampled is also shown for each habitat in the Total Nekton category; this equals 100% of the individual species biomasses.

Community Composition (High Tide) June 1995



HIGHTIDE SAV (N = 0)

Species	inds/m2±SE	%B
(not sampled)		

HIGHTIDE UNVEG. (N = 3)

Species	inds/m2±SE	%B
C. sapidus	0.8 ± 0.3	96%
L. xanthurus	0.4 ± 0.1	4%
Crustaceans	0.8 ± 0.3	96%
Fishes	0.4 ± 0.1	4%
Total Nekton	1.1 ± 0.4	*4.27 g*

MARSH EDGE (N = 3)

Species	inds/m2±SE	%B
C. sapidus	0.4 ± 0.1	82%
F. heteroclitus	0.8 ± 0.3	12%
M. menidia	0.2 ± 0.1	3%
P. pugio	0.8 ± 0.2	3%
Crustaceans	1.1 ± 0.2	85%
Fishes	1.0 ± 0.4	15%
Total Nekton	2.1 ± 0.3	*1.87 g*

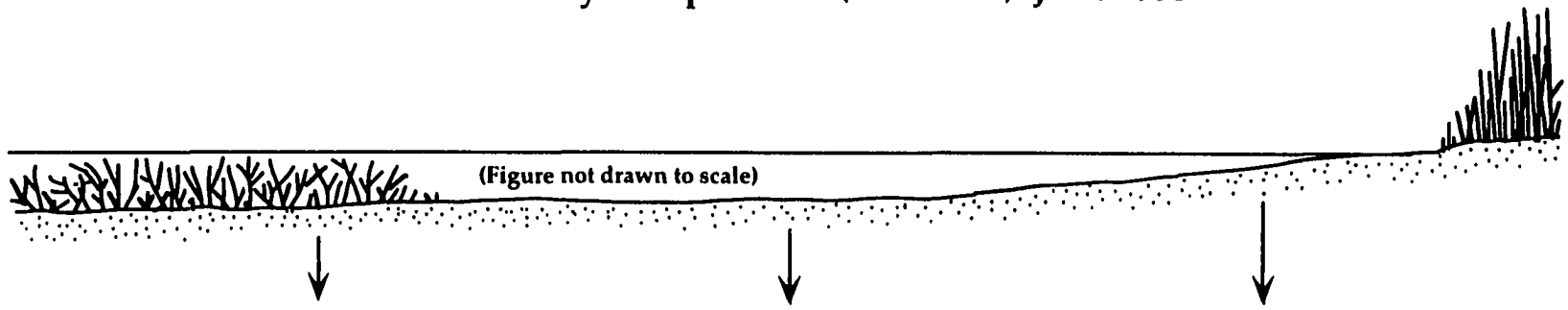
MARSH FRINGE (N = 0)

Species	inds/m2±SE	%B
(not sampled)		

MARSH INTERIOR (N = 4)

Species	inds/m2±SE	%B
F. majalis	0.3 ± 0.1	56%
F. heteroclitus	1.7 ± 0.6	33%
C. variegatus	0.1 ± 0.1	5%
P. pugio	0.1 ± 0.1	3%
M. menidia	0.1 ± 0.1	3%
Crustaceans	0.1 ± 0.1	3%
Fishes	2.3 ± 0.5	97%
Total Nekton	2.4 ± 0.5	*0.52 g*

Community Composition (Low Tide) June 1995



LOWTIDE SAV (N = 0)

Species	inds/m2±SE	%B
(not sampled)		

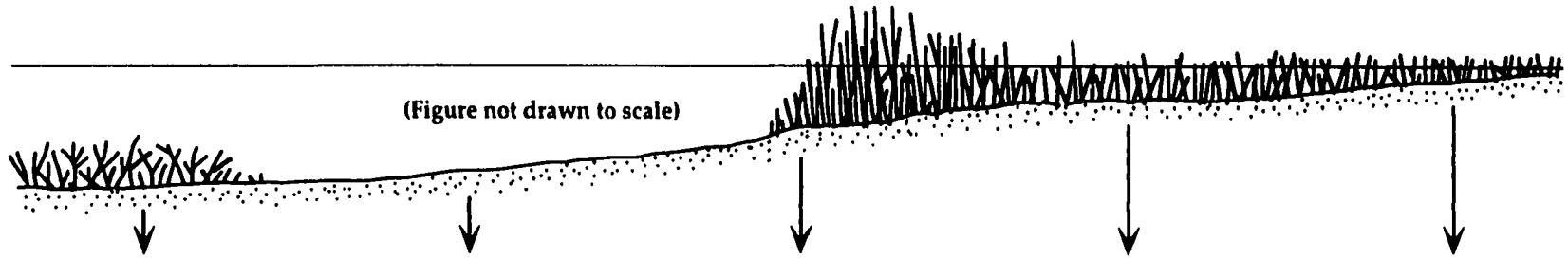
LOWTIDE DEEP (N = 5)

Species	inds/m2±SE	%B
C. sapidus	1.0 ± 0.2	79%
S. plagiusa	0.2 ± 0.1	11%
P. pugio	1.1 ± 0.4	9%
F. heteroclitus	2.2 ± 0.7	1%
Crustaceans	2.2 ± 0.5	87%
Fishes	2.4 ± 0.7	13%
Total Nekton	4.6 ± 0.8	*1.24 g*

LOWTIDE SHALLOW (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.3 ± 0.1	93%
F. heteroclitus	1.3 ± 0.3	5%
P. pugio	0.5 ± 0.1	2%
Crustaceans	0.8 ± 0.1	95%
Fishes	1.3 ± 0.3	5%
Total Nekton	2.1 ± 0.3	*0.29 g*

Community Composition (High Tide) July 1995



HIGHTIDE SAV (N = 0)

Species	inds/m2±SE	%B
(not sampled)		

HIGHTIDE UNVEG. (N = 5)

Species	inds/m2±SE	%B
M. cephalus	0.3 ± 0.2	74%
C. sapidus	0.1 ± 0.1	21%
M. menidia	0.1 ± 0.1	3%
F. heteroclitus	0.1 ± 0.1	2%
Crustaceans	0.1 ± 0.1	21%
Fishes	0.6 ± 0.1	79%
Total Nekton	0.7 ± 0.1	*1.03 g*

MARSH EDGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.2 ± 0.1	71%
P. pugio	13.4 ± 3.3	21%
F. heteroclitus	0.3 ± 0.1	7%
M. menidia	0.5 ± 0.1	1%
Crustaceans	13.6 ± 3.4	92%
Fishes	0.8 ± 0.2	8%
Total Nekton	14.4 ± 3.7	*5.17 g*

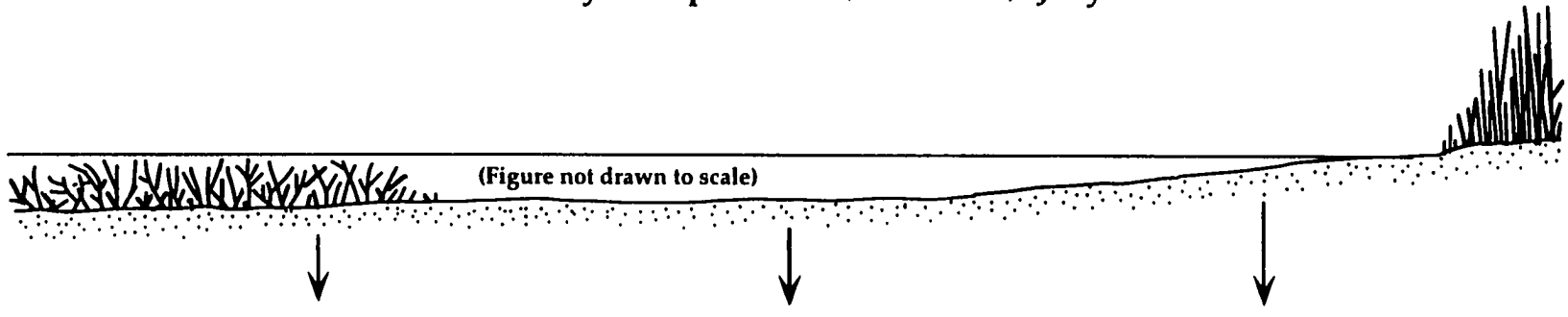
MARSH FRINGE (N = 5)

Species	inds/m2±SE	%B
P. pugio	19.0 ± 6.6	54%
F. heteroclitus	2.7 ± 0.6	26%
C. sapidus	0.1 ± 0.1	13%
L. parva	0.1 ± 0.1	6%
C. variegatus	0.2 ± 0.1	2%
Crustaceans	19.1 ± 6.6	66%
Fishes	3.1 ± 0.6	34%
Total Nekton	22.2 ± 6.7	*1.71 g*

MARSH INTERIOR (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.1 ± 0.1	37%
F. heteroclitus	2.5 ± 0.5	34%
P. pugio	3.4 ± 0.6	29%
Crustaceans	3.5 ± 0.6	66%
Fishes	2.5 ± 0.5	34%
Total Nekton	6.1 ± 0.9	*0.38 g*

Community Composition (Low Tide) July 1995



LOWTIDE SAV (N = 3)

Species	inds/m2±SE	%B
C. sapidus	0.4 ± 0.2	86%
P. pugio	7.0 ± 3.3	6%
L. parva	4.0 ± 1.4	5%
F. heteroclitus	1.0 ± 0.3	2%
M. menidia	0.2 ± 0.1	1%
O. tau	0.2 ± 0.1	<1%
Crustaceans	7.4 ± 3.5	92%
Fishes	5.3 ± 1.4	8%
Total Nekton	12.8 ± 4.9	*4.60 g*

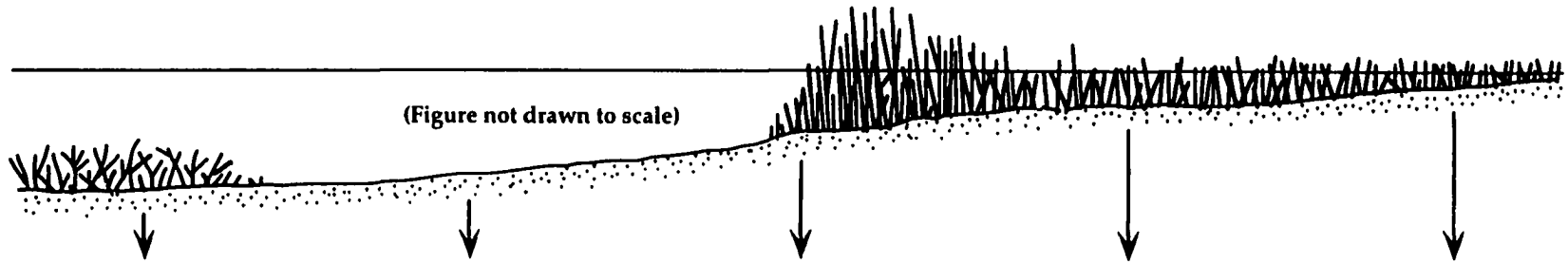
LOWTIDE DEEP (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.1 ± 0.1	83%
F. heteroclitus	0.3 ± 0.1	15%
P. pugio	0.1 ± 0.1	1%
Crustaceans	0.2 ± 0.1	85%
Fishes	0.3 ± 0.1	15%
Total Nekton	0.6 ± 0.1	*0.22 g*

LOWTIDE SHALLOW (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.2 ± 0.1	82%
P. pugio	8.8 ± 1.9	12%
F. heteroclitus	3.1 ± 0.8	6%
C. variegatus	0.1 ± 0.1	<1%
Crustaceans	9.0 ± 1.9	94%
Fishes	3.2 ± 0.8	6%
Total Nekton	12.2 ± 1.4	*1.20 g*

Community Composition (High Tide) August 1995



HIGHTIDE SAV (N = 2)

Species	inds/m2±SE	%B
C. sapidus	8.6 ± 1.2	61%
G. bosc	10.0 ± 0.6	14%
P. vulgaris	10.3 ± 1.2	9%
B. chrysoura	0.3 ± 0.2	5%
S. plagiusa	0.9 ± 0.2	3%
O. tau	0.3 ± 0.2	2%
S. fuscus	1.4 ± 0.6	2%
Penaeus spp	0.9 ± 0.6	2%
P. pugio	2.6 ± 0.6	1%
S. floridae	0.3 ± 0.2	<1%
A. mitchelli	0.9 ± 0.6	<1%
Hippolyte spp	1.4 ± 0.2	<1%
Palaemnts. spp	0.6 ± 0.4	<1%
Crustaceans	24.3 ± 1.8	73%
Fishes	14.0 ± 1.4	27%
Total Nekton	38.3 ± 3.2	*2.94 g*

HIGHTIDE UNVEG. (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.3 ± 0.1	88%
M. menidia	0.7 ± 0.1	12%
S. plagiusa	0.2 ± 0.1	<1%
Crustaceans	0.3 ± 0.1	88%
Fishes	0.9 ± 0.2	12%
Total Nekton	1.3 ± 0.2	*2.60 g*

MARSH EDGE (N = 5)

Species	inds/m2±SE	%B
F. heteroclitus	1.1 ± 0.4	36%
C. sapidus	0.7 ± 0.2	33%
M. menidia	1.5 ± 0.3	6%
L. parva	2.6 ± 0.9	6%
B. chrysoura	0.2 ± 0.1	6%
F. majalis	0.6 ± 0.3	5%
P. pugio	5.6 ± 1.4	5%
C. nebulosus	0.1 ± 0.1	3%
G. strumosus	0.1 ± 0.1	1%
Palaemnts. spp	0.1 ± 0.1	<1%
G. bosc	0.1 ± 0.1	<1%
Crustaceans	6.4 ± 1.3	38%
Fishes	6.4 ± 1.1	62%
Total Nekton	12.8 ± 2.1	*5.97 g*

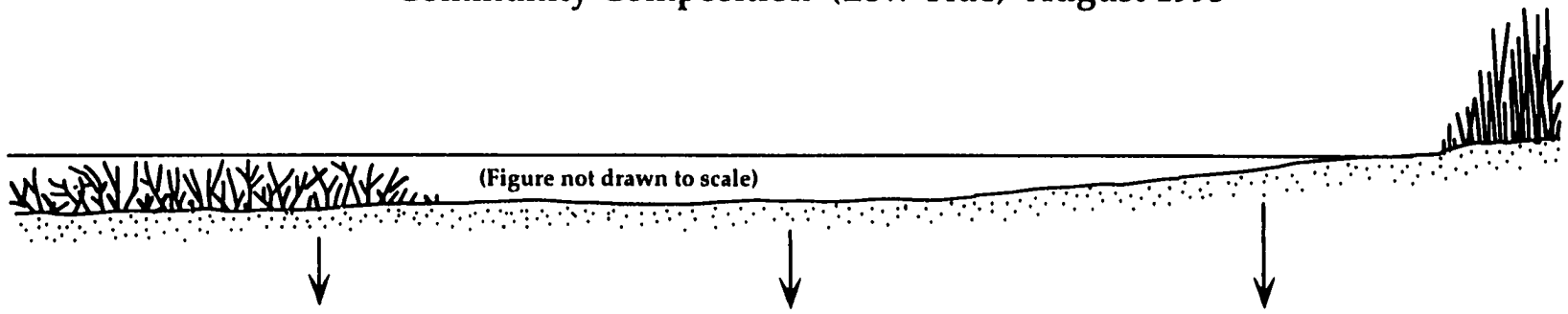
MARSH FRINGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.1 ± 0.1	59%
F. heteroclitus	2.4 ± 0.6	30%
P. pugio	7.9 ± 1.9	11%
Palaemnts. spp	0.2 ± 0.1	<1%
Crustaceans	8.2 ± 2.0	70%
Fishes	2.4 ± 0.6	30%
Total Nekton	10.6 ± 1.8	*2.43 g*

MARSH INTERIOR (N = 5)

Species	inds/m2±SE	%B
F. heteroclitus	3.1 ± 0.3	53%
F. majalis	0.5 ± 0.2	18%
B. chrysoura	0.1 ± 0.1	16%
P. pugio	2.1 ± 0.5	7%
M. menidia	0.1 ± 0.1	3%
L. parva	0.1 ± 0.1	2%
Crustaceans	2.1 ± 0.5	7%
Fishes	3.9 ± 0.4	93%
Total Nekton	5.9 ± 0.7	*0.75 g*

Community Composition (Low Tide) August 1995



LOWTIDE SAV (N = 4)

Species	inds/m2±SE	%B
C. sapidus	3.9 ± 0.6	86%
P. vulgaris	33.7 ± 16.9	7%
P. pugio	43.6 ± 7.3	3%
L. parva	14.7 ± 1.5	2%
F. heteroclitus	3.1 ± 0.7	1%
P. intermedius	4.9 ± 2.4	<1%
G. bosc	1.9 ± 0.6	<1%
O. tau	0.4 ± 0.2	<1%
C. variegatus	0.1 ± 0.1	<1%
S. fuscus	0.1 ± 0.1	<1%
C. nebulosus	0.1 ± 0.1	<1%
S. floridae	0.1 ± 0.1	<1%
A. quadracus	0.1 ± 0.1	<1%
Hippolyte spp	2.9 ± 1.4	<1%
Palaemonetes spp	1.3 ± 0.6	<1%
Crustaceans	90.1 ± 26.9	96%
Fishes	20.9 ± 1.7	4%
Total Nekton	111.0 ± 28.6	*29.56 g*

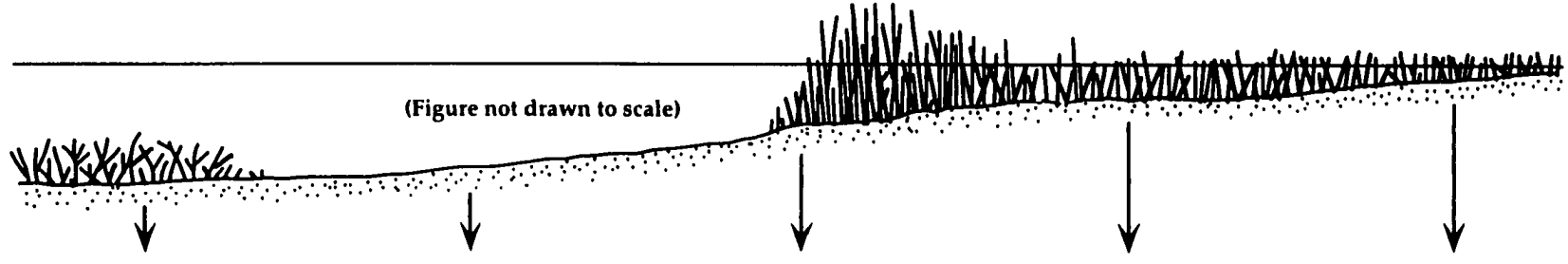
LOWTIDE DEEP (N = 5)

Species	inds/m2±SE	%B
C. sapidus	0.5 ± 0.1	93%
F. heteroclitus	0.1 ± 0.1	3%
C. faber	0.2 ± 0.1	2%
Palaemonetes spp	0.1 ± 0.1	<1%
P. pugio	0.3 ± 0.1	<1%
Penaeus spp	0.1 ± 0.1	<1%
S. plagiusa	0.2 ± 0.1	<1%
G. bosc	0.1 ± 0.1	<1%
Crustaceans	1.0 ± 0.2	94%
Fishes	0.7 ± 0.2	6%
Total Nekton	1.7 ± 0.4	*1.61 g*

LOWTIDE SHALLOW (N = 5)

Species	inds/m2±SE	%B
P. pugio	37.5 ± 10.8	82%
F. majalis	0.6 ± 0.2	11%
C. sapidus	0.7 ± 0.3	4%
G. bosc	0.3 ± 0.1	1%
M. cephalus	0.1 ± 0.1	1%
Palaemonetes spp	0.2 ± 0.1	<1%
F. heteroclitus	0.3 ± 0.2	<1%
L. parva	0.1 ± 0.1	<1%
C. variegatus	0.3 ± 0.2	<1%
Crustaceans	38.4 ± 10.8	86%
Fishes	1.8 ± 0.4	14%
Total Nekton	40.2 ± 11.1	*0.57 g*

Community Composition (High Tide) September 1995



HIGHTIDE SAV (N = 5)

Species	inds/m2±SE	%B
C. sapidus	15.5 ± 1.0	72%
A. rostrata	0.5 ± 0.1	18%
P. vulgaris	22.3 ± 4.0	4%
G. bosc	4.2 ± 0.5	2%
P. pugio	5.7 ± 1.5	1%
Penaeus spp	0.5 ± 0.1	1%
S. floridae	0.3 ± 0.1	1%
Palaemnts. spp	3.4 ± 0.9	1%
C. nebulosus	0.1 ± 0.1	<1%
S. fuscus	0.7 ± 0.1	<1%
S. plagiusa	0.2 ± 0.1	<1%
G. strumosus	0.2 ± 0.1	<1%
H. hentzi	0.1 ± 0.1	<1%
L. parva	0.1 ± 0.1	<1%
P. intermedius	0.8 ± 0.3	<1%
C. septemspin.	0.3 ± 0.1	<1%
Hippolyte spp	1.3 ± 0.3	<1%
Crustaceans	49.7 ± 6.6	78%
Fishes	6.5 ± 0.5	22%
Total Nekton	56.2 ± 6.7	*11.05 g*

HIGHTIDE UNVEG. (N = 5)

Species	inds/m2±SE	%B
C. sapidus	6.5 ± 0.7	60%
S. plagiusa	0.7 ± 0.1	22%
Penaeus spp	0.3 ± 0.1	10%
M. thalassinus	0.2 ± 0.1	2%
G. bosc	0.3 ± 0.1	2%
L. xanthurus	0.6 ± 0.2	2%
L. parva	0.1 ± 0.1	2%
P. pugio	1.5 ± 0.7	1%
S. fuscus	0.1 ± 0.1	1%
Crustaceans	8.3 ± 1.3	70%
Fishes	2.1 ± 0.3	30%
Total Nekton	10.4 ± 1.4	*0.72 g*

MARSH EDGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	11.4 ± 1.3	77%
P. pugio	32.9 ± 8.9	9%
F. heteroclitus	0.3 ± 0.1	5%
C. nebulosus	0.1 ± 0.1	3%
L. parva	1.1 ± 0.3	2%
Palaemnts. spp	9.1 ± 4.1	2%
C. bosquianus	0.1 ± 0.1	1%
S. plagiusa	0.1 ± 0.1	<1%
L. xanthurus	0.2 ± 0.1	<1%
G. bosc	0.1 ± 0.1	<1%
P. vulgaris	0.1 ± 0.1	<1%
Crustaceans	53.6 ± 12.0	88%
Fishes	2.2 ± 0.3	12%
Total Nekton	55.8 ± 12.0	*9.30 g*

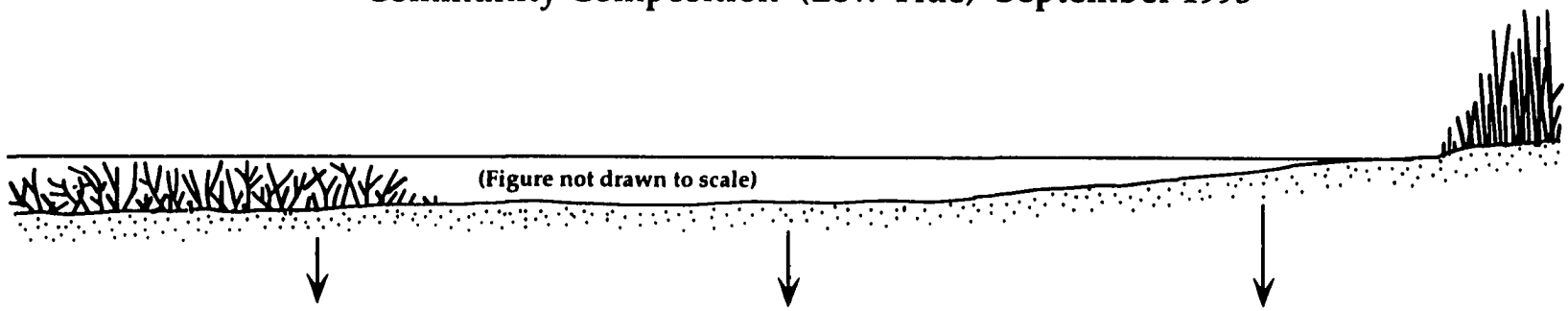
MARSH FRINGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	1.8 ± 0.3	61%
F. heteroclitus	1.4 ± 0.3	22%
M. menidia	0.8 ± 0.4	10%
F. majalis	0.2 ± 0.1	5%
L. parva	0.3 ± 0.2	2%
P. pugio	1.3 ± 0.3	1%
Crustaceans	3.1 ± 0.6	61%
Fishes	2.7 ± 0.4	39%
Total Nekton	5.8 ± 0.9	*2.18 g*

MARSH INTERIOR (N = 5)

Species	inds/m2±SE	%B
C. sapidus	1.0 ± 0.3	63%
F. heteroclitus	1.8 ± 0.3	25%
F. majalis	0.9 ± 0.3	8%
P. pugio	5.6 ± 1.2	3%
L. parva	0.9 ± 0.2	2%
Palaemnts. spp	0.1 ± 0.1	<1%
P. vulgaris	0.2 ± 0.1	<1%
Crustaceans	7.0 ± 1.1	65%
Fishes	3.7 ± 0.6	35%
Total Nekton	10.6 ± 1.2	*5.24 g*

Community Composition (Low Tide) September 1995



LOWTIDE SAV (N = 4)

Species	inds/m2±SE	%B
C. sapidus	12.6 ± 2.0	73%
P. vulgaris	26.1 ± 8.8	8%
G. bosc	4.4 ± 0.3	6%
B. chrysoura	0.1 ± 0.1	5%
Penaeus spp	0.9 ± 0.2	2%
Palaemonetes spp	5.4 ± 1.6	2%
G. strumosus	0.1 ± 0.1	1%
S. fuscus	0.6 ± 0.1	1%
P. intermedius	2.4 ± 1.2	1%
S. plagiusa	0.3 ± 0.1	<1%
M. thalassinus	0.1 ± 0.1	<1%
C. nebulosus	0.1 ± 0.1	<1%
P. pugio	1.9 ± 0.2	<1%
S. floridae	0.1 ± 0.1	<1%
Hippolyte spp	2.7 ± 0.9	<1%
C. septemspinosa	0.1 ± 0.1	<1%
Crustaceans	52.0 ± 14.7	86%
Fishes	6.0 ± 0.5	14%
Total Nekton	58.0 ± 14.7	*4.48 g*

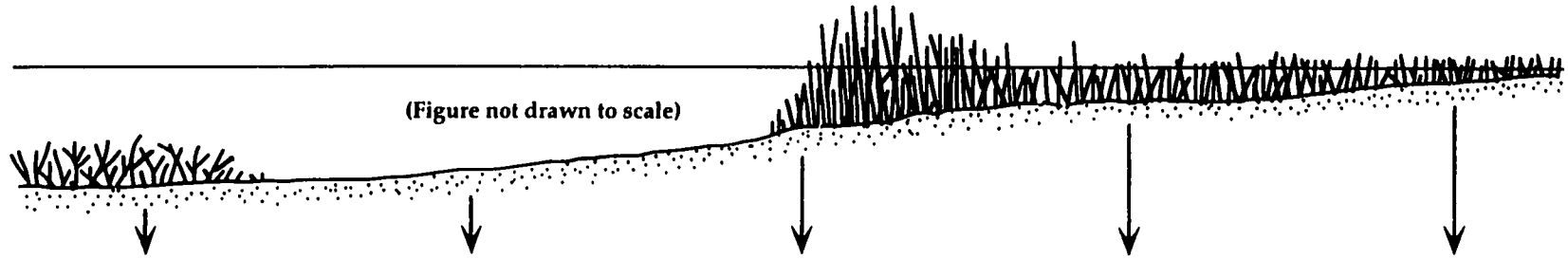
LOWTIDE DEEP (N = 5)

Species	inds/m2±SE	%B
C. sapidus	9.7 ± 1.0	84%
F. heteroclitus	0.5 ± 0.2	8%
S. plagiusa	0.5 ± 0.1	2%
Penaeus spp	0.2 ± 0.1	1%
G. bosc	0.9 ± 0.1	1%
F. majalis	0.1 ± 0.1	1%
G. strumosus	0.1 ± 0.1	1%
S. floridae	0.1 ± 0.1	<1%
P. vulgaris	3.9 ± 1.7	<1%
L. parva	0.1 ± 0.1	<1%
P. pugio	0.5 ± 0.1	<1%
C. septemspinosa	0.2 ± 0.1	<1%
Palaemonetes spp	0.7 ± 0.3	<1%
H. hentzi	0.1 ± 0.1	<1%
S. ocellatus	0.1 ± 0.1	<1%
Crustaceans	15.2 ± 2.5	86%
Fishes	2.5 ± 0.3	14%
Total Nekton	17.7 ± 2.6	*6.32 g*

LOWTIDE SHALLOW (N = 5)

Species	inds/m2±SE	%B
P. pugio	41.8 ± 16.3	56%
C. sapidus	5.7 ± 0.5	21%
F. majalis	1.1 ± 0.4	10%
F. heteroclitus	0.3 ± 0.2	9%
G. strumosus	0.2 ± 0.1	2%
Palaemonetes spp	0.9 ± 0.2	1%
P. vulgaris	0.1 ± 0.1	<1%
Crustaceans	48.5 ± 16.9	79%
Fishes	1.7 ± 0.4	21%
Total Nekton	50.2 ± 17.0	*2.03 g*

Community Composition (High Tide) October 1995



HIGHTIDE SAV (N = 5)

Species	inds/m2±SE	%B
P. vulgaris	61.0 ± 4.4	33%
C. sapidus	21.1 ± 2.7	25%
G. bosc	4.6 ± 0.4	10%
P. pugio	17.5 ± 2.5	10%
Penaeus spp	1.3 ± 0.2	7%
S. plagiusa	0.5 ± 0.1	4%
Palaemnts. spp	8.6 ± 1.5	4%
P. intermedius	9.6 ± 2.7	4%
Hippolyte spp	13.9 ± 1.7	1%
S. fuscus	0.6 ± 0.1	1%
S. floridae	0.1 ± 0.1	<1%
C. septemspin.	0.5 ± 0.1	<1%
G. strumosus	0.1 ± 0.1	<1%
Crustaceans	133.4 ± 6.7	84%
Fishes	5.8 ± 0.4	16%
Total Nekton	139.3 ± 7.0	*4.05 g*

HIGHTIDE UNVEG. (N = 5)

Species	inds/m2±SE	%B
C. sapidus	3.2 ± 0.6	97%
G. bosc	0.1 ± 0.1	2%
P. pugio	1.1 ± 0.5	1%
Crustaceans	4.3 ± 1.1	98%
Fishes	0.1 ± 0.1	2%
Total Nekton	4.5 ± 1.0	*1.21 g*

MARSH EDGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	5.4 ± 0.6	84%
F. majalis	0.2 ± 0.1	7%
P. pugio	8.8 ± 1.5	4%
F. heteroclitus	0.2 ± 0.1	3%
L. parva	0.6 ± 0.2	1%
G. strumosus	0.1 ± 0.1	1%
Palaemnts. spp	0.9 ± 0.3	1%
G. bosc	0.1 ± 0.1	<1%
P. vulgaris	0.1 ± 0.1	<1%
Crustaceans	15.2 ± 1.9	88%
Fishes	1.3 ± 0.3	12%
Total Nekton	16.5 ± 2.0	*5.84 g*

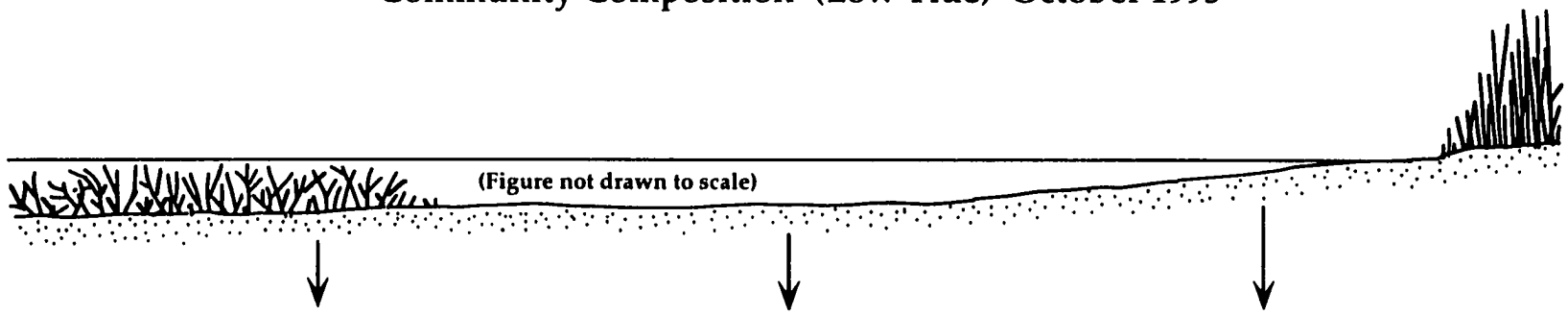
MARSH FRINGE (N = 5)

Species	inds/m2±SE	%B
C. sapidus	2.5 ± 0.4	70%
F. majalis	0.2 ± 0.1	16%
F. heteroclitus	0.9 ± 0.2	8%
P. pugio	5.8 ± 0.6	4%
P. vulgaris	0.9 ± 0.4	2%
L. parva	0.3 ± 0.1	1%
Crustaceans	9.3 ± 0.6	75%
Fishes	1.5 ± 0.4	25%
Total Nekton	10.7 ± 1.0	*4.42 g*

MARSH INTERIOR (N = 4)

Species	inds/m2±SE	%B
C. sapidus	1.4 ± 0.4	33%
P. pugio	20.7 ± 3.8	29%
F. heteroclitus	1.0 ± 0.1	19%
F. majalis	0.7 ± 0.3	16%
L. parva	0.3 ± 0.1	2%
F. luciae	0.1 ± 0.1	1%
Palaemnts. spp	0.6 ± 0.2	1%
Crustaceans	22.7 ± 4.2	62%
Fishes	2.1 ± 0.3	38%
Total Nekton	24.9 ± 4.5	*1.64 g*

Community Composition (Low Tide) October 1995



LOWTIDE SAV (N = 5)

Species	inds/m2±SE	%B
C. sapidus	16.1 ± 1.4	38%
P. vulgaris	41.0 ± 6.9	21%
Palaemonetes spp	24.2 ± 9.6	12%
G. bosc	2.3 ± 0.3	6%
L. parva	2.2 ± 0.5	6%
P. pugio	8.2 ± 1.8	3%
Penaeus spp	0.2 ± 0.1	3%
G. strumosus	0.3 ± 0.1	2%
P. intermedius	4.0 ± 0.7	2%
F. heteroclitus	0.1 ± 0.1	2%
S. plagiusa	0.2 ± 0.1	1%
Hippolyte spp	14.9 ± 1.5	1%
C. septemspinosa	0.6 ± 0.1	1%
S. fuscus	0.5 ± 0.1	<1%
S. floridae	0.3 ± 0.2	<1%
L. xanthurus	0.1 ± 0.1	<1%
S. ocellatus	0.1 ± 0.1	<1%
Crustaceans	109.1 ± 6.9	80%
Fishes	6.2 ± 0.7	20%
Total Nekton	115.2 ± 7.4	*4.38 g*

LOWTIDE DEEP (N = 4)

Species	inds/m2±SE	%B
P. pugio	32.3 ± 15.7	49%
C. sapidus	7.3 ± 0.5	39%
S. plagiusa	0.6 ± 0.2	5%
G. bosc	0.6 ± 0.1	2%
F. majalis	0.1 ± 0.1	2%
C. septemspinosa	3.4 ± 1.7	1%
G. strumosus	0.1 ± 0.1	1%
S. ocellatus	0.1 ± 0.1	1%
Palaemonetes spp	0.6 ± 0.3	<1%
L. parva	0.1 ± 0.1	<1%
Crustaceans	43.6 ± 15.5	89%
Fishes	1.7 ± 0.2	11%
Total Nekton	45.3 ± 15.7	*3.88 g*

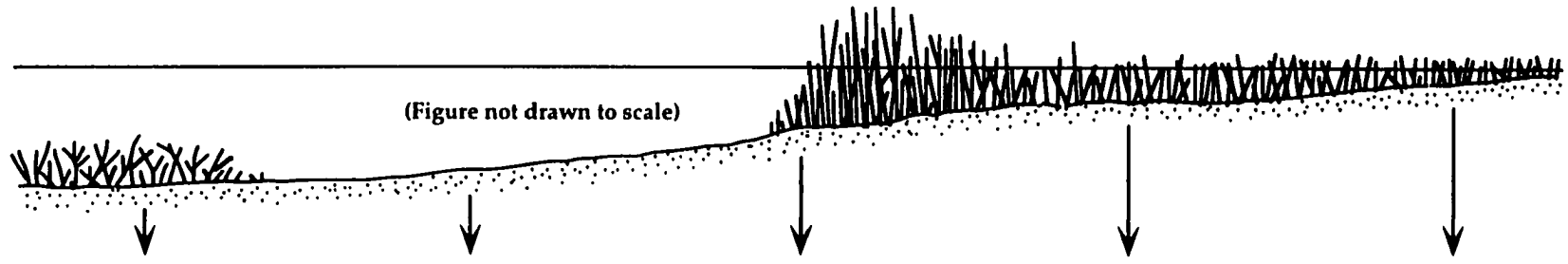
LOWTIDE SHALLOW (N = 5)

Species	inds/m2±SE	%B
P. pugio	82.6 ± 23.2	59%
F. heteroclitus	3.3 ± 1.2	19%
F. majalis	1.8 ± 0.8	10%
C. sapidus	4.9 ± 1.0	9%
Palaemonetes spp	9.0 ± 2.9	4%
Hippolyte spp	0.9 ± 0.4	<1%
P. intermedius	0.1 ± 0.1	<1%
P. vulgaris	0.1 ± 0.1	<1%
Crustaceans	97.6 ± 27.3	72%
Fishes	5.1 ± 1.2	28%
Total Nekton	102.7 ± 28.0	*4.39 g*

Figure 4. Community Composition of Habitats, June - October

Community composition per square meter is shown for all species captured in each high tide and low tide habitat. Species are arranged in each habitat column in order of decreasing biomass. The number of samples used to compile each estimate is given (N). Standard errors (SE) are provided for the abundance estimates. Biomass estimates are percents of the total biomass in that habitat. The total biomass for each habitat is listed in the Total Nekton category and equals 100% of the individual species biomasses. Numbers given are means from all samples collected in that habitat, not averages of the monthly mean data provided in Figure 3.

Community Composition (High Tide) June - October 1995



HIGHTIDE SAV (N = 12)

20 Species	inds/m2±SE	%B
C. sapidus	16.71 ± 0.83	59%
A. rostrata	0.19 ± 0.04	13%
P. vulgaris	36.42 ± 2.37	11%
G. bosc	5.33 ± 0.24	5%
P. pugio	10.09 ± 0.92	3%
Penaeus spp	0.86 ± 0.08	2%
S. plagiusa	0.43 ± 0.04	1%
Palaemnts. spp	5.08 ± 0.51	1%
P. intermedius	4.30 ± 0.79	1%
S. floridae	0.24 ± 0.03	1%
S. fuscus	0.76 ± 0.06	<1%
B. chrysoura	0.05 ± 0.01	<1%
Hippolyte spp	6.57 ± 0.69	<1%
O. tau	0.05 ± 0.01	<1%
C. nebulosus	0.05 ± 0.01	<1%
G. strumosus	0.14 ± 0.02	<1%
C. septemspin.	0.33 ± 0.04	<1%
H. hentzi	0.05 ± 0.01	<1%
L. parva	0.05 ± 0.01	<1%
A. mitchelli	0.14 ± 0.04	<1%
Crustaceans	80.36 ± 4.63	78%
Fishes	7.48 ± 0.31	22%
Total Nekton	87.83 ± 4.53	6.78 g

HIGHTIDE UNVEG. (N = 23)

13 Species	inds/m2±SE	%B
C. sapidus	2.31 ± 0.14	81%
M. cephalus	0.07 ± 0.02	9%
M. menidia	0.17 ± 0.02	4%
S. plagiusa	0.20 ± 0.01	2%
L. xanthurus	0.17 ± 0.02	1%
Penaeus spp	0.07 ± 0.01	1%
G. bosc	0.10 ± 0.01	<1%
F. heteroclitus	0.02 ± 0.01	<1%
P. pugio	0.57 ± 0.08	<1%
M. thalassinus	0.05 ± 0.01	<1%
L. parva	0.02 ± 0.01	<1%
S. fuscus	0.02 ± 0.01	<1%
Crustaceans	2.96 ± 0.21	82%
Fishes	0.84 ± 0.05	18%
Total Nekton	3.80 ± 0.23	1.76 g

MARSH EDGE (N = 23)

14 Species	inds/m2±SE	%B
C. sapidus	3.90 ± 0.24	68%
F. heteroclitus	0.55 ± 0.04	12%
P. pugio	13.29 ± 1.02	9%
F. majalis	0.17 ± 0.03	3%
L. parva	0.94 ± 0.10	2%
C. nebulosus	0.05 ± 0.01	2%
M. menidia	0.45 ± 0.04	2%
B. chrysoura	0.05 ± 0.01	1%
Palaemnts. spp	2.21 ± 0.41	1%
C. bosquianus	0.02 ± 0.01	<1%
G. strumosus	0.05 ± 0.01	<1%
S. plagiusa	0.02 ± 0.01	<1%
G. bosc	0.07 ± 0.01	<1%
L. xanthurus	0.05 ± 0.01	<1%
P. vulgaris	0.05 ± 0.01	<1%
Crustaceans	19.45 ± 1.44	78%
Fishes	2.43 ± 0.15	22%
Total Nekton	21.89 ± 1.45	5.96 g

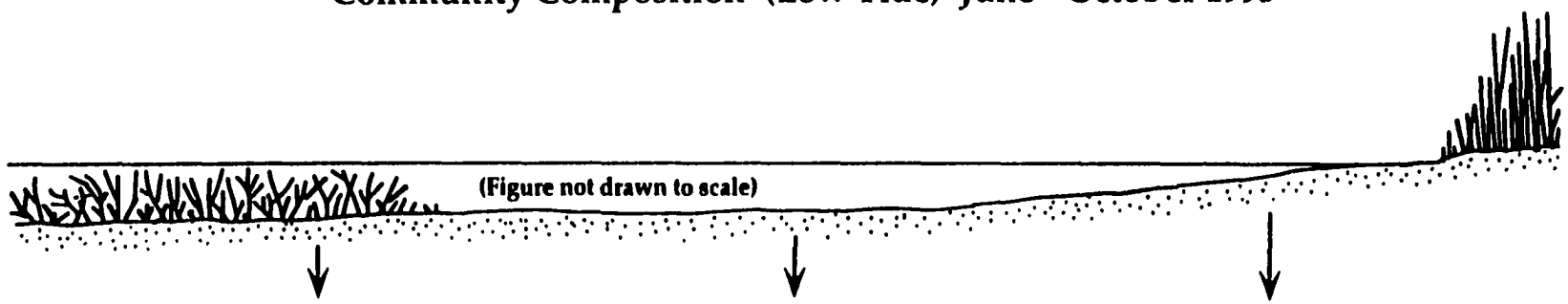
MARSH FRINGE (N = 20)

8 Species	inds/m2±SE	%B
C. sapidus	1.14 ± 0.08	56%
F. heteroclitus	1.86 ± 0.11	19%
P. pugio	8.49 ± 0.86	13%
F. majalis	0.11 ± 0.02	7%
M. menidia	0.20 ± 0.04	2%
L. parva	0.20 ± 0.02	2%
P. vulgaris	0.23 ± 0.05	1%
C. variegatus	0.06 ± 0.01	<1%
Palaemnts. spp	0.06 ± 0.01	<1%
Crustaceans	9.91 ± 0.85	70%
Fishes	2.43 ± 0.12	30%
Total Nekton	12.34 ± 0.86	2.68 g

MARSH INTERIOR (N = 23)

10 Species	inds/m2±SE	%B
C. sapidus	0.50 ± 0.05	47%
F. heteroclitus	2.09 ± 0.08	28%
F. majalis	0.47 ± 0.04	12%
P. pugio	6.04 ± 0.41	9%
L. parva	0.27 ± 0.03	2%
B. chrysoura	0.02 ± 0.01	1%
M. menidia	0.05 ± 0.01	<1%
C. variegatus	0.02 ± 0.01	<1%
Palaemnts. spp	0.12 ± 0.02	<1%
F. luciae	0.02 ± 0.01	<1%
P. vulgaris	0.05 ± 0.01	<1%
Crustaceans	6.71 ± 0.45	56%
Fishes	2.96 ± 0.09	44%
Total Nekton	9.66 ± 0.46	1.76 g

Community Composition (Low Tide) June - October 1995



LOWTIDE SAV (N = 16)

24 Species	inds/m2±SE	%B
C. sapidus	9.21 ± 0.52	79%
P. vulgaris	27.75 ± 2.58	8%
P. pugio	15.25 ± 1.39	3%
L. parva	5.11 ± 0.42	2%
G. bosc	2.29 ± 0.13	2%
Palaemonetes spp	9.21 ± 1.70	2%
F. heteroclitus	1.00 ± 0.12	1%
P. intermedius	3.04 ± 0.34	1%
Penaeus spp	0.29 ± 0.04	1%
B. chrysoura	0.04 ± 0.01	0%
G. strumosus	0.14 ± 0.02	0%
S. fuscus	0.32 ± 0.03	0%
S. plagiusa	0.14 ± 0.02	0%
Hippolyte spp	6.04 ± 0.50	0%
O. tau	0.14 ± 0.03	0%
C. variegatus	0.04 ± 0.01	0%
S. floridae	0.18 ± 0.03	0%
C. nebulosus	0.07 ± 0.01	0%
C. septemspinosa	0.21 ± 0.03	0%
M. menidia	0.04 ± 0.01	0%
L. xanthurus	0.04 ± 0.01	0%
M. thalassinus	0.04 ± 0.01	0%
S. ocellatus	0.04 ± 0.01	0%
A. quadracus	0.04 ± 0.01	0%

LOWTIDE DEEP (N = 24)

16 Species	inds/m2±SE	%B
C. sapidus	3.57 ± 0.20	73%
P. pugio	5.81 ± 1.07	13%
F. heteroclitus	0.64 ± 0.07	5%
S. plagiusa	0.29 ± 0.02	4%
G. bosc	0.31 ± 0.02	1%
F. majalis	0.05 ± 0.01	1%
G. strumosus	0.05 ± 0.01	1%
Penaeus spp	0.07 ± 0.01	1%
C. septemspinosa	0.62 ± 0.12	0%
C. faber	0.05 ± 0.01	0%
S. floridae	0.02 ± 0.005	0%
S. ocellatus	0.05 ± 0.01	0%
P. vulgaris	0.81 ± 0.16	0%
L. parva	0.05 ± 0.01	0%
Palaemonetes spp	0.26 ± 0.03	0%
H. hentzi	0.02 ± 0.005	0%
Crustaceans	11.14 ± 1.17	88%
Fishes	1.52 ± 0.08	12%
Total Nekton	12.67 ± 1.19	2.60 g

LOWTIDE SHALLOW (N = 25)

12 Species	inds/m2±SE	%B
P. pugio	34.21 ± 2.75	51%
C. sapidus	2.38 ± 0.14	25%
F. heteroclitus	1.67 ± 0.13	13%
F. majalis	0.71 ± 0.08	8%
Palaemonetes spp	2.02 ± 0.28	2%
G. strumosus	0.05 ± 0.01	0%
P. vulgaris	0.05 ± 0.01	0%
G. bosc	0.07 ± 0.01	0%
C. variegatus	0.09 ± 0.01	0%
M. cephalus	0.02 ± 0.005	0%
Hippolyte spp	0.18 ± 0.04	0%
P. intermedius	0.02 ± 0.00	0%
L. parva	0.02 ± 0.005	0%
Crustaceans	38.86 ± 3.11	78%
Fishes	2.63 ± 0.14	22%
Total Nekton	41.49 ± 3.17	1.69 g

LOWTIDE SAV TOTALS

Species	inds/m2±SE	%B
Crustaceans	71.01 ± 4.34	93%
Fishes	9.64 ± 0.48	7%
Total Nekton	80.65 ± 4.60	10.74 g

Table 4. Tests for Statistical Differences among Habitats

This table shows the results of statistical testing for differences among habitats. All data are presented per sample, not per square meter; each sample consisted of 1.75 square meters. Only data from August through October are used in these comparisons, as all habitats were sampled during those months only. The non-parametric Kruskal-Wallace test, which evaluates median ranks, was used to determine if differences existed at the $p = 0.05$ level (as calculated by SAS, SAS Institute). If a significant difference did exist, then the Dunn test (Zar 1996) was used to create groupings to show where the differences existed. Groups with the same letter designation were not significantly different at the $p = 0.05$ level. Groups are always clustered from greatest values (A) to lowest values (C or D). Abundant species were tested on numbers of individuals per sample and are listed in alphabetical order; groups of species were tested on grams dry weight per sample and are listed at the end of the table. Other columns in the table include N, the sample minimum, the first quartile, the median, the third quartile, the maximum, the mean, and the standard error of the mean. Significant differences among habitats as determined by the Dunn test are summarized underneath each table.

Tests for Statistical Differences among Habitats
August - October 1995

A.

Callinectes sapidus (blue crab), inds/sample			Kruskal-Wallace statistic = 48.46, P = .0001							
Habitat	Dunn groupings		N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A		12	12.00	17.50	25.00	37.00	73.00	29.25	1.45
Hightide Unveg.	B	C	15	0.00	1.00	2.00	10.00	19.00	5.87	0.42
Hightide Edge	A B	C	15	0.00	1.50	9.00	14.50	33.00	10.20	0.69
Hightide Fringe		C	15	0.00	0.50	1.00	4.50	10.00	2.60	0.20
Hightide Interior		C	14	0.00	0.00	0.00	1.75	6.00	1.36	0.16
Lowtide SAV	A B		13	1.00	9.00	17.00	27.00	40.00	19.69	1.06
Lowtide Deep	A B	C	14	0.00	1.50	10.50	15.75	30.00	10.00	0.65
Lowtide Shallow	B	C	15	0.00	0.50	7.00	8.00	23.00	6.60	0.44
Significant differences:			HV > LS, HU, HF, HI							
			HV, LV > HF, HI							

B.

Fundulus heteroclitus (mummichog), inds/sample			Kruskal-Wallace stat. = 43.01, P = .0001							
Habitat	Dunn groupings		N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV		C	12	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hightide Unveg.		C	15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hightide Edge	A B	C	15	0.00	0.00	0.00	1.00	7.00	1.00	0.13
Hightide Fringe	A B		15	0.00	0.00	1.00	4.00	12.00	2.73	0.23
Hightide Interior	A		14	0.00	2.00	2.50	6.00	8.00	3.57	0.18
Lowtide SAV	B	C	13	0.00	0.00	0.00	1.00	12.00	1.77	0.28
Lowtide Deep	B	C	14	0.00	0.00	0.00	0.00	4.00	0.36	0.08
Lowtide Shallow	A B	C	15	0.00	0.00	0.00	2.00	24.00	2.33	0.41
Significant differences:			HI > LV, LD, HU, HV							
			HI, HF > HU, HV							

C.

Gobiosoma bosc (naked goby), inds/sample			Kruskal-Wallace statistic = 75.66, P = .0001							
Habitat	Dunn groupings		N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A		12	4.00	5.75	8.00	13.25	19.00	9.33	0.41
Hightide Unveg.		C	15	0.00	0.00	0.00	0.00	2.00	0.27	0.04
Hightide Edge		C	15	0.00	0.00	0.00	0.00	1.00	0.20	0.03
Hightide Fringe		C	15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hightide Interior		C	14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lowtide SAV	A B		13	0.00	2.00	4.00	8.00	9.00	4.92	0.26
Lowtide Deep	B	C	14	0.00	0.00	1.00	1.75	3.00	0.93	0.07
Lowtide Shallow		C	15	0.00	0.00	0.00	0.00	2.00	0.20	0.04
Significant differences:			HV > LD, HU, HE, LS, HF, HI							
			HV, LV > HU, HE, LS, HF, HI							

D.

Lucania parva (rainwater killifish), inds/sample							Kruskal-Wallace stat. = 23.59, P = .0013			
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	B	12	0.00	0.00	0.00	0.00	1.00	0.08	0.02
Hightide Unveg.	B	15	0.00	0.00	0.00	0.00	1.00	0.07	0.02
Hightide Edge	A B	15	0.00	0.00	0.00	3.50	19.00	2.53	0.33
Hightide Fringe	A B	15	0.00	0.00	0.00	0.00	3.00	0.40	0.06
Hightide Interior	A B	14	0.00	0.00	0.00	1.00	5.00	0.79	0.10
Lowtide SAV	A	13	0.00	0.00	3.00	15.00	39.00	9.38	0.99
Lowtide Deep	A B	14	0.00	0.00	0.00	0.00	1.00	0.14	0.03
Lowtide Shallow	B	15	0.00	0.00	0.00	0.00	1.00	0.07	0.02
Significant differences:			LV > HV, HU, LS						

E.

Palaemonetes pugio (grass shrimp), inds/sample							Kruskal-Wallace stat. = 33.96, P = .0001		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A B	12	0.00	4.50	13.00	22.36	62.00	17.65	1.60
Hightide Unveg.	C	15	0.00	0.00	0.00	0.00	13.00	1.53	0.27
Hightide Edge	A B	15	0.00	2.00	4.00	25.00	162.00	27.60	3.20
Hightide Fringe	A B C	15	0.00	2.00	6.00	11.00	42.00	8.73	0.72
Hightide Interior	A B	14	0.00	2.50	6.00	22.75	70.00	15.14	1.42
Lowtide SAV	A B	13	0.00	3.33	9.20	42.00	139.00	30.01	3.26
Lowtide Deep	B C	14	0.00	0.00	0.00	1.75	221.00	16.64	4.20
Lowtide Shallow	A	15	0.00	2.50	27.00	100.10	504.00	94.38	9.76
Significant differences:			LS > LD, HU						
			LS, LV, HV, HI, HE > HU						

F.

Palaemonetes vulgaris (grass shrimp), inds/samp.							Kruskal-Wallace stat. = 69.45, P = .0001		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A	12	14.00	19.75	48.25	100.20	156.00	63.73	4.14
Hightide Unveg.	B	15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hightide Edge	B	15	0.00	0.00	0.00	0.00	1.00	0.13	0.02
Hightide Fringe	B	15	0.00	0.00	0.00	0.00	8.00	0.53	0.14
Hightide Interior	B	14	0.00	0.00	0.00	0.00	2.00	0.14	0.04
Lowtide SAV	A	13	0.00	0.00	21.00	126.60	236.00	59.76	5.85
Lowtide Deep	B	14	0.00	0.00	0.00	0.00	33.00	2.43	0.63
Lowtide Shallow	B	15	0.00	0.00	0.00	0.00	1.00	0.13	0.02
Significant differences:			HV, LV > LD, HE, LS, HI, HF, HU						

G.

Crustaceans, gdw/sample							Kruskal-Wallace statistic = 25.98, P = .0005		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A	12	1.04	2.77	4.68	6.64	64.06	9.37	1.45
Hightide Unveg.	A B	15	0.00	0.06	0.58	3.38	10.18	2.32	0.22
Hightide Edge	A B	15	0.14	1.12	2.61	9.38	52.37	9.12	0.99
Hightide Fringe	A B	15	0.00	0.25	0.56	4.89	16.72	3.69	0.36
Hightide Interior	B	14	0.00	0.06	0.21	0.86	28.67	2.69	0.54
Lowtide SAV	A	13	1.19	2.66	5.42	10.54	136.06	19.80	2.95
Lowtide Deep	A B	14	0.00	1.65	4.99	9.22	16.57	6.07	0.40
Lowtide Shallow	A B	15	0.00	0.48	1.05	2.52	18.82	3.05	0.34
Significant differences:				LV, HV > HI					

H.

Fundulids, gdw/sample							Kruskal-Wallace statistic = 47.64, P = .0001		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	D	12	0.00	0.00	0.00	0.00	0.10	0.01	0.00
Hightide Unveg.	D	15	0.00	0.00	0.00	0.00	0.10	0.01	0.00
Hightide Edge	A B	15	0.00	0.21	0.99	3.08	13.73	2.35	0.24
Hightide Fringe	A B C	15	0.00	0.22	0.52	1.47	8.53	1.44	0.15
Hightide Interior	A	14	0.20	0.30	1.17	1.88	7.39	1.79	0.16
Lowtide SAV	A B C D	13	0.00	0.00	0.41	1.36	1.86	0.63	0.06
Lowtide Deep	C D	14	0.00	0.00	0.00	0.00	5.18	0.44	0.10
Lowtide Shallow	A B C D	15	0.00	0.00	0.17	1.17	6.14	1.00	0.12
Significant differences:				HI, HE > LD, HV, HU HI, HE, HF > HV, HU					

I.

Fishes, gdw/sample							Kruskal-Wallace statistic = 28.31, P = .0002		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A	12	0.61	0.71	1.21	1.46	9.87	2.49	0.28
Hightide Unveg.	B	15	0.00	0.00	0.22	0.40	1.49	0.32	0.03
Hightide Edge	A	15	0.00	0.70	1.26	4.54	13.98	3.19	0.25
Hightide Fringe	A B	15	0.00	0.22	0.71	1.80	8.53	1.57	0.15
Hightide Interior	A	14	0.20	0.49	1.38	1.88	7.39	1.88	0.16
Lowtide SAV	A	13	0.28	0.69	1.82	2.17	2.96	1.48	0.07
Lowtide Deep	A B	14	0.00	0.11	0.46	0.72	5.68	0.83	0.10
Lowtide Shallow	A B	15	0.00	0.03	0.20	1.23	6.14	1.02	0.12
Significant differences:				HE, LV, HV, HI > HU					

J.

Nekton, gdw/sample								Kruskal-Wallace statistic = 26.09, P = .0005		
Habitat	Dunn groupings	N	min	1st qrt	median	3rd qrt	max	mean	SE
Hightide SAV	A B	12	2.30	3.43	6.18	8.65	73.75	11.86	1.65
Hightide Unveg.	B	15	0.00	0.25	0.95	3.71	11.25	2.64	0.23
Hightide Edge	A	15	1.25	4.10	5.74	14.54	57.44	12.32	1.02
Hightide Fringe	A B	15	0.26	0.50	2.99	6.82	17.48	5.26	0.41
Hightide Interior	A B	14	0.24	0.93	1.92	2.85	36.06	4.56	0.66
Lowtide SAV	A	13	1.84	4.97	7.19	10.82	139.02	21.28	2.98
Lowtide Deep	A B	14	0.00	2.32	6.57	10.59	18.06	6.90	0.41
Lowtide Shallow	A B	15	0.00	0.61	1.96	2.93	22.68	4.07	0.42
Significant differences:				LV, HE > HU					

RESULTS AND DISCUSSION

OVERALL RESULTS

Thirty-two species of nekton were captured in the sampled habitats within the narrow 30 meter band of shoreline extending from marsh interior to shallow SAV bed (Table 2). Ten of these species are commercially valuable (Table 2). Only 6 drop samples out of 166 were devoid of nekton; all of these samples were taken from unvegetated habitats. The 166 samples (1.75 m^2 each) produced 8305 individual nektonic animals, with a total dry weight of 1102 grams. The overall mean density was 28.6 inds m^{-2} with a mean biomass of 3.79 gdw m^{-2} (note that these figures are slightly lower than the results seen in Table 3, which calculates summary statistics as averages of the monthly and habitat means). Blue crabs, *Callinectes sapidus*, were the biomass dominants in the study; palaemonid shrimp were the numeric dominants (Table 2, Figure 4). Most of the species captured (75%) were fishes (Table 2).

SPECIES SPECIFIC FINDINGS

For clarity, this section will evaluate use patterns by individual species of nekton in turn. Fishes are discussed together, then crustaceans. In several cases, species used habitats differently than is reported in the literature for other geographic regions. This is interpreted as behavioral flexibility, and is discussed in detail at the end of this section.

FISHES

Mummichogs, *Fundulus heteroclitus*

Abundance. Mummichogs were the most abundant fish in this study, making up 32% of the individual fishes captured (52% of marsh resident fishes). Mean densities between June and October at high tide (± SE) in marsh Edge, Fringe, and Interior habitats were 0.6 ± 0.04 inds

m^{-2}, 1.9 ± 0.1 inds m^{-2}, and 2.1 ± 0.1 inds m^{-2}, respectively. This mean density of mummichogs was almost identical to the density reported by Ayers (1995) for her comparable open embayment marsh habitat at the Goodwin Islands.

Habitat preferences. Mummichogs had an affinity for marsh habitat in this study at high tide. Of 300 mummichogs captured quantitatively, only 1 was caught in an unvegetated habitat at high tide, and none were caught in SAV at high tide. Bearing in mind that quantitative sampling did not begin until June, numbers and biomass of mummichogs peaked in July (Table 3). A trend towards increasing numbers of mummichogs further up on the marsh surface was observed (Tables 3 and 5). The conservative Kruskal-Wallace/Dunn tests did not detect significant differences between marsh surface habitats (Table 4 B), but more powerful tests for linear association did show that mummichog abundance at high tide increased significantly with habitat distance from the marsh edge (Cochran-Mantel-Haenszel test for linear association, SAS Proc FREQ, $Q = 6.79$, $p = 0.009$). This result has been shown in other studies for mummichogs (Kneib 1984a) and for other killifishes as well (Rozas and Reed 1993).

Relationships between habitat and fish size. The mean size of mummichogs decreased with increasing distance from the marsh edge (Cochran-Mantel-Haenszel test for linear association, SAS Proc FREQ, $Q = 49.59$, $p = 0.001$). This result is in contrast to the results of Kneib and Wagner (1994) who found that the larger classes of nekton (including *F. heteroclitus*) penetrated further into the marsh interior at spring tide than did the smallest size classes. The marsh system of Kneib and Wagner floods much more extensively than does my system, and the two sampling stations of their study were 25 and 90 meters from the marsh edge. Kneib and Wagner suggest that the penetration of larger individuals farther into their marsh interior may have been due to the more limited mobility of smaller nekton, and their increased risk of being stranded (Kneib and Wagner 1994). In my marsh, mean flooding distance into the marsh is 16 meters (23 meters at spring tides), and risk of stranding is therefore of much less importance in determining the distance to which different size classes of nekton will penetrate into the marsh. It is likely that factors other than risk of stranding are

governing penetration of different sizes of fish into the interior of this small marsh. Small nekton are found in high marsh habitats of other marshes as well (Talbot and Able 1984). The different distribution of size classes of mummichogs on the marsh surface may be an example of behavioral flexibility that is driven by physical differences between habitats in different regions.

Low tide refuge. At low tide, mummichogs retreated to refugia adjacent to the marsh or took refuge on the marsh surface, as evidenced by pit trap data (Figure 5). The mummichogs caught in my pit traps were far less abundant and considerably larger than is reported in other pit trap studies (Kneib 1984b; Talbot and Able 1984; Yozzo *et al.* 1994a; Yozzo *et al.* 1994b; Kneib 1997b; Yozzo and Smith 1998). I did not install pit traps on the marsh surface until September of 1995. Pit traps are selective for small larval and juvenile fishes (Yozzo and Smith 1998) which are most abundant in spring and early summer. Consequently, the timing of pit trap deployment is probably responsible for the large size and low numbers of captured mummichogs.

Mummichogs were also captured at low tide using throw traps in open water. Figures 3 and 4 and Table 3 quantitatively describe use of the open water refugia adjacent to the marsh. Mummichogs were present in all lowtide habitats, with a non-significant trend (Table 4) towards greater use of shallow (0 - 10 cm) unvegetated habitats followed by SAV habitats followed by deeper (10 - 30 cm) unvegetated habitats. Mummichogs used all possible lowtide refugia to some degree.

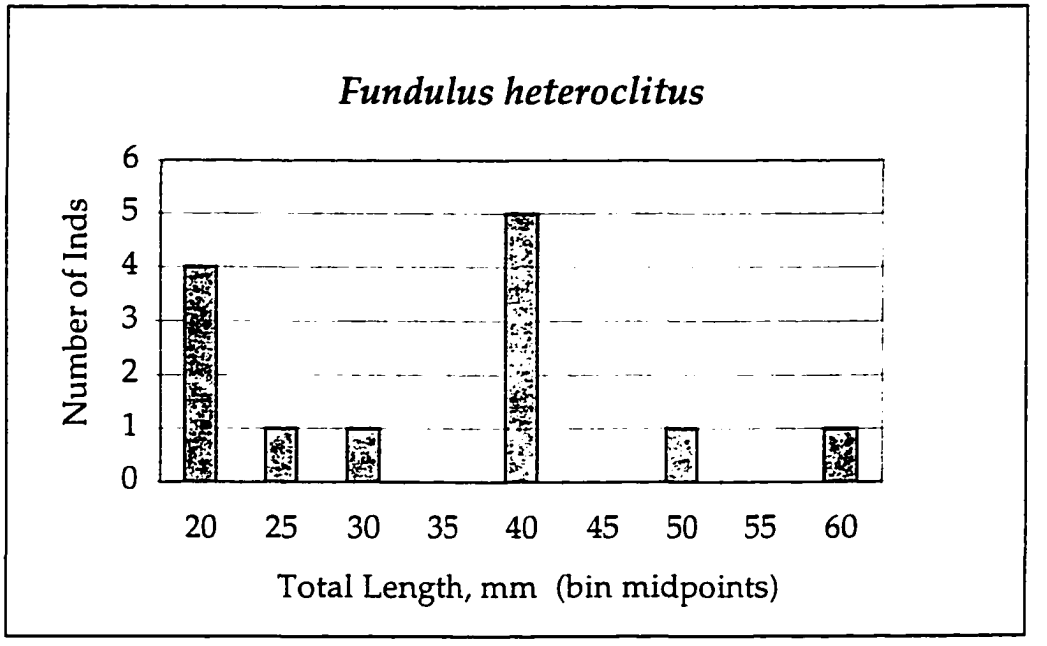
Striped killifish, *Fundulus majalis*

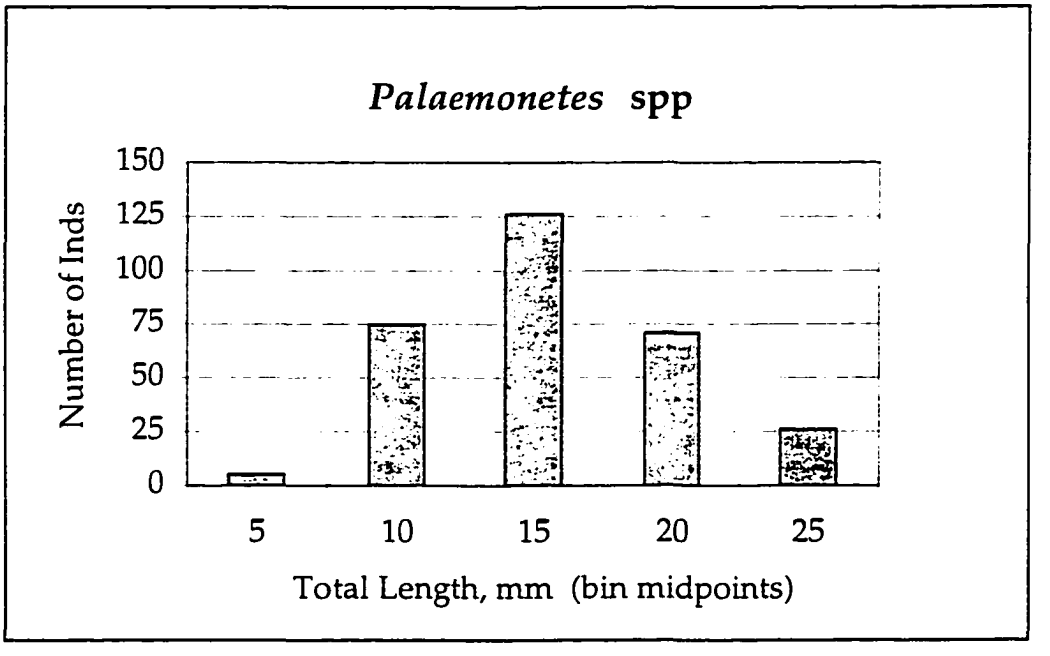
These fish were not particularly abundant in this sampling area (63 individuals captured quantitatively) and constituted about 10% of all sampled marsh resident fishes. Of the 63 individuals captured, 30 were taken on the marsh surface, 63% of which were in the marsh interior habitat. Thirty-three individuals were captured in lowtide unvegetated habitats, 94% of which were in the shallow (< 10 cm) habitat. No fish were taken in SAV

Figure 5. Nekton Captured in Pit Traps

Length-frequency data are given for the two nekton species that were abundant in pit traps between September 1995 and November 1995. Other nekton species captured are described at the bottom. No data is provided for *Uca*, *Sesarma*, and other species that are not nekton, although these species were captured in the traps as well. Four pit traps were deployed; two of these were located in the irregularly flooded high marsh and rarely caught nekton. This figure shows the grand total of all individuals caught in the twelve times that the four traps were checked.

Nekton Captured in Pit Traps, September - November 1995





Also Captured:

Callinectes sapidus (1 individual, 17 mm CW)

Fundulus majalis (1 individual, 41 mm TL)

habitats at high tide or at low tide, and no fish were taken in unvegetated habitat at high tide. Weisberg (1986) states that *Fundulus majalis* on the Atlantic coast are found primarily in subtidal areas and do not venture onto the marsh surface. My data and the work of Werme (1981) in Massachusetts suggest that *F. majalis* does use the marsh surface on the Atlantic coast. Kneib and Wagner (1994) also captured *F. majalis* on the marsh surface, but in very low numbers (11 individuals in 6000 m^2 sampled). It is unclear whether the low numbers of Kneib and Wagner are due to rarity of this species in their area, or to reluctance of these fishes to use marsh surface habitat in Georgia. It is possible that regional differences between use of marsh vs. unvegetated habitat by *F. majalis* at high tide exist along the Atlantic coast. These differences may result from behavioral selection of different habitats in various regions of the Atlantic coast.

In my study, the mean size of striped killifish was 49 mm TL, with a range of 26 - 108 mm. These fish were most abundant in the Hightide Interior and Lowtide Shallow habitats, with mean densities (± SE) of 0.5 ± 0.04 and 0.7 ± 0.1 in these areas (Table 3). Only one striped killifish (41 mm TL) was captured in a pit trap, but the concerns about pit trap sampling for mummichogs in this study (see above) apply here as well. Although the Kruskal-Wallace and Dunn tests were not conducted between habitats due to the small number of striped killifishes captured, a primary pattern of migration between the marsh interior (> 3 m from the edge) at high tide, and the shallow unvegetated (< 10 cm deep) at low tide is suggested in these data. The absence of striped killifish in SAV habitats suggests an avoidance of these habitats even as low tide refuge. In contrast, mummichogs and other marsh resident fishes were commonly captured in the SAV habitat at low tide (Table 3). Striped killifishes were never captured at high tide in any habitat other than the marsh surface.

Rainwater killifish, *Lucania parva*

The rainwater killifish, *Lucania parva*, was the second most abundant fish captured after *Fundulus heteroclitus*, and made up 22% of all fishes captured (35% of marsh resident

fishes). Rainwater killifish were found in all marsh surface habitats with a trend towards higher density at the Hightide Edge habitat relative to Hightide Fringe and Hightide Interior habitats (Table 3). This trend was not statistically significant, however (Table 4 D). Rainwater killifishes had more of a preference for SAV habitats as lowtide refuge than did other marsh resident fishes, and the Kruskal-Wallace/Dunn tests showed a significant difference between SAV and shallow (<10 cm) unvegetated habitats at low tide. These fishes can occur in schools or shoals of 20 - 100 fish (G. Cicchetti, unpublished 1997 videotape data at erosional marsh edges). The Kruskal-Wallace and Dunn tests (which analyze ranked data) consider the number of fish in a large sample only as a rank value. Consequently, these tests may not be the most appropriate means to evaluate habitat use by these aggregating fish, which mostly occur in drop samples at zero abundance, but with a few stragglers and occasional high abundance. Only 2 of these fish were captured in the Lowtide Deep unvegetated habitat (10 - 30 cm), yet the Kruskal-Wallace and Dunn tests find no significant difference between this habitat and the Lowtide SAV habitat, where 122 fish were captured between August and October. Despite the non-significant result of the statistical tests, the data suggest that SAV is preferred as a low tide refuge over unvegetated habitats by these fish. At high tide in my study, essentially the entire population of *L. parva* had moved into marsh habitat (Table 3), as was true of other marsh resident fishes as well (Table 4 H). Only one rainwater killifish was caught in the unvegetated habitat during the study, likewise only one was caught in SAV habitat at high tide. In contrast, Rozas and Minello (1998 in press) found no significant differences between *L. parva* densities in SAV and marsh habitats when both were flooded, though this species was somewhat more abundant in marsh habitats. Inundation regimes between their sampling area and my area were different; the marsh surface and SAV areas sampled by Rozas and Minello were nearly continuously flooded during the time period of their study. These and other differences between the sampled areas are probably responsible for flexibility in habitat use by *L. parva*.

Marsh transient fishes

Weinstein and Brooks (1983) remark on the "notable absence of transient (marine) species that are dependent on polyhaline, shallow nursery habitats [SAV and marsh creek] in the Chesapeake Bay" relative to other geographic regions. I also found that the abundance of transients was generally low. August and September were the peak months for use of the marsh by non-resident fishes, and most transients were found in marsh edge habitats (Figures 3 and 4). The total density of transient fishes in marsh edge habitats for the peak months of August and September was 1.3 ± 0.4 (SE) inds m^{-2}. This is a respectable number of fishes, but densities in other marsh habitats were quite low (Figures 3 and 4). In all, thirty-three marsh transient fishes were captured in the 30 drop samples taken in all marsh habitats during August and September: 21 silversides, 3 silver perch, 2 spotted seatrout, 2 naked gobies, 2 spot, 1 striped blenny, 1 blackcheek tonguefish, and 1 skilletfish (Table 3). An additional 6 silversides, 1 naked goby, and 1 skilletfish were captured in the 36 drop samples taken in all marsh habitats during the remaining months of June, July, and October. Only silver perch and silversides ventured away from marsh edge habitat and onto the interior marsh surface (Table 3). Some evidence exists for increased use of the marsh surface by transient fish species during night high tides (see diel section below) but in general marsh fish communities were heavily dominated by the resident fundulids. To conclude, marsh edge habitat in August and September supported marsh transient fish species, but other habitats and other months saw low use. The most important marsh transient species in this study was the crustacean, *Callinectes sapidus*, which is discussed below.

Naked goby, *Gobiosoma bosc*

This species deserves special consideration as it is very commonly reported as a numeric dominant in marsh studies of the Gulf of Mexico (Zimmerman and Minello 1984, Rakocinski *et al.* 1992, Peterson and Turner 1994). Rozas and Minello (1998 in press) found no significant differences between densities of this species in SAV vs. marsh edge habitats in Texas. In my

study, this species was never caught on the marsh surface, and was caught only rarely at the marsh edge (3 individuals total in the habitat study, but one 1995 marsh edge drop sample in the year-to-year variability study contained 7 individuals). It was, however, the most abundant fish captured in SAV habitats. Table 4 C shows significant differences between use of SAV and marsh surface habitats for *G. bosc*.

The gear used in my project to remove nekton from drop rings (Chapter 1) was almost certainly less effective at removing small benthic forms such as gobies. However, the high abundance of gobies captured with this gear in SAV habitats suggests that their reported absence in marsh habitats in is in fact a true result. Also, gobies have been captured in low numbers in other studies of the marsh surface at the Goodwin Islands. Densities reported by Ayers (1995) for marsh edge habitats were comparable to those of my study (< 0.1 ind m^{-2}). Gobies were never caught in pit traps installed on the marsh surface in my study (Figure 5). In contrast, Yozzo and Smith (1998) caught significant numbers of *Gobiosoma bosc* using pit traps in salt marshes on Virginia's Eastern Shore. *G. bosc* was more abundant at one of Yozzo and Smith's sites than at the other. Since *G. bosc* does use marsh surface habitat in some Virginia salt marshes, behavioral flexibility in habitat use between local marshes may play a role in determining patterns of use by this species.

Other fishes

In all, 24 species of fishes were captured in the study and are listed in Table 2. Most of those which are not discussed above were captured so rarely that habitat use evaluations cannot properly be made. Six fish species were captured only in SAV habitats, and deserve special mention: northern pipefish (*Syngnathus fuscus*, 26 individuals), dusky pipefish (*Syngnathus floridae*, 11 individuals), juvenile oyster toadfish (*Opsanus tau*, 5 individuals), American eel (*Anguilla rostrata*, 4 individuals), bay anchovy (*Anchoa mitchelli*, 3 individuals), and fourspine stickleback (*Apeltes quadracus*, 1 individual). The eels are of interest in that they were the biomass dominant fish in the hightide SAV habitat despite

their low numbers. Moreover, eels occurred only in the month of September, when they were present in SAV only at high tide, at a mean abundance of 0.5 ± 0.1 (SE) inds m^{-2}. These eels ranged from 73 to 299 mm TL, with a mean of 211 mm TL. In addition to eels and other visitors, seagrass provides habitat for several species such as pipefishes and sticklebacks which have been noted to show strong selection for areas of SAV (Lippson and Lippson 1984).

Total fishes: comparisons to other studies

Ayers (1995) used enclosure-style flume weirs in a quantitative study of protected (creekbank) marsh sites versus exposed (open embayment) marshes at the Goodwin Islands. Her gear sampled an area that extended 2.5 m onto the marsh surface and utilized a very fine mesh size. Ayers' open embayment site was my Area 3 (Figure 1, Chapter 1). She found that overall densities for all fishes from May to November of 1994 were 2.6 m^{-2} for the exposed marsh and 10.8 m^{-2} for the protected marsh. My study took place from June to October of 1995. To eliminate any seasonal bias in comparison (though of course site, year-to-year, and gear differences still exist), Ayers' total fish numbers for June to October, 1994 in the exposed and protected sites were calculated as 1.5 m^{-2} and 8.9 m^{-2} respectively (data from Ayers 1995). The number of fishes captured in my study are slightly higher than in Ayers' analogous exposed site, but lower than in her protected site (mean of my study: 2.4 m^{-2} for June to October, 1995, for habitats comparable to those used by Ayers). I conclude that my study provides numbers that are comparable to those obtained in other local quantitative studies.

Some other geographic regions that have been sampled quantitatively, however, have shown much greater use of marsh habitats. Baltz *et al.* (1993) captured 16,864 fishes in 658 m^{-2} sampled in Gulf of Mexico marsh edge habitat. This mean of 25.6 fish m^{-2} (57 species captured) is an order of magnitude greater than my estimates from Chesapeake Bay. In fact, Rozas (1993) suggests that the difference in nekton abundance between Gulf coast marshes and Atlantic coast marshes is about an order of magnitude. Zimmerman and Minello (1984), in a drop ring study of marsh and unvegetated habitats in Texas, found densities of crustaceans to be

much higher than in my study, while fish densities of Zimmerman and Minello were comparable to my study. Zimmerman and Minello captured 29 species of fishes; I captured 20 in my marsh and unvegetated habitats. Relative to some other geographic regions and in particular to Gulf coast marshes, the abundance and diversity of nekton captured in my study is low. Again, differences between regions may be due to tides, marsh morphology, or various other factors.

CRUSTACEANS

Callinectes sapidus

As noted above, blue crabs were the biomass dominant in every habitat except in the unvegetated Lowtide Shallow habitat, where large blue crabs were mostly absent. A comparative analysis of habitat use by crabs at high tide during the months of August through September (when all habitats were sampled) found highest densities of crabs in SAV habitats (mean 16.7 ± 0.8 (SE) inds m^{-2}). Densities in this habitat were significantly different from those in unvegetated (3.4 ± 0.2 inds m^{-2}), marsh fringe (1.5 ± 0.1 inds m^{-2}), and marsh interior (0.8 ± 0.1 inds m^{-2}) habitats (Kruskal-Wallace and Dunn tests, Table 4 A). The marsh edge habitat (5.8 ± 0.4 inds m^{-2}) was significantly similar to SAV and to the low density habitats for these months (Table 4 A). These abundance patterns are primarily driven by blue crab recruitment, which will be discussed further below. Note that mean abundances are provided for informative purposes, and are not meant to be correlated with Kruskal-Wallace/Dunn results; these tests examine median rank values, not mean values. The marsh edge crabs were larger than those found in seagrass habitats at high tide, and biomasses at the two areas were comparable at mean 4.03 gdw m^{-2} in SAV, mean 4.69 gdw m^{-2} at the marsh edge. The marsh edge was seen in this study to support a large biomass and abundance of blue crabs, but numbers sampled were greater in SAV habitats.

Blue crab juveniles recruited heavily into the sampled habitats in the months of September and October; similar timing of this recruitment pulse has also been seen in other

local studies (Orth and van Montfrans 1987). Densities of juvenile crabs in SAV in my study are within the range reported by Orth and van Montfrans (1987). Marsh edge densities in September (11.4 ± 1.3 inds m^{-2}) and October (5.4 ± 0.6 inds m^{-2}) are higher in my study than was reported for marsh creeks in Orth and van Montfrans (1987). Crabs began recruiting to SAV areas in August, while crabs did not recruit heavily to marsh or unvegetated habitats until September (Table 3); a similar delay in recruitment to marsh creeks was seen in Orth and van Montfrans (1987).

In considering habitat use by juvenile crabs, the removal efficiency of the gear may have caused crab densities in marsh habitats to be significantly underestimated relative to SAV habitats. Table 1 in Chapter 1 shows a removal efficiency of 39% ± 15% (95% CI) for SAV habitats and 16% ± 12% (95% CI) for marsh habitats. If we correct the data for the known removal efficiencies, then SAV and marsh edge densities may be similar, on the order of 30 - 40 inds m^{-2}. These densities are comparable to the 13 - 90 inds m^{-2} reported for SAV beds in Chesapeake Bay at this time of year using more efficient suction sampling gear (Orth and van Montfrans 1987). Unvegetated habitat was not examined for removal efficiency for blue crabs, but it is thought that removal efficiency here would be greater than for either vegetated habitat. Both vegetated habitats had substrates which crabs < 20 mm could burrow into (G. Cicchetti, personal observation). In marsh and SAV habitats, the clearing device was raked through the vegetation and sediment at the top of the root mass and did not remove substantial amounts of sediment. In unvegetated habitats, the clearing device was used to scrape much of the top 2 - 5 cm of sediment into the mesh collecting bag/cod end. The collected mud was then sieved *in situ* through the 2 mm mesh cod end, and it is assumed that small burrowing crabs were caught with efficiency.

There were significant differences in crab use of marsh habitat between fall 1995 and fall 1996 (Table 6, Wilcoxon-Mann-Whitney test result chi-sq = 4.31, p = 0.038). Much of this difference was due to the low numbers of small crabs ≤ 25 mm on the marsh surface in 1996. Year-to-year variability in recruitment of small juvenile crabs has also been noted in SAV beds

in this region (Orth and van Montfrans 1987). These authors linked recruitment of crabs to SAV beds with supply of megalopae from the plankton, but noted that dispersal into shallow water habitat might also be important. Year-to-year variability may be a consistent feature of blue crab recruitment to these habitats.

Forward *et al.* (1996) found that metamorphosis of blue crab megalopae was induced by chemical cues from either *Spartina alterniflora*, various seagrasses or certain algae. This finding supports the notion that *Spartina* may provide an important recruitment substrate for *Callinectes sapidus*. Recruitment of blue crabs to marsh habitats is known to be important in other geographic regions. Thomas *et al.* (1990) reported 13 - 22 juvenile blue crabs per square meter in marsh habitats in Texas during the period of peak recruitment. In areas where seagrass beds existed, crab recruitment to marsh habitat was about half that of recruitment to seagrass habitat. Thomas *et al.* (1990) suggested that salt marshes were an important nursery for juvenile blue crabs in Texas. Also in Texas, Rozas and Minello (1998 in press) found that juvenile blue crabs were significantly more abundant in salt marsh edge habitat than in seagrass habitat in both seasons sampled (spring and fall). Zimmerman and Minello (1984) and Thomas *et al.* (1990) found crab densities to be significantly higher in *Spartina* vs. unvegetated habitats in Texas, but these trends may not apply to all geographic regions. In South Carolina, Mense and Wenner (1989) found greater densities of crabs in unvegetated substrates than in marshes. Both Mense and Wenner and Thomas *et al.* suggest that differences in tidal inundation may play a role in creating these differences.

My dissertation is the first study in Chesapeake Bay to specifically examine the marsh edge habitat for blue crab recruitment. Marsh edge is available throughout Chesapeake Bay and most other estuaries. Orth and van Montfrans (1990) report that Chesapeake Bay contains 146,000 hectares of salt marsh and 17,000 hectares of SAV. It is possible that recruitment of blue crabs to marsh edge habitats is an important and underestimated aspect of blue crab biology in this region.

Larger blue crabs also made considerable use of marsh habitats in my study area. In fact, blue crab biomass from August through October was comparable between the marsh edge habitat (mean 4.69 gdw m^{-2}) and the hightide SAV habitat (4.03 gdw m^{-2}). The lowtide SAV habitat had the highest crab biomass (9.47 gdw m^{-2}) for this time period; much of that biomass is due to one drop ring sample in August that contained 5 large blue crabs with a combined biomass of 118 grams dry weight. Blue crabs were also the biomass dominant in all marsh surface habitats, although biomass of blue crabs was much lower here. Marsh Fringe and Marsh Interior habitats were characterized by blue crab biomass of 1.94 gdw m^{-2} and 1.32 gdw m^{-2} respectively as means for August through October. It is clear that marsh habitat is important to blue crabs in this area at several different stages in their development.

The only habitat in which blue crabs were not consistently the biomass dominant was the Lowtide Shallow (unvegetated) habitat, with water depths of less than 10 cm. This habitat had the lowest mean biomass of crabs between August and October (0.28 gdw m^{-2}) and was characterized by small blue crabs (mean carapace width = 13.6 mm). Mean density of crabs here was 3.8 ± 0.25 (SE) inds m^{-2}. Of 104 crabs captured in this habitat, only 3 were larger than 35 mm, and these three crabs accounted for 59% of the biomass in this habitat. The largest crab captured here had a carapace width of 64 mm. These results are consistent with the findings of other workers. Ruiz *et al.* (1993) classified larger blue crabs as a deep zone species (> 30 cm of water) in a drop ring study in Chesapeake Bay; Dittel et al. (1995) showed that shallow water provided a refuge from cannibalism for smaller crabs.

Other researchers have shown that large blue crabs forage on the marsh surface at high tide, and take refuge in subtidal waters at low tide (Ryer 1987, Fitz and Wiegert 1991). Data of my study supports this conclusion for larger crabs as well, in that only one blue crab (17 mm CW) was captured in a pit trap on the marsh surface (Figure 5) and in that larger blue crabs > 30 mm CW were never observed in burrows or natural aquatic microhabitats in the intertidal at low tide. My drop trap data are not informative as to preferred low tide habitat of juvenile blue crabs, however. Pit traps were set up only in marsh interior habitat, and

juvenile blue crabs recruited most heavily to marsh edge habitat (Table 3). Juvenile blue crabs do have the ability to take refuge on the salt marsh surface at low tide (Kneib 1997b, Yozzo and Smith 1998). Other studies indicate that larger crabs retreat to the subtidal at low tide (Ryer 1987, Fitz and Wiegert 1991).

Blue crabs have been found to be numeric or biomass dominants in many studies of marsh habitat in other geographic regions. After palaemonids, blue crabs were the second most abundant organism collected in marsh surface flumes by Peterson and Turner (1994) in Louisiana. Blue crabs were the biomass dominant in Hettler's (1989a) flume study of North Carolina marshes. These areas are characterized by extensive marshes and it is inferred that marsh habitat is important to populations of blue crabs in these more southerly regions. If extrapolated beyond the Goodwin Islands, my data suggest that marshes may be very important to populations of blue crabs in Chesapeake Bay as well.

Blue crabs can be considered habitat opportunists. Although SAV seems to be preferred habitat for crabs in Chesapeake Bay, populations of crabs also exist where seagrass is locally absent. Likewise, if all marsh in an area were to be destroyed, blue crabs would no doubt still exist in unvegetated areas. Indeed, it is quite possible that a substantial number of individual blue crabs never enter either an SAV bed or a marsh. Marsh and SAV habitat nonetheless offers important benefits to those individuals that do exploit these habitats, and expand the range of habitat open to this particular species. Consequently, opportunistic marsh use may be of great importance towards the maintenance of blue crabs in Chesapeake Bay at a certain population level, even if the species does not depend on marsh habitat in the strictest sense.

Palaemonetes pugio

These small shrimp were the most abundant nekton captured in this study, as has been found for other studies that have considered the entire marsh community as well (Nixon and Oviatt 1973, Zimmerman and Minello 1984, Rozas and Reed 1993). In all, 3478 individual *Palaemonetes pugio* were captured in 166 drop samples. Peak habitat use was in the fall, and

mean densities from August to September in marsh edge habitat were 15.8 ± 1.8 (SE) inds m^{-2}, with 53.9 ± 5.6 inds m^{-2} in the shallow unvegetated lowtide habitat. At high tide, *P. pugio* was distributed over the marsh surface and in SAV habitats with no obvious preference for marsh over SAV or vice versa (Kruskal-Wallace and Dunn tests, no significant differences, Table 4 E). As was seen for *Fundulus heteroclitus*, the mean size of *P. pugio* decreased with distance into the marsh (Cochran-Mantel-Haenszel test for linear association, SAS Proc FREQ, Q = 8.19, p = 0.004). *P. pugio* exhibited a strong aversion to unvegetated habitats at high tide (Kruskal-Wallace and Dunn tests, significant differences at p = 0.05, Table 4 E). Only 2 samples out of 23 taken between June and October in this habitat contained these shrimp, and one of these samples contained appreciable quantities of drifting dead *Zostera marina*.

At low tide, *Palaemonetes pugio* was found to take refuge on the marsh surface as evidenced by pit traps, where 303 individuals were captured (Figure 5). *P. pugio* also took refuge in SAV beds and in the shallow (0 - 10 cm deep) habitat at the water's edge. *P. pugio* was significantly more abundant in this shallow water habitat than in the adjacent deeper (10 - 30 cm) habitat (Table 4 E, significant difference at p = 0.05). In fact, of the total 244 *P. pugio* captured in 24 drop samples taken in the lowtide unvegetated deep habitat, 221 were found in one sample that also contained drifting dead *Zostera marina* and a large drifting clump of red algae. This preference for shallow water and for vegetation is presumably to take refuge from deeper aquatic predators (see Ruiz *et al.* 1993).

Other palaemonids

Palaemonetes pugio, *P. vulgaris*, and *P. intermedius* coexisted in my sampling area. In spite of morphological similarity, *P. vulgaris* and *P. pugio* are ecologically distinct, and showed different patterns of habitat use in my study. Although both shrimp are euryhaline (Knowlton and Kirby 1984), in many areas *P. vulgaris* and *P. pugio* are separated by the different salinity tolerances of the two species, with *P. vulgaris* being more prevalent at

higher salinities (Knowlton *et al.* 1994). In areas where the two species coexist, it has been suggested that *P. vulgaris* has an ability to competitively displace *P. pugio* from preferred habitat (Thorp 1976). As discussed above, *P. pugio* was distributed over marsh surface and SAV habitats at high tide, and took low tide refuge on the marsh surface, in very shallow unvegetated areas, and in SAV habitat (Tables 3 and 5, Figure 5). *P. vulgaris* showed different patterns of habitat use. *P. vulgaris* had a very clear preference for SAV habitat in this study at high tide and at low tide, and was significantly more abundant in SAV habitats than in any of the other sampled habitats (Kruskal-Wallace and Dunn tests at $p = 0.05$, Table 4 F). Mean densities in SAV during the peak months of August - September were 36.4 ± 2.4 (SE) inds m^{-2} at high tide and 34.2 ± 3.3 inds m^{-2} at low tide. A total of 1590 individual *P. vulgaris* were captured; of these only 48 were found in habitats other than SAV.

Palaemonetes intermedius was also present in this area, though it was much less abundant than the other two species. *P. intermedius* were positively identified in this study when at least two distinguishing morphological characteristics could be determined. Interestingly, *P. intermedius* seemed to share a distribution pattern with *P. vulgaris*, and exhibited a strong preference for SAV habitat. Out of the 177 individual *P. intermedius* shrimp captured, 176 were taken in SAV habitats at high tide or low tide. Rozas and Minello (1998 in press) found the opposite result, that *P. intermedius* was more abundant in marsh habitats than in SAV habitats. Inundation differences between the study areas of Rozas and Minello and my area are considerable; both their marsh and SAV habitats were almost continuously inundated during the time period of their study. Flexibility in habitat use by *P. intermedius* between my marsh and these Texas marshes may very well be forced by these differences in inundation.

Palaemonetes pugio and *P. vulgaris* were allopatric species with overlap in habitat use in my study. *P. vulgaris* and *P. intermedius* appeared to be sympatric. Given the obvious morphological similarities of the three species, this situation is interesting for evolutionary reasons, and merits further study.

Other natant crustaceans

Other nektonic crustaceans were captured primarily in SAV habitats. None were captured in marsh habitats, though benthic *Uca*, *Sesarma*, and xanthid crabs were abundant in marsh habitats. These benthic crabs were not quantified in this study and are not discussed in this chapter. Of the natant crustaceans, the *Hippolyte* shrimp were found almost exclusively in SAV beds (Table 3). Juveniles of the commercial shrimps *Penaeus aztecus* and *Penaeus duorarum* were also present in SAV habitats, but at densities typically less than 1 ind m^{-2} (Table 3). *Callinectes sapidus* and palaemonid shrimp made up by far the greatest part of natant crustaceans, especially in marsh and unvegetated habitats.

GENERAL FINDINGS

Behavioral flexibility between geographic regions

Behavioral flexibility in feeding is considered a characteristic feature of estuarine fish (Day et al. 1989). This flexibility allows better exploitation of the variable resources typical in estuaries. Behavioral flexibility in habitat use between regions is less commonly documented, but has been shown in estuarine species ranging from mummichogs (Able 1984) to salmonids (Healey 1994) to oystercatchers (Lauro and Burger 1989). Flexibility in behavior between regions is adaptive, and allows species to better exploit the different characteristics of each area. Differences in behavior between regions may be linked to cues from the environment, may be forced by the availability or unavailability of a resource, or may be genetic in nature.

Estuaries provide suitable conditions for the genetic development of behavioral flexibility between regions. Different estuaries are separated spatially, and many marsh species never leave the estuary. Moreover, each estuary provides a unique environment which could favor specific genetic adaptations (Ayvazian *et al.* 1994). These features can create genetic divergence in fish species between different estuaries and different regions (Ayvazian *et al.* 1994). Genetic divergence may manifest itself in behavior, or in other ways.

In my study, several species used habitats differently from what is reported for other geographic regions. Size of mummichogs decreased with distance into the marsh; the opposite result was reported by Kneib and Wagner (1994) in expansive Georgia marshes. This may be a result of forcing from the environment rather than a behavioral choice, in that only larger mummichogs can swim fast enough to return to low tide refuge in Kneib's extensively flooded Georgia marshes. Nonetheless this shows what the species is capable of adapting to, and can be considered as flexibility in this way. Rainwater killifish were seen to significantly prefer marsh habitat over SAV habitat at high tide; they were abundant in both marsh and SAV at high water in a Texas marsh that was almost constantly inundated (Rozas and Minello 1998 in press). Rainwater killifish seem to exhibit a behavioral choice that differs between regions. In my marsh *Palaemonetes intermedius* were found almost exclusively in SAV habitats; they were more abundant in marsh habitats than in SAV habitats in the long inundation period Texas marsh (Rozas and Minello 1998 in press). Naked gobies are common on the marsh surface in Gulf of Mexico marshes (Zimmerman and Minello 1984, Rakocinski *et al.* 1992, Peterson and Turner 1994) and in some Virginia marshes (Yozzo and Smith 1998) but were extremely rare on the surface of my marsh despite their abundance in the adjacent subtidal. *Cyprinodon variegatus* uses habitats differently in different areas as well (Herke 1971). In fact, behavioral differences between regions were noted for the majority of marsh resident species captured in my study.

While it may be difficult to separate chosen behavioral differences from forced behavior differences, behavioral flexibility in marsh resident use of estuarine habitat does occur between regions. This is not surprising, given that estuaries are isolative and unique environments. Behavioral flexibility allows estuarine organisms to better deal with the particular combinations of tidal regime, food resource, and predation risk found in each area. If forced by the environment (say, by availability or unavailability of a habitat), this variation in use indicates a flexible ability to persist in differing situations. If behavioral differences are by choice linked entirely to environmental cues, then behavioral flexibility

between regions offers a rich opportunity for experimental work to examine the underlying factors driving habitat use. If genetic in nature, behavioral flexibility in habitat use has evolutionary implications; genetic behavioral variation between isolated populations may be the first outward indication that the populations are diverging.

Differences between areas of the Goodwin Islands

A separate study was carried out to determine how typical the primary sampling area was of open embayment marshes on the Goodwin Islands. All the previously discussed results were obtained from the primary sampling area (Figure 1, Chapter 1). Two additional areas were selected for study (Figure 1, Chapter 1), and the marsh fringe habitat was sampled at all three areas in July and August of 1996 as described in the methods section above. Table 5 shows the results of this comparison.

No statistical differences among areas were found for abundance of any individual species. The trend for three of the four abundant species, however, was for greatest numbers at Area 3 and lowest numbers at Area 2 (Table 5). A significant difference was found among areas for grams dry weight of total nekton (Kruskal-Wallace test, $p = 0.018$, Table 5). The Dunn test showed that total biomass in Area 3 was significantly greater than in Area 2, but that biomass in Area 1 was not significantly different from either Area 2 or Area 3, consistent with the trend seen for the individual species.

An analysis of total nekton by grams dry weight per sample may be thought to be heavily influenced by large blue crabs, especially in this case where crab numbers mirrored the pattern of total nekton biomass (Table 5). To test for this influence, the Kruskal-Wallace analysis was also run on total nekton excluding blue crabs. Results from the test excluding blue crabs also led to a significant conclusion (Table 5). Consequently, the results of the test on total nekton biomass are accepted as indicative of community trends and not just of blue crab trends. The test on total nekton excluding blue crabs is not meant to be evaluated as a separate test, as

Table 5. Site Comparisons

Results of Kruskal-Wallace tests for differences among sampling Areas 1, 2, and 3 (arrows 1, 2, and 3, Figure 1, Chapter 1) on the Goodwin Islands are shown (as calculated by SAS, SAS Institute). Significance was taken at the $p = 0.05$ level. Individual species were tested on numbers of individuals per sample, total nekton were tested on grams dry weight per sample. Only abundant species were tested, but total numbers captured are provided for all nekton encountered. Sampling took place in four days in July and August, 1996, in the Marsh Fringe habitat only (see habitat diagram Figure 5, Chapter 1). Eight replicate samples were used to characterize each area, equivalent to 14 square meters sampled per site. The test on total nekton less crabs is explained in the text of this dissertation.

Site Comparison: Nekton use of Marsh Fringe Habitat, Fall 1996

Species	Area 1 (14 m2)	Area 2 (14 m2)	Area 3 (14 m2)	Test result (K-W stat.)	Test result (signif.)
Callinectes sapidus (inds)	9	4	13	3.41	p = 0.181
Fundulus heteroclitus (inds)	74	60	51	0.96	p = 0.612
Menidia menidia (inds)	26	14	75	0.18	p = 0.914
Palaemonetes spp (inds)	42	15	56	3.31	p = 0.191
Bairdiella chrysoura (inds)	1	0	0	(test was not done)	
Cyprinodon variegatus (inds)	4	0	6	(test was not done)	
Fundulus majalis (inds)	6	2	4	(test was not done)	
Lucania parva (inds)	0	1	6	(test was not done)	
* Total Nekton (gdw)	85.32	56.42	158.05	8.02	p = 0.018
[Total Nekton less crabs (gdw)	32.92	15.97	51.16	6.25	p = 0.044]

Kruskal-Wallace test

* = significant at p = 0.05

this would involve issues of inflated alpha. It is intended only to aid in the interpretation of the test run on grams dry weight of total nekton.

The lack of significant differences in use patterns by any individual species suggests that community composition was similar among areas. The standing stocks of the entire communities did differ among areas, however. The most obvious differences in physical appearance among these areas relate to the energy regimes they experience. Area 1, the primary site, is exposed directly to Chesapeake Bay and receives a fair amount of wave energy on a regular basis. Area 2 (arrow 2, Figure 1, Chapter 1) is similar in gross morphology to Area 1 but lies inshore of several small islands and a series of shallow sand bars. Area 2 is more protected from the wave energy of Chesapeake Bay, and the small bay that abuts Area 2 is somewhat shallower than the similar bay of Area 1. Area 3 sees a very different energy regime from Areas 1 and 2 and the small channel passing between islands here (arrow 3, Figure 1, Chapter 1) experiences strong tidal currents at every tide as water is exchanged between the York River to the north and the open area to the south. Area 3 is morphologically different from both Areas 1 and 2. The marsh edge in places is reticulated with tiny marsh-islands that are a few meters across. The water adjacent to the marsh in Area 3 is somewhat deeper than in the other areas, sediments in general are coarser, and the ratio of tall form/short form *Spartina alterniflora* is greater. Associated with the differences in energy regime between Areas 1, 2, and 3 are many linked factors including sediment type, flora, detrital exchange rates from the marsh surface, water depth, and more. While it is premature at this point to assign causes to the differences in nekton biomass seen among these areas, it seems likely that energy regimes, or factors correlated to energy regimes, may play a part in determining these differences.

Area 1, the primary sampling area, appears to be fairly representative of bay-exposed marshes at the Goodwin Islands since no significant differences were found between it and either sites 2 or 3. Ayers (1995), however, conducted a comparison study between bay-exposed and protected creekbank marshes at the Goodwin Islands in 1994 and found significant

differences between these types of areas. Ayers' creek sites were located in the small tidal creek that separates the easternmost main island from the smaller islands, about 400 m east of my Area 1 (Figure 1, Chapter 1). Her exposed sites were located at my Area 3. Ayers' creek marsh was characterized by considerably higher fish densities and biomass, mostly of marsh resident fishes, than was the exposed site. Species composition in the exposed marsh was less dominated by marsh resident fishes, and was more variable over the sampling season than it was in the creek marsh. While my Area 1 may be representative of bay-exposed marshes within the Goodwin Islands system, it almost certainly sees very different use by nekton in comparison to local creekbank marshes such as studied by Ayers.

Year-to-year variation in nekton use of the salt marsh surface

Utilization of the marsh surface was compared between 1995 and 1996 by sampling in all marsh surface habitats. The design of this comparison is described in the methods section. This study found a significant difference in abundance of blue crabs (*Callinectes sapidus*) on the marsh surface between 1995 and 1996 (Wilcoxon-Mann-Whitney test, chi-sq = 4.31, p = 0.038, Table 6). No statistical differences were found between years for biomass of total nekton, or for use by any individual species other than blue crabs (Table 6). The difference in use by blue crabs was primarily due to a poor recruitment of juvenile crabs to these habitats in 1996; similar year-to-year variation for juvenile blue crab recruitment has also been seen in seagrass beds (Orth and van Montfrans 1987). To conclude, I found that significant year-to-year variation in use of the marsh surface did exist for the blue crab, but not for any of the other species that were abundant in these years. Similar variation in use of marsh habitat by one or more species is documented in Werme (1981), Orth and van Montfrans (1987), Rulifson (1991), Rountree and Able (1992) and Yozzo and Smith (1998).

Table 6. Year-to-Year Comparisons

Results of Wilcoxon-Mann-Whitney tests for differences in abundance of nekton between 1995 and 1996 are given. Significance was taken at the $p = 0.05$ level. Individual species were tested on numbers of individuals per sample, total nekton were tested on grams dry weight per sample. Only abundant species were tested, but total numbers captured are provided for all nekton encountered. Sampling took place on four dates in August and September, 1995, and on the same dates in August and September, 1996, in all marsh surface habitats (see habitat diagram, Figure 5, Chapter 1). Twelve replicate samples were used to characterize each time period, equivalent to 21 square meters sampled per year.

Year-to-Year Comparison:
Nekton use of the Marsh Surface, Fall 1995 and 1996 (Area 1)

Species	1995 (21 m2)	1996 (21 m2)	Test result (chi-sq)	Test result (significance)
* *Callinectes sapidus* (inds)	76	7	4.31	p = 0.038
Fundulus heteroclitus (inds)	27	50	0.83	p = 0.363
Lucania parva (inds)	10	51	1.19	p = 0.276
Palaemonetes spp (inds)	214	659	2.93	p = 0.087
Bairdiella chrysoura (inds)	0	1	(test was not done)	
Chasmodes bosquianus (inds)	1	0	(test was not done)	
Cynoscion nebulosus (inds)	2	0	(test was not done)	
Fundulus majalis (inds)	11	3	(test was not done)	
Gobiosoma bosc (inds)	9	6	(test was not done)	
Gobiesox strumosus (inds)	3	0	(test was not done)	
Hippolyte spp (inds)	0	1	(test was not done)	
Menidia menidia (inds)	10	13	(test was not done)	
Total Nekton (gdw)	121.35	110.14	0.05	p = 0.817

Wilcoxon-Mann-Whitney test
* = significant at p = 0.05

Table 7. Diel Use of the Marsh Surface

Results of Wilcoxon-Mann-Whitney tests for differences in abundance of nekton on the marsh surface between day and night high tides are given. Significance was taken at the $p = 0.05$ level. Individual species were tested on numbers of individuals per sample, total nekton were tested on grams dry weight per sample. Only abundant species were tested, but total numbers captured are provided for all nekton encountered. Sampling took place on four paired day/night high tides in August and September, 1996, in all marsh surface habitats (Figure 5, Chapter 1). Twelve replicate samples were used to characterize each time period, equivalent to 21 square meters sampled.

Diel Use of the Marsh Surface, August - September 1996 (Area 1)

Species	Day (21 m2)	Night (21 m2)	Test result (chi-sq)	Test result (significance)
Fundulus heteroclitus (inds)	50	17	2.85	p = 0.092
Lucania parva (inds)	51	8	2.23	p = 0.136
* *Menidia menidia* (inds)	13	50	7.74	p = 0.005
Palaemonetes spp (inds)	659	640	0.19	p = 0.664
Bairdiella chrysoura (inds)	1	0	(test was not done)	
Callinectes sapidus (inds)	7	5	(test was not done)	
Cyprinodon variegatus (inds)	0	5	(test was not done)	
Fundulus majalis (inds)	3	0	(test was not done)	
Gobiosoma bosc (inds)	6	2	(test was not done)	
Hippolyte spp (inds)	1	0	(test was not done)	
Morone saxatilis (inds)	0	2	(test was not done)	
Total Nekton (gdw)	110.14	73.06	0.08	p = 0.773

Wilcoxon-Mann-Whitney test
* = significant at p = 0.05

Diel patterns of nekton use of the salt marsh surface

Significant differences in diel use patterns were seen in Atlantic silversides, *Menidia menidia*, but not for any other species or group (Table 7). Several species were not sufficiently abundant to include in the statistical analysis; for these only the total numbers caught are listed in Table 7. Palaemonid use of the marsh surface was very similar between day and night. No significant differences between day and night use were detected for abundances of any species of fundulid. Interestingly, a trend existed towards greater abundance of marsh resident fishes during the day, but this trend was not statistically significant. It is also of interest that two juvenile striped bass were captured in marsh habitats at night. One was sampled on the marsh edge, the other was captured 5 meters onto the marsh surface. No striped bass were ever caught during the day in almost 300 drop samples I have taken during the three years of this and other drop ring projects at the Goodwin Islands.

Menidia menidia was seen to be significantly more abundant on the marsh surface at night high tides than at day high tides (Wilcoxon-Mann-Whitney test, chi-sq = 7.74, p = 0.005, Table 7). During the day, *M. menidia* was present in only two of twelve samples, and one marsh edge sample of 11 fish accounted for 85% of the sampled individuals. At night, *M. menidia* was captured in 10 of 12 samples, with the largest sample (19 fish) accounting for 37% of the sampled individuals. Moreover, *M. menidia* was found in all habitats on the marsh surface at night and was most abundant in the marsh interior. Unfortunately, sample sizes were too small for analysis with the Cochran-Mantel-Haenszel test for linear association. Despite this, results suggest that patterns of distribution on the marsh surface (as well as the overall abundance of silversides) differ between day and night high tides.

These fishes are reported to be more abundant at night than during the day in drainage ditches (Schmelz 1964) and tidal creeks (Rountree and Able 1993, but see Reis and Dean 1981). To my knowledge this dissertation is the first study to capture silversides on the marsh surface at night, though night use of intertidal marsh creeks has been documented (Shenker and Dean 1979, Rountree and Able 1993). Atlantic silversides are known to deposit eggs in intertidal

habitats (Tewksbury and Conover 1987) but this may occur primarily during daytime high tides (Rountree and Able 1993). *Menidia menidia* are visual daytime feeders (Adams 1976c) and gut content examinations of my night-caught fishes did not give any indications of active feeding at night. Only 10% (4 out of 39) of night-caught fish had even a minimal amount of food in the guts, compared to 92% (12 of 13) for day-caught fish. Spawning in this species takes place through July (Fay *et al.* 1983) and my sampling dates for the diel study were between August 29 and September 14, 1996. Neither feeding nor reproduction can explain this night time use of the marsh surface by silversides. The spatial pattern of silversides on the marsh surface at night high tides appears to be a spreading out over the marsh interior. Rountree and Able (1993) suggest that *M. menidia* uses marsh habitats at night as refuge from predation. Similarly, I suggest that *M. menidia* swims onto the marsh surface at night for the primary purpose of obtaining refuge from predation by larger fishes in deeper waters.

Comparisons to SAV and unvegetated habitat

SAV habitats supported greater numbers of species than did marsh or unvegetated habitats (Figure 4). SAV habitats also supported a significantly higher biomass of crustaceans than did the marsh interior habitat (Table 4 G). Of marsh habitats, the marsh edge at high tide had the highest abundance, biomass, and diversity of nekton, though this trend was in general not statistically significant (Table 4). The marsh edge supported a biomass of crustaceans and of fishes that was very close to that supported by the SAV habitat at high tide (Table 4 G, I, J). Numbers of individuals and species richness, however, were generally lower at the marsh edge than in the seagrass bed (Figure 4).

Lowtide unvegetated and SAV habitats were used as a refuge for marsh surface species, which were rarely caught in these habitats at high tide. This lowtide refuge use probably accounts for the generally greater densities and biomasses in unvegetated and SAV habitats at low tide compared to the same habitats at high tide.

At high tide most species of fishes and crustaceans were significantly more abundant and numerous in marsh or SAV habitats than in unvegetated habitats (Table 4 A - F). This was also true for total fish biomass (Table 4 I) and for total nekton biomass (Table 4 J). At low tide, however, the shallow unvegetated habitats supported large numbers of nekton, primarily of those species found on the marsh surface at high tide (Figure 3).

Most of the abundant species were found to use all three habitat types (marsh, unvegetated, and SAV) at one stage of tide or another. Blue crabs, the biomass dominant of the study, were present in every habitat at every tide. *Palaemonetes pugio*, the numerical dominant of the study, also occupied marsh, SAV and unvegetated habitats in large numbers. In fact, the Lowtide Shallow (unvegetated) habitat supported the greatest densities of *P. pugio*, though the species showed a clear aversion to deeper unvegetated habitats. Fundulids, the numerically dominant group of fishes, preferred marsh surface habitats over SAV habitats at high tide. At low tide, marsh resident fishes sought refuge in especially the Lowtide Shallow and Lowtide SAV habitats (Table 4 H, non-significant trend). Of abundant species, *Palaemonetes vulgaris*, *Palaemonetes intermedius*, *Hippolyte spp*, and *Gobiosoma bosc* had the greatest affinity for SAV habitats over marsh and unvegetated habitats. *Fundulus majalis* was the only abundant species never found in SAV beds, even at low tide.

Nine species were found in all three habitat types. In order of abundance, these were *Palaemonetes pugio*, *Callinectes sapidus*, *Fundulus heteroclitus*, *Lucania parva*, *Symphurus plagiusa*, *Gobiesox strumosus*, *Leiostomus xanthurus*, *Bairdiella chrysoura*, and *Cyprinodon variegatus*. In the months of August through October (when all habitats were sampled) these nine species made up 65% of the total numbers and 86% of the total biomass collected. Since organisms were redistributed at every tidal cycle, it is reasonable to assume that a fair amount of exchange does take place between the three habitat types. It is important to note that these numbers (65% and 86%) do not represent the percent of the community that actually moves from habitat to habitat, since certain individuals of a species may remain in a single habitat. These numbers show the potential importance of movements between habitats. The

species which used all three habitat types at one stage of tide or another represented the largest part of the sampled communities.

In this sampling area, SAV, unvegetated, and marsh habitats are found in close proximity and together characterize the shallow nearshore region. This is in part due to the shallow water depths, and to the presence of *Ruppia maritima* as the dominant seagrass. *Ruppia* exists inshore of *Zostera marina* at the Goodwin Islands (Buzzelli 1995); *Ruppia* occurs within 5 to 15 meters of marsh habitat at most of this area. Similar habitat structure can be provided by *Halodule wrightii* as well (Thomas *et al.* 1990) but, at least at the Goodwin Islands, *Zostera marina* exists further from the marsh surface (Buzzelli 1995). Most of the species inhabiting the shallow waters I sampled move from marsh to unvegetated to SAV depending on tide stage. In this sampling area, these habitats are intimately connected by mobile fauna. Indeed, the regular use of all 3 habitat types by so many of these species may be considered as evidence for the importance of this juxtaposition of habitats to these populations of nekton.

CONCLUSIONS

General findings

Diversity, abundance, and biomass of nekton were high in this study; 32 different species were captured with a mean abundance for all habitats, dates and tides of 28.6 inds m^{-2} and a mean biomass of 3.8 gdw m^{-2}. Nonetheless, these numbers are low in comparison to similar studies in different geographic regions (notably the western and central Gulf of Mexico). Crustaceans were clearly the dominant natant taxon in my study. Blue crabs were the biomass dominant in every habitat except the Shallow Unvegetated at low tide (where palaemonid shrimp were dominant). Palaemonid shrimp were the numeric dominant in every habitat except the Hightide Unvegetated (where blue crabs were most abundant). Mummichogs were the fish species captured in highest numbers, although naked gobies were the most abundant fish in seagrass beds, and sampling effort was not equal between SAV and marsh habitat. Fishes made up 75% of the number of species captured and contributed most to the diversity (richness) of these habitats.

Species-specific findings

This study found that patterns of habitat use for several species differed from reports from other geographic regions. These and other species-specific findings are outlined below. It seems clear from these results that generalizations in patterns of use by shallow water fishes should be applied from one region to another only with caution.

Mummichogs were the dominant fundulid species, as has been found in other studies. At high tide, they and other fundulids were found almost exclusively on the marsh surface. At slack high tide, the density of mummichogs increased significantly with distance onto the marsh surface, but mean size of fish decreased significantly with distance onto the marsh surface.

Rainwater killifish, the second most abundant fundulid captured in my study, was seen primarily to move out of SAV and unvegetated habitats and into marsh habitats at high tide. *L. parva* is reported in other regions as abundant in both SAV and marsh areas at high tide (Rozas and Minello 1998 in press).

Striped killifishes were found to use marsh interior habitats at high tide, whereas Weisberg (1986) reported that they primarily used subtidal areas at high tide along the Atlantic coast.

Naked gobies were only rarely caught on the marsh edge and never in the marsh interior in my study, but were the most abundant fish in SAV beds at high tide; in other Virginia and Gulf coast studies they are reported as very abundant in marsh habitats (Zimmerman and Minello 1984, Rakocinski *et al.* 1992, Peterson and Turner 1994, Yozzo and Smith 1998, Rozas and Minello 1998 in press.)

Atlantic silversides were seen to use the marsh surface in high numbers at night, but apparently not for purposes of feeding or reproduction. Their pattern of spatial distribution on the marsh surface at night appeared to be a spreading out over marsh interior areas.

Marsh transient fish species were relatively abundant in August and September at marsh edge habitats (1.3 ± 0.4 inds m^{-2}) but were not abundant in other marsh habitats at other times of year during the day. Two juvenile striped bass were caught on the marsh surface at night in 1996.

Blue crab recruitment to marsh edge habitats is hypothesized to be an important aspect of blue crab life history in Chesapeake Bay; this has been found in other areas but not in Chesapeake Bay (Thomas *et al.* 1990, Rozas and Minello 1998 in press). However, year-to-year variation in this recruitment was also found to be statistically significant, with lower recruitment in 1996. Biomass of larger blue crabs were found to be especially large in SAV and marsh edge habitats.

Palaemonids were the numeric dominant in all areas except the deeper unvegetated habitats. At low tide, *Palaemonetes pugio* was more abundant in shallow (0 - 10 cm) unvegetated habitats than in deeper (10 - 30 cm) unvegetated habitats. *P. pugio* showed a clear spatial partitioning with *P. vulgaris* and *P. intermedius*, but *P. vulgaris* and *P. intermedius* appeared to be sympatric.

Habitat flexibility.

Regional differences in fish use of shallow water habitats were seen between this study and those conducted at other marshes. This was true for mummichogs, rainwater killifish, striped killifish, naked gobies, *Palaemonetes intermedius*, and blue crabs. Other examples can be found in the literature of variation in use of shallow water habitats by the same species in different regions (Herke 1971, Able 1984). I suggest that marsh nekton show behavioral flexibility in regional utilization of habitats. This flexibility may be in response to differences in hydroperiod, tidal regime, marsh morphology, prey availability, predation, or other factors.

Habitat-specific findings

Each of the 8 sampled habitats was used differently by nekton, pointing out the complexity of animal-habitat interactions in these shallow water areas. In general, SAV habitats were inhabited by the greatest numbers of species and of individuals. Marsh habitats showed clear differences between marsh edge and marsh interior areas, with greater numbers, diversity and biomass captured on the edge. Marsh interior habitat saw greater use by certain marsh resident species, however, notably mummichogs and striped killifish. The marsh edge habitat was similar in biomass to SAV habitats at high tide, but as a general trend contained fewer individuals and lower numbers of species than did the SAV habitats. The unvegetated habitat at high tide contained significantly lower abundance and biomass of most species and groups than did either vegetated habitat at high tide, but was used

extensively as a refuge at low tide by marsh residents. This was especially true of the shallow unvegetated habitat, which supported very high numbers of the smaller marsh residents at low tide. Most of the individuals (65%) and biomass (86%) of nekton sampled were species found in all three habitat types (marsh, unvegetated, and SAV) at different stages of tide. It is likely that considerable exchange takes place between these three habitat types as organisms are redistributed with each tidal cycle.

Summary

The shallow SAV bed, the intertidal unvegetated, and the marsh surface make up a strip of habitat that borders many undeveloped shorelines. My study and other studies show that this nearshore region supports a diversity and abundance of marine life. Interactions between animals and habitats are very complex here, and are dependent on a great many interconnected factors. Due to the intricacies of these connections in natural ecosystems, every effort should be made to preserve these areas in their pristine state.

CHAPTER III. SECONDARY PRODUCTION OF DOMINANT SALT MARSH NEKTON

ABSTRACT

Marshes are generally thought to be very productive ecosystems, yet production studies of marsh nekton are rare. I used the size-frequency and allometric equation techniques to estimate the secondary production of marsh nekton, including *Fundulus heteroclitus* and *F. majalis*, *Lucania parva*, and *Palaemonetes pugio*. The results from the two techniques were similar. Total marsh surface production was estimated at 7.4 - 8.0 gdw m^{-2} 150 d^{-1} (28.4 - 30.7 gww m^{-2} 150 d^{-1}) for the area flooded at mean high tide if corrected for poorly sampled small size classes and for the removal efficiency of the gear. These community estimates are lower than what has previously been reported for production of *F. heteroclitus* alone. An argument is developed to show that previously reported high estimates for this species may not truly be applicable. Marsh surface production of the larger size classes of resident fishes may be less than is generally believed. Marsh-derived production of transient users was evaluated using allometric equation techniques. Production was estimated at 1.1 gdw m^{-2} 150 d^{-1} (4.2 gww m^{-2} 150 d^{-1}) for the entire marsh area flooded at mean high tide if corrected for gear removal efficiency; the value of blue crab (*Callinectes sapidus*) production per square meter of marsh edge habitat was estimated at 6.0 gdw m^{-2} 150 d^{-1}, or 22.1 gww m^{-2} 150 d^{-1}. These results are within the ranges reported for other productive shallow water ecosystems. As is true of previous marsh production studies, my work did not quantitatively sample the smallest size classes of nekton. The results described above were corrected conservatively to account for this. Recent quantitative work indicates that production of the smallest size classes may be very high, yet at this point it is unclear how high. A study to examine production of larval and juvenile nekton on the marsh surface is much needed.

The contribution of marshes to estuarine secondary production includes the quantified production values as well as unquantifiable marsh functions. Marshes have a refuge value, particularly for small size classes of nekton; this refugia allows populations to develop. Marshes are available over broad spatial scales and are relatively stable on temporal scales from seasons to years to decades in the Mid-Atlantic and elsewhere. The value of marshes may be of greater importance when considered on time scales longer than one year. These and other unquantifiable marsh attributes that contribute to estuarine production should not be overlooked.

INTRODUCTION

ESTIMATES OF THE PRODUCTION OF SALT MARSH NEKTON

The value of estimating production

Quantitative studies of marine ecosystems provide estimates of abundance and/or biomass; these are well recognized as vital descriptors of populations and communities. However, analysis of standing stocks alone can be misleading in studies of ecosystem dynamics (Minello and Zimmerman 1992). The analysis of production provides a better characterization of energy flow, growth, and yield (Diaz and Schaffner 1990). The estimation of production is an important step in understanding ecosystem function, and is of particular value in understanding predator-prey relationships (Minello and Zimmerman 1992). At the same time, in some cases the more basic estimation of prey standing stocks can be equally critical. Miller and Dunn (1980) remark that, for transient predators, standing stocks of prey may be a more important factor than production of prey in determining use of an area. Since marsh nekton are both predators and prey, determinations of production as well as standing stock provides a more complete approach to understanding ecosystem function.

Production and growth estimates for salt marsh resident fishes

Production estimates for marsh surface fishes can vary considerably even within one species and one zoogeographic province. Day *et al.* (1989) provide a range of productivity estimates for *Fundulus heteroclitus* from 12.5 to 64.0 gww $m^{-2} yr^{-1}$ (based on 3 studies) and for *F. majalis* of 2.1 to 6.3 gww $m^{-2} yr^{-1}$ (within one study). In general, salt marshes are thought to support very high rates of fish production (Valiela *et al.* 1977, Meredith and Lotrich 1979, Weisberg and Lotrich 1982a). Growth of individuals is directly linked to production, and growth studies of marsh nekton show a rapid accumulation of tissue. Marsh fishes in their first

season can grow at a rate of 5% of their body weight per day during mid summer (Kneib and Stiven 1978). Weisberg and Lotrich (1982b) report a growth of larger mummichogs in experimental pens at natural density and with free access to the marsh and subtidal areas at 0.342% of body weight per day. While estimates of growth and production vary between marshes, the literature suggests that these areas support high rates of growth and production.

Valiela *et al.* (1977) reported production of mummichogs on the salt marsh surface as 9.1 gdw m^{-2} per season. This was corrected to 16 gdw m^{-2} (64 gww m^{-2}) per season when an estimate for the unsampled smallest age classes was added in. This study was a pioneering work in the field of salt marsh fish ecology, and presents a tremendous amount of valuable information on the dynamics and energetics of salt marsh fish populations. It is possible, however, that the 9.1 gdw m^{-2} and 16 gdw m^{-2} figures represent an error in calculation. An examination of the data in Valiela *et al.* suggests that these numbers may be a ten-fold overestimate. When the mean lengths of fish in each size class of Table 1 of Valiela *et al.* (1977) are entered into the length-weight regressions on page 137 of Valiela *et al.* (1977), values in milligrams are produced which are exactly ten times smaller than what is reported in Table 2 (Valiela *et al.* 1977) as the corresponding mean weights for these fish. For example, the 4.5 cm fish in the upper left of Table 1 (Valiela *et al.* 1977) should have a mean weight of 221 mgdw or 0.221 gdw using the regression on page 137 of Valiela *et al.* (1977). These 4.5 cm fish are shown in Table 2 with a mean weight of 2.21 gdw, and the error is repeated for every group of fish in the table. This error is also evident in Figures 4 and 5 and Tables 2 through 4 in Wright (1972), the thesis upon which this part of Valiela *et al.* (1977) is based.

Furthermore, comparisons to other studies indicate that the weights of fish in Table 2 of Valiela *et al.* (and in the corresponding tables of Wright 1972) are about ten times larger than expected for mummichogs of each size. In my study, 45 mm fish weighed under 0.3 gdw. As above, Table 2 reports 45 mm fish as having a mean weight of 2.21 gdw. The largest fish in Table 2 of Valiela *et al.* (96 mm females) are reported with a weight of 34.52 gdw; similar sized fish in my study weighed just over 3 gdw. Other workers show length-weight

relationships of mummichogs to be similar to those of my study (Meredith and Lotrich 1979, when converted to dry weight). Since the biomass estimates of Table 2 (Valiela *et al.* 1977) are carried throughout the rest of the production estimates in this work, I suggest that the calculations of Valiela *et al.* (1977) represent a ten fold overestimate. If so, then production in dry weight would be 0.91 gdw m^{-2} per season for these fishes, or 1.6 gdw m^{-2} per season if an estimate for the small size classes is added in. The numeric value of the production estimates in Valiela *et al.* (1977) may need revision for reasons of arithmetic, but this does not in any way detract from the ideas presented in this original and insightful paper.

Meredith and Lotrich (1979) investigated marsh creek populations of mummichogs using mark-recapture techniques to develop biomass and production estimates. They calculated an annual production of 40.7 gww m^{-2} yr^{-1} (8 - 10 gdw m^{-2} yr^{-1}) for the subtidal creek area. This calculation is based on an area of tidal creek extending 3 m from the creek bank to the center of the creek. This estimate does not consider the area of marsh surface which the fish would have access to at high tide. Meredith and Lotrich reported that the marsh surface at this site floods for 2.5 hours of a 12.5 hour tidal cycle (20% of the time), and concluded that the fish obtained much of their food from the subtidal areas. Later work at this site by the same lab group, however, showed that mummichogs were in fact deriving a substantial part of their daily ration from the marsh surface (Weisberg *et al.* 1981, Weisberg and Lotrich 1982). The estimate of Meredith and Lotrich was not intended to estimate marsh surface production, and is difficult to interpret with reference to production per m^2 of marsh. It remains, however, an important work as regards production in a creek population of mummichogs.

The data reported in Wright (1972), Valiela *et al.* (1977) and Meredith and Lotrich (1979) are the evidence most often cited for high fish production on the marsh surface. In my opinion, none of the values cited in these papers actually represent production of fish per m^2 of marsh surface. The estimate of Meredith and Lotrich (1979) is based on a subtidal habitat, and the other two studies may include an error of arithmetic. Production values for mummichogs in

marsh surface habitats may be somewhat less than 40 - 64 gww m^{-2} yr^{-1}, as is often quoted from these studies.

In spite of this, it is quite possible that production of marsh surface fish is relatively high. Most studies of production of marsh surface nekton sampled only the larger size classes (Wright 1972, Valiela *et al.* 1977, Meredith and Lotrich 1979, my study). While these production studies include estimates for the contributions of the very small fishes, the estimates were not based on actual sampling and were intended as minimum estimates by the authors. These studies (my own included) may substantially underestimate production by failing to properly sample the smallest size classes and by using very conservative estimates for their production.

Fish production estimates for salt marsh tidal creeks

Several excellent production studies exist for nekton in tidal creeks. Weinstein *et al.* (1984) found high densities and production of spot (*Leiostomus xanthurus*) in polyhaline marsh tidal creeks of the York River (Virginia). Production was estimated at 4.6 gdw m^{-2} over a 90 day period. Weinstein and Walters (1981) found lower spot production in a North Carolina creek and estimated that 0.05 gdw m^{-2} were produced over a 7 month period from March through September. The extent to which the nekton in tidal creeks may benefit from marsh surface resources remains unknown, but in particular the study by Weinstein *et al.* (1984) shows that creek habitats can be highly productive.

Production of palaemonid shrimp

Welsh (1975) conducted a very thorough study of the ecology of *Palaemonetes pugio* in a Rhode Island embayment. Production of shrimp biomass and eggs during the late summer ranged from about 0.1 to 0.25 gdw m^{-2} d^{-1}, equivalent to between 3 and 7.5 gdw m^{-2} per month. This study took place in a very shallow, highly productive salt marsh embayment that was also vegetated with seagrass (*Ruppia maritima*) and macroalgae (primarily *Ulva lactuca*).

The subtidal embayment was literally packed with shrimp, particularly in the late summer and fall, when mean densities in the 6600 m^2 subtidal area were around 200 - 300 inds m^{-2}. This embayment was surrounded by 16,800 m^2 of intertidal marsh to form a total area of 23,400 m^2 (Nixon and Oviatt 1973). It is unclear if shrimp in the shallow embayment were making substantial use of the vegetated salt marsh surface at high tide. While Welsh (1975) does not estimate use of the marsh surface itself by these shrimp, this study nonetheless shows the tremendous potential for shrimp production in shallow water habitats.

Sikora (1977) estimated production of *Palaemonetes pugio* in South Carolina at 0.56 g afdw m^{-2} yr^{-1} for the inundated marsh area. This is equivalent to 0.68 gdw m^{-2} yr^{-1} as calculated using approximate conversions from Cummins and Wuycheck (1971). The mean standing crop responsible for this production was 0.11 g afdw m^{-2}, equivalent to 0.13 gdw m^{-2}. Mean densities were highest in early January, at 8.63 inds m^{-2} but were considerably lower in spring and early summer. This marsh surface production estimate is considerably lower than the embayment estimates of Welsh (1975), but densities of shrimp in Sikora are closer to those of my study and of other marsh surface studies. Kneib (1997a) reports ranges of densities of palaemonids on the marsh surface as between 0.6 and 32 ind m^{-2} in a review paper.

Total production of nekton on the marsh surface

To my knowledge, no study has directly estimated the total community production of nekton on the marsh surface during a single year or season. While it is certainly possible to estimate total production by summing species-specific results from disparate studies, this approach is less satisfying because of differences in species use patterns between years and regions. My study provides an estimate of community production by nekton in a single marsh system.

The production of marsh transient species on the marsh surface is particularly difficult to evaluate. Most methods of studying production rely on cohort identification or at least on the assumption of a closed population of organisms. This problem is also encountered in studies of

the production of estuarine transient species as they enter and leave the larger estuary (Deegan and Thompson 1985). The allometric equation methods of Edgar (1990) and of Edgar and Shaw (1995a) can be used in these cases because they do not assume a closed population. These techniques estimate production of somatic tissue per day based on temperature and on size of individual, and are potentially very useful in estimating the production of transient species. These allometric equations do not consider species-specific differences in growth, or take food availability into account, however (Edgar 1990). The equations are unable to account for differences in production as populations move between areas that offer different opportunities for feeding. Nonetheless, since in some cases no other methods can properly be used to evaluate production, allometric equations offer at least a first-order approach to the estimation of production in difficult situations. The estimation of marsh surface-derived production by transient species that migrate between habitats with the tides and use the marsh surface opportunistically is such a difficult situation.

METHODS

SAMPLING AND REPORTING OF THE DATA

Sampling

Drop samples collected for the primary habitat study were also used to estimate production. Quantitative drop ring samples were taken in habitats as depicted in Figure 5, Chapter 1, between June 1995 and October 1995. A full description of the drop ring gear, techniques, and sampling design is provided in Chapter 1 of this dissertation.

Selection of data for cohort or size-frequency production estimates

Two biweekly spring tide sampling periods were collapsed to create monthly estimates of nekton populations in the habitat study (Chapter 2) and the trophic exchange study (Chapter 4). This was done to improve replication, to simplify analysis, and to provide a more even data structure. Poor weather occasionally prevented full replication on three consecutive days per biweekly sampling period. Five replicates, as used in monthly estimates of Chapters 2 and 4, were generally obtained per habitat per month. Collapsing the data set in this way does not violate the assumptions of the habitat or trophic exchange studies, which evaluate patterns of use based on monthly mean values.

In studying production, it would be a violation of assumptions to base cohort or size-frequency calculations on a monthly estimate that was taken as the compilation of two biweekly estimates. Cohort methods of estimating production rely ultimately on the identification of individual cohorts from length frequency histograms. If each histogram contained data from two biweekly periods, then growth of animals during the two weeks between biweekly sampling periods would muddy cohorts, or would create the appearance of two cohorts where in reality only one existed. The cohort-free size-frequency method calculates production on the assumption that collection dates are evenly spaced in time. If two

unequal biweekly sampling periods were combined to form a single monthly estimate, the result would be a data structure in which the animal collections were not evenly spaced in time. Although monthly reporting of the data would bury this violation from view, it would still exist. For these reasons it was considered unacceptable to use the data sets of Chapters 2 and 4 for production estimates. A subset of the data was selected to use single biweekly sampling periods as the basis for these calculations. It is assumed that growth of animals over the three days of each sampling period is negligible in comparison to their growth during the longer interval between sampling periods.

Sampling periods for production work were selected to achieve maximal replication in periods that were evenly spaced in time. In general, sampling periods from June through October took place near the middle of the month, and near the end of the month. Replication was poor in the late August and late October sampling periods, with only five drop samples taken in all habitats on the marsh surface in each of these periods. Of even greater concern, only one drop sample was taken in marsh interior areas during each of these sampling periods. These sampling periods were therefore not considered acceptable for production estimates. To achieve uniform spacing of the remaining sampling periods, samples from the middle period of each month were used for analysis. The end-of-month periods, which were coincidentally more afflicted by poor replication, were ignored. This provided the best available compromise between requirements for replication and for even spacing in time without violating the assumptions of the methods used to calculate production.

Reporting of the data

Production for this study is reported in units of grams per square meter of marsh surface available per time. However, as was seen in the habitat study (Chapter 2) nekton do not use all areas of the marsh surface equally. Abundance of mummichogs was found to increase significantly with distance from the marsh edge, while mean size of these fish decreased significantly with distance from the edge (Chapter 2). Striped killifishes were more abundant

in marsh interior areas (Chapter 2, Table 3) though this was not tested statistically. Mean size of *Palaemonetes pugio* decreased significantly with distance from the marsh edge (Chapter 2). Given the redistribution of nekton with every tidal cycle, it was assumed that mummichogs and *P. pugio* shifted their selection of marsh habitat based on body size (rather than the same individuals remaining in each habitat and, say, growing more rapidly in one habitat than in another). Both cohort and size-frequency methods of determining production depend on an accurate portrayal of the size structure of the entire population. Therefore, the entire horizontal flooding distance of the marsh surface was assessed as a single unit. This accounts for the shifting use of marsh surface sub-habitats by different size classes of nekton.

Sampling for this dissertation took place on spring high tides. Marsh elevation and tidal data revealed that the mean horizontal flooding distance on the dates of sampling was 23 m from the marsh edge. To evaluate production of the entire population of nekton on the marsh at sampled high tides, a hypothetical mean transect of marsh 23 meters long by 1 meter wide is used as a unit of marsh surface, and production is calculated for the entire 23 m^2 area. Figure 5, Chapter 1 shows that sampling took place in habitats on the marsh edge itself, in the marsh "Fringe" habitat < 3 m from the marsh edge, and in the marsh interior > 3 m from the marsh edge. For production calculations, the abundances determined for each habitat were multiplied by the areal extent of each habitat within the hypothetical 23 m^2 transect described above. This provides an estimate of the entire population using the 23 m^2 transect.

It is customary in studies of production to run calculations on the area encompassed by a single sample. In my study, a different approach is necessitated by the mobile nature of the investigated populations, and by their shifts in habitat use with size. The method chosen places unequal emphasis on the samples taken in the different habitats, but it was felt that this approach was conceptually necessary. Production is therefore estimated for the population of marsh nekton assumed to inhabit a 1 m x 23 m transect of marsh that would be inundated during spring high tides. Production is also reported per square meter of marsh at spring high tide, achieved by dividing values obtained for the 23 m^2 transect by 23.

The value of production per m^2 at mean high tide may be a more accurate depiction of nekton use of the available marsh surface than is the value per m^2 at spring high tide. Mean high tide represents the habitat which is regularly available to support these populations. The spring high tide estimates can easily be converted into values per m^2 at mean high tide. It is assumed that the population of marsh resident nekton disperses itself over whatever marsh surface is flooded and available at any tide. The sampled marsh flooded a distance of 16 m at mean high tide, based on marsh elevation and tidal data. The population of resident nekton is assumed not to change between neap, mean, and spring tides, but to be more or less compressed spatially on the marsh surface. Values of production per m^2 obtained at spring high tides for the resident marsh nekton population are multiplied by 23/16 or 1.44 to give values per m^2 at mean high tides. Values are reported both per m^2 at spring high tide and per m^2 at mean high tide.

Populations of marsh resident nekton also feed actively in low tide refuge habitats (Chapter 4). Populations could be quantified or reported from these low tide habitats as well, as in Meredith and Lotrich (1979). In my study, methodological problems prevent this. First, precise surveys of the areal extent and relative elevations of the three sampled low tide habitats were not conducted; this work was only done for marsh surface habitats. Second, and more importantly, the shallow water depths and lack of emergent vegetation almost certainly made gear avoidance by fishes a greater problem in these habitats, though this may be partially compensated for by higher gear removal efficiencies in unvegetated habitats. It is assumed that the dense cover of emergent stems on the marsh surface worked to minimize problems of gear avoidance by fishes. I consider drop ring quantifications taken on the marsh surface to be more reliable than those taken in unvegetated low tide refuge habitat. For these reasons, nekton production is reported per unit of marsh surface available to the populations. Marsh resident fishes and crustaceans also feed at low tide, however, and the resources of the unvegetated and SAV areas contribute significantly to their production.

COHORT METHODS TO ESTIMATE PRODUCTION

Cohort methods

The estimation of fish production is most commonly done using cohort methods. Winberg (1971), Waters (1977), and Bagenal (1978) provide a complete description of these techniques, as do several other authors. All cohort methods (increment-summation, removal-summation, instantaneous growth, Allen curve) rely ultimately on the ability to separately identify cohorts where several are present, or alternatively, to determine that all collected individuals belong to the same cohort (Gillespie and Benke 1979).

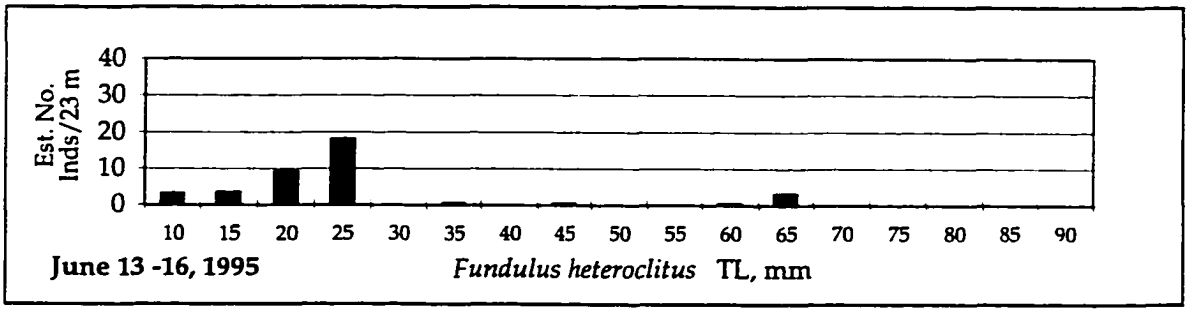
Rejection of cohort methods

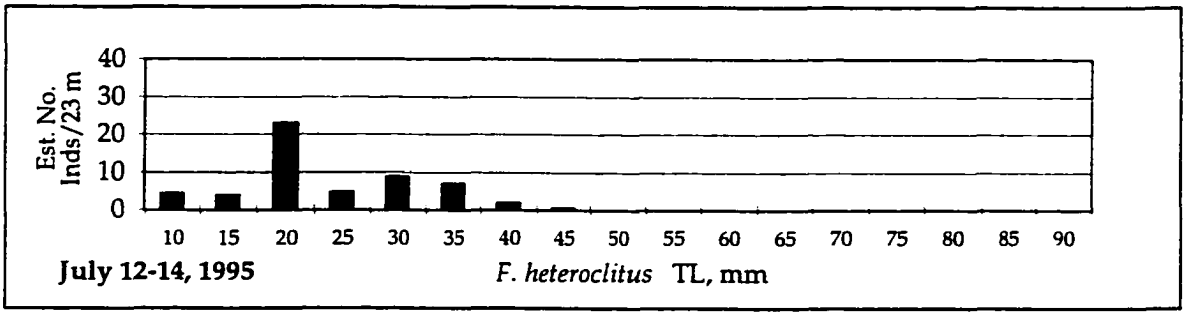
In the case of *Fundulus heteroclitus*, cohorts were not clearly distinguishable (Figure 1). In part this is due to small sample sizes; Anderson and Gutreuter (1983) recommend that at least 100 fish be used to generate each length-frequency histogram; in my case the mean number used was 20 fish ± 1.9 (SE). In contrast, each length-frequency histogram for *Palaemonetes pugio* (Figure 2) was based on well over 100 individuals, except for the June 13 - 16 sampling period when shrimp were much less abundant (note that Sikora 1977 also reported lowest numbers around this time period). Despite these higher sample sizes, Figure 2 does not show clearly separable cohorts for *P. pugio*. This may in part be due to a lack of precision in measuring shrimp; previous workers have measured to 0.5 mm (Sikora 1977, Alon and Stancyk 1982) or 0.2 mm (Kneib 1987b). Precision in measurement of shrimp was not as good in my study.

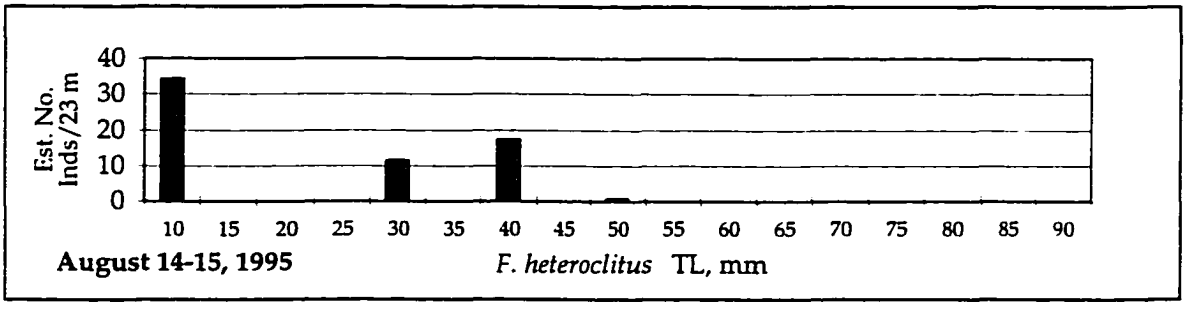
A close examination of Figure 2 suggests that shrimp may be recruiting and growing to a length of 17 - 20 mm or more in the time period between reported samples; this would muddy a cohort analysis. *Palaemonetes pugio* grows rapidly (Wood 1967, Welsh 1975, Sikora 1977, Kneib 1987b). To address this possibility, Figure 3 shows data for all biweekly sampling dates which were properly replicated. Figure 3 also does not reveal recognizable cohorts that would justify a cohort-based analysis of production. It is likely that sampling to recognize cohorts in

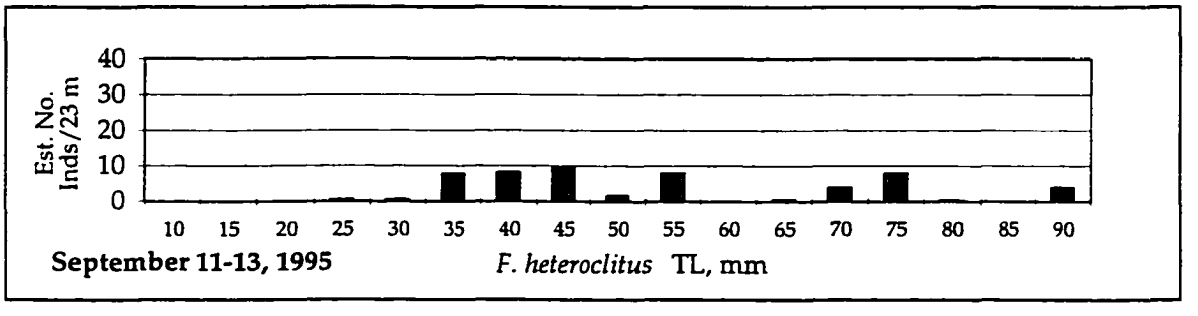
Figure 1. Monthly Length-Frequency Histograms for *Fundulus heteroclitus*

Data are reported per 1 m x 23 m transect of marsh surface, as discussed in the text. Length measurements are in Total Length and represent bin midpoints.









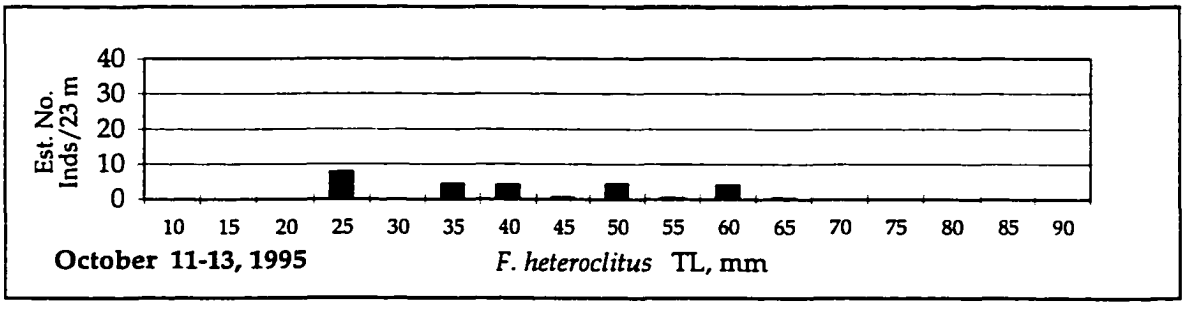
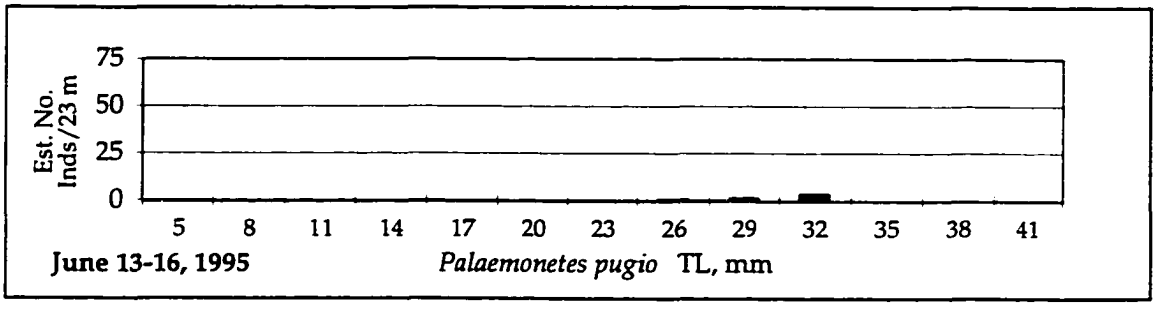
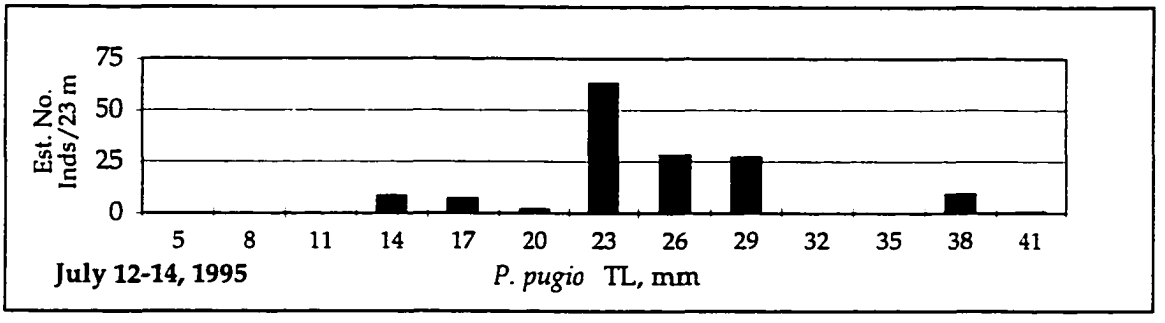
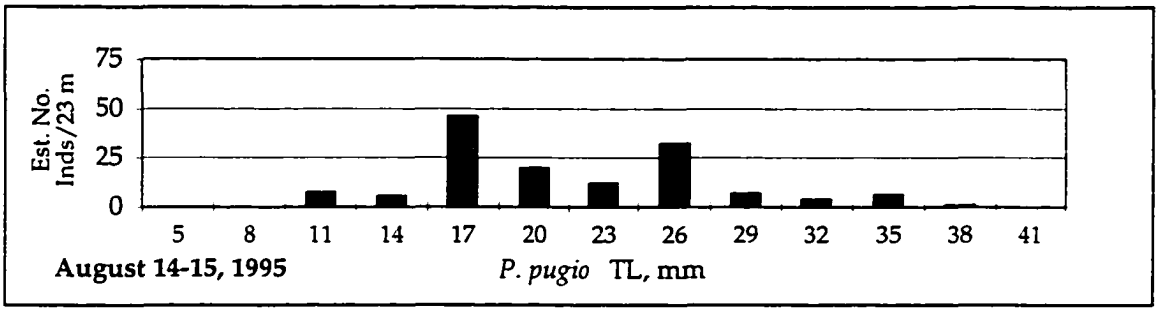


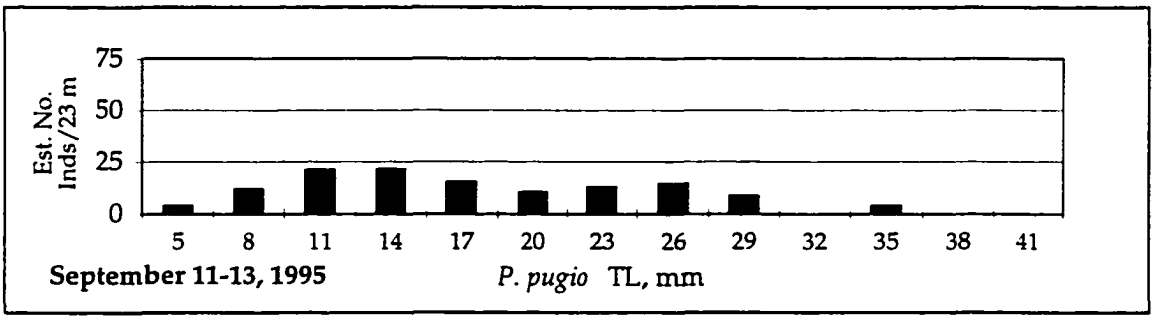
Figure 2. Monthly Length-Frequency Histograms for *Palaemonetes pugio*

Data are reported per 1 m x 23 m transect of marsh surface, as discussed in the text. Length measurements are in Total Length and represent bin midpoints. Note the change of scale in the last graph.









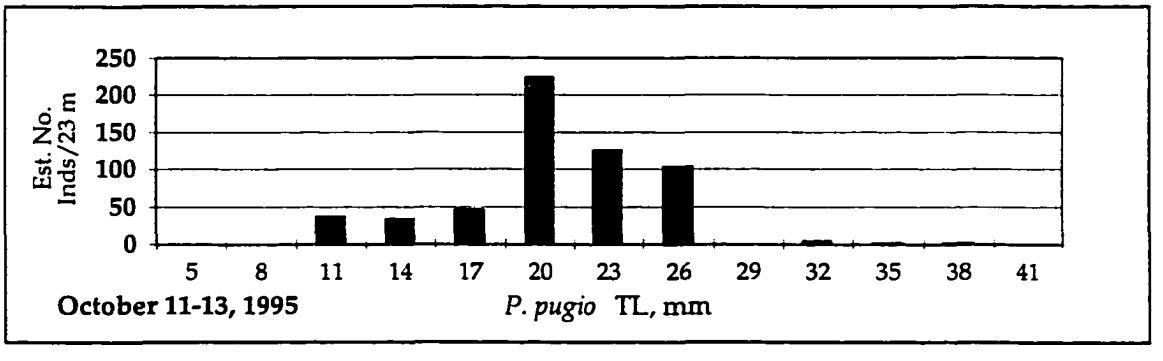
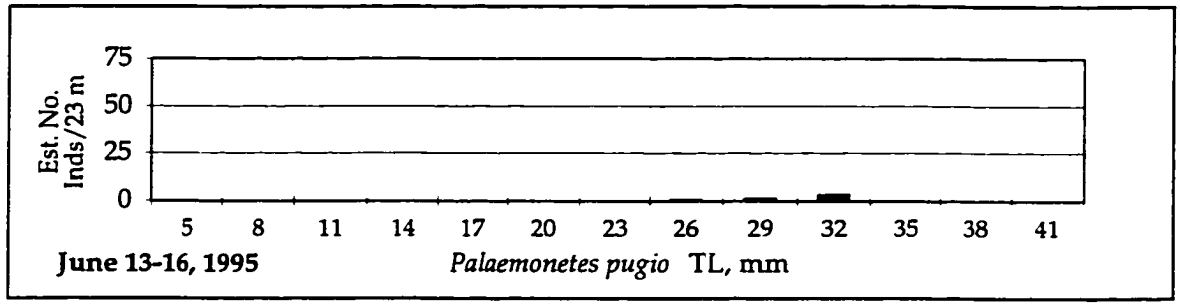
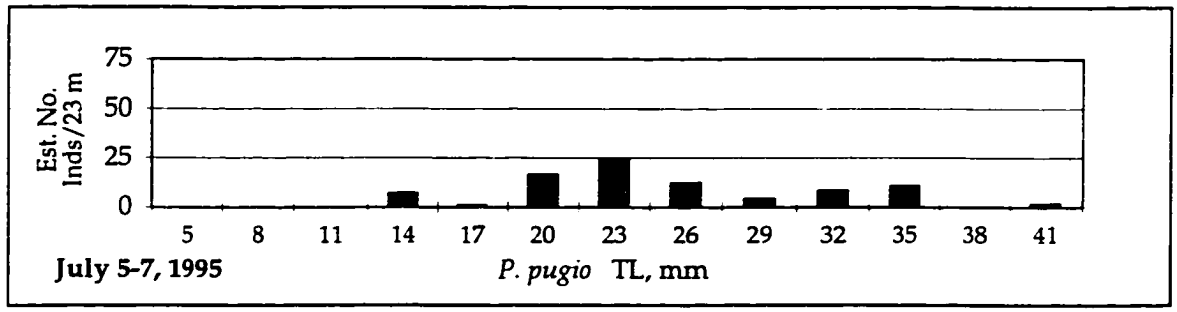
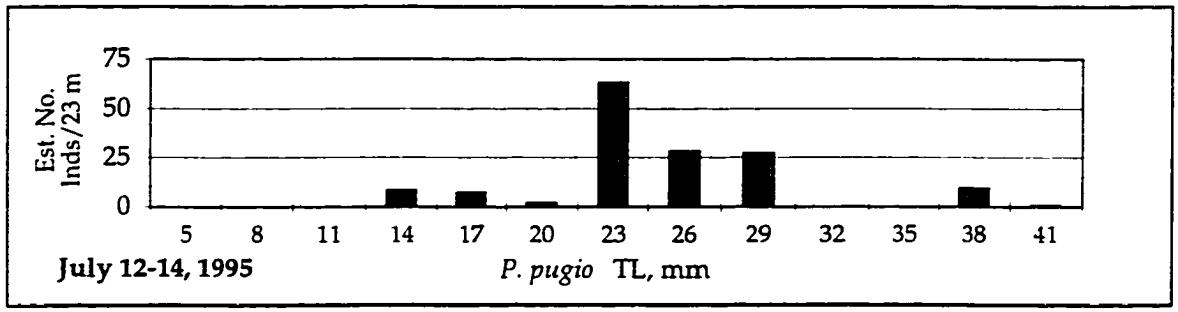


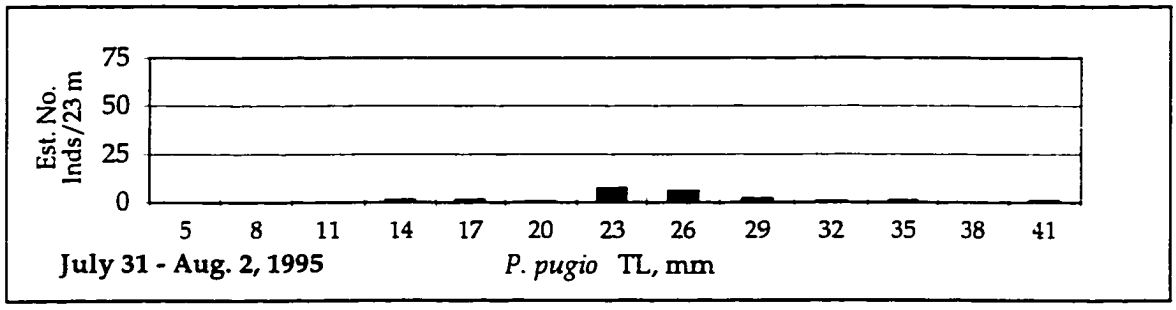
Figure 3. Biweekly Length-Frequency Histograms for *Palaemonetes pugio*

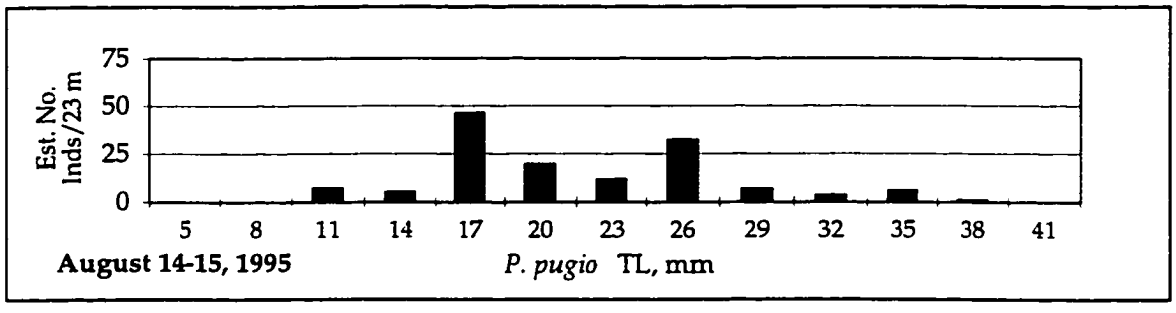
Data are reported per 1 m x 23 m transect of marsh surface. Length measurements are in Total Length and represent bin midpoints. Data for late August and late October are not displayed due to insufficient replication during those sampling periods. Note the change of scale in the last two graphs.

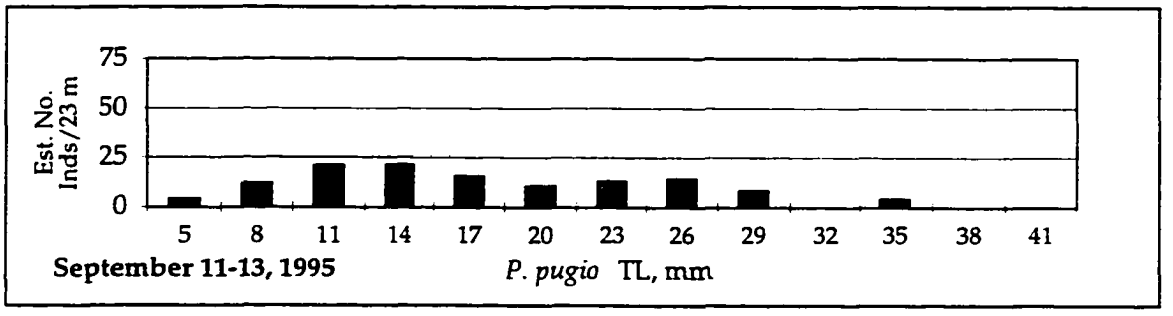


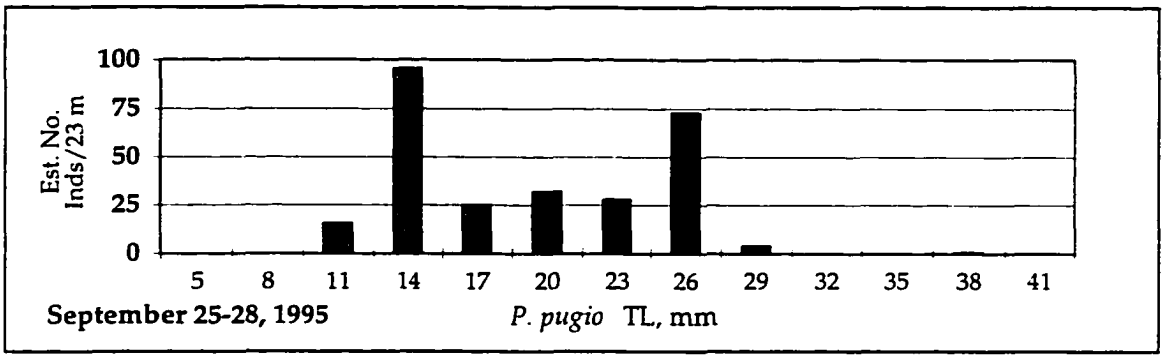


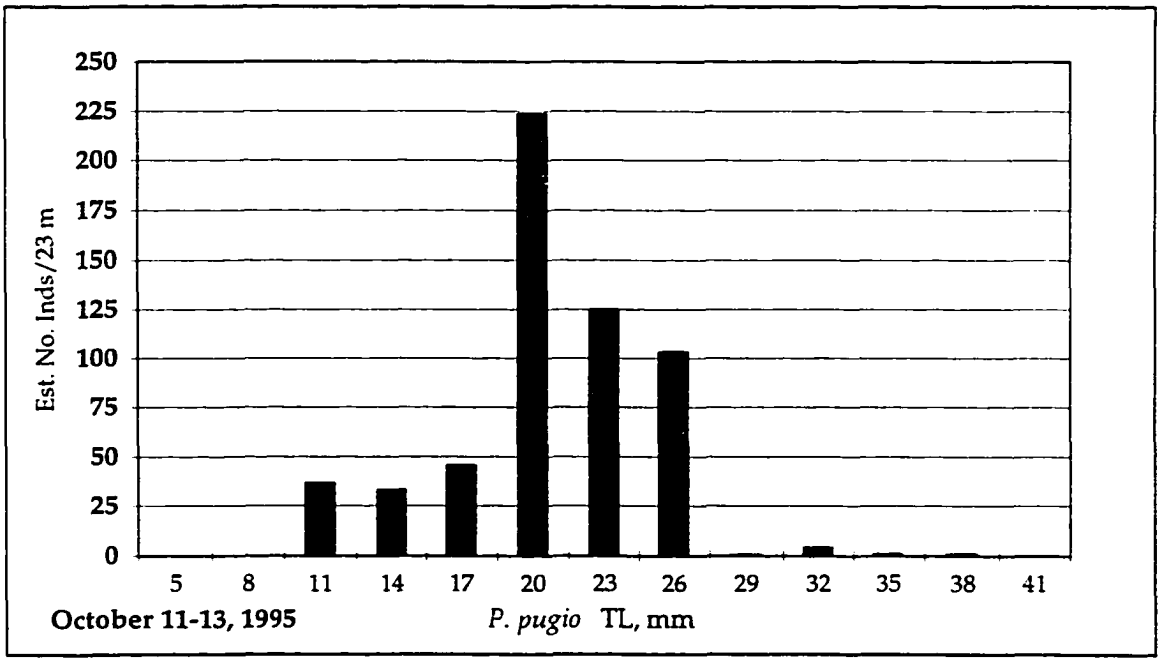












P. pugio would need to take place more frequently than biweekly. Kneib (1987b) sampled shrimp every three days to distinguish cohort patterns, but Sikora (1977) identified cohorts of *P. pugio* based on monthly sampling.

In any case, cohort methods of estimating production were not applied in my study. My data did not allow the clear recognition of cohorts in the common species. Fortunately, methods to estimate production can be employed that do not rely on an ability to separate multiple cohorts. Several of these methods are well described in Waters (1977).

COHORT-FREE SIZE-FREQUENCY METHODS

General explanation

I used the size-frequency method, which prior to 1980 was known as the Hynes method (Hynes 1980) to calculate production. This method examines the abundance and size structure of the entire investigated population over the total time of sampling to estimate production. The size-frequency method is related conceptually to removal-summation techniques (Waters 1977), which use changes in the numbers and size structure of each individual cohort between sampling periods to estimate productivity. The size-frequency method can be applied to a single species or even to mixed groups of similar species. Essentially, the entire sampled population is divided into equal-interval size groups once sampling is complete. Mean biomass per individual and mean abundance is calculated for each size group. The change in numbers between size groups is multiplied by the average change in weight per individual between size groups, and the total of all these calculations is summed to provide an estimate of production.

The size-frequency method has been used primarily to calculate invertebrate production, and has been less commonly applied to the calculation of fish production. Waters (1977) points out, however, that this technique is fully applicable to fish work as well as to invertebrate work. In situations where cohort methods can be applied, modern versions of the size-frequency method have invariably provided estimates of secondary production that are similar to those calculated using cohort methods (Waters 1979). Waters (1979) states that this

method is "well accepted as valid in its basic procedure". Concerns over the accuracy of the method apply primarily to situations in which the basic life history parameters of the species involved are unknown (Waters 1979). In salt marsh ecology, the basic life history parameters of the dominant species have been well studied, and it is expected that the size-frequency method will provide accurate results in this application.

Menzie (1980) compiles ideas from the original papers dealing with the size-frequency method and provides an easily used version of this technique. This is the version which I employ in my study. The basic equation used is:

$$P = \sum_{j=1}^{i} (N_j - N_{j+1}) * (W_j * W_{j+1})^{0.5} \quad \text{where:}$$

P is production over the time period (one year)

i is the number of size categories used

j is used to denote each size category, with j=1 composed of the smallest organisms

W_j is the mean weight of an individual in the j th size category

N_j is the number of individuals that developed into a particular size category during the sampled time period, and where:

$N_j = i * n_j * Pe/Pa * 365/CPI$ such that i and j are as above and:

n is the mean number of individuals in size category j

Pe (= 1/i) is the estimated proportion of the life cycle spent in a particular size category

Pa is the actual proportion of the life cycle spent in a particular size category, to correct for non-linear growth between size categories and the resulting different lengths of time spent in each category

CPI is the cohort production interval in days, from hatching until the largest size class is reached, to correct for voltinism

This equation is very easy to use, at least in comparison to other techniques for estimating production.

Assumptions

The size-frequency method is dependent on several assumptions, and certain requirements of the data must be met. This technique assumes that a closed population has been sampled quantitatively. Sampling must be evenly spaced in time (Hamilton 1969). Population parameters to correct for non-linear growth and voltinism must be known (Menzie 1980). All sampled species or sexes included in a single calculation must potentially grow to the maximum length sampled (Hamilton 1969). The number of samples must be equal to or greater than the number of size intervals used (Fager 1969). Given these assumptions, this method can generate accurate estimates of secondary production (Waters 1979). Further assumptions that are specific to my study are discussed below.

Cohort-free size-frequency methods: application to data

My use of this technique differs from previous studies in that I am estimating production over a time period other than one year. My study took place between June and October, however, and several authors (Valiela *et al.* 1977, Kneib and Stiven 1978) have shown that the great part of growth for mummichogs takes place during this interval. Valiela *et al.* (1977) did not find great changes in population structure between early November fish in a certain age-class and June fish of the next age-class. Therefore, winter growth by the 1 age-class and older fish who survive during the unsampled months is assumed not to drastically affect my production results. My size categories 3 - 5 (Table 1) were grouped to encompass entire age-classes of fish (based on data of Valiela *et al.* 1977), and the value of Pe/Pa was adjusted for each size category to reflect very little growth during the winter months. The same

approach was taken for other marsh resident fishes. Unlike mummichogs, *Palaemonetes* shrimp do experience dramatic population changes over the unsampled months (Sikora 1977). However, this species can reach maturity in 2 to 3 months between June and September (Wood 1967) and since few individuals live from one June through to the next (Sikora 1977), it was assumed that a time period of less than one year could be used in the production estimate without introducing excessive error for this species. Other than the duration of time for which production was calculated, the size-frequency method was used as specified in Hamilton (1969), Waters (1977), and Menzie (1980), and met all the requirements spelled out by these authors.

Cohort-free size-frequency methods: marsh resident fishes

Mummichogs and striped killifishes achieved about the same maximum size in my study, and were grouped together for size-frequency analyses. Values of Pa and CPI were estimated for *Fundulus heteroclitus* from data in Valiela *et al.* (1977), Kneib and Stiven (1978), and Meredith and Lotrich (1979). Of these studies, the size structure of the population reported in Valiela *et al.* (1977) was closest to that of the population I sampled, and this paper provided the primary information used. Values used for Pa and CPI are shown in Table 1. *Lucania parva*, the rainwater killifish, did not attain the same maximum size as *F. heteroclitus* and *F. majalis*. Therefore, a separate size-frequency analysis was conducted for *L. parva*. Pa (relative growth rates between the five size categories) for *L. parva* was assumed to be similar to *F. heteroclitus* and *F. majalis*. *L. parva* is a smaller fish though, and was assumed to grow to a maximum size in two seasons, giving a 365/CPI ratio of 0.5. Values used for *L. parva* are shown in Table 2.

Cohort-free size-frequency methods: *Palaemonetes pugio*

Size-frequency analysis was also carried out for the grass shrimp *Palaemonetes pugio*. Values for Pa were estimated based on the observation by Kneib (1987b) that growth in juveniles is about twice as rapid as in adults. Sikora (1977) found that growth rates remained

constant as adults increased in size. This is also incorporated into estimates of Pa, and accounts for the lack of change in Pe/Pa between the larger size classes (Table 3). The CPI for *P. pugio* was estimated at 5 months based on Wood (1967) and Welsh (1975). The values of Pe/Pa and CPI used in these calculations are shown in Table 3.

Correction for poorly sampled small size classes

The clearing device used to remove creatures from drop rings in my study was ineffective in very shallow marsh surface habitats (Chapter 1). These areas may be used extensively by the smallest size classes of marsh resident nekton (Talbot and Able 1984, Kneib 1997b). I captured very low numbers of small nekton (Figures 1 and 2), and assume that the smallest size classes of nekton were poorly sampled in my project.

Previous studies of production of marsh surface nekton have also sampled only the larger size classes of marsh nekton (Wright 1972, Valiela *et al.* 1977, Sikora 1977, Meredith and Lotrich 1979). Several production studies (Valiela *et al.* 1977, Meredith and Lotrich 1979) include estimates for the contributions of the small individuals. Valiela *et al.* (1977) estimated that production of the small size classes (< 45 mm) was at minimum 44% of the total production by considering that the production of the unsampled 0 age-class fish was equal to the biomass of the captured 1 age-class fish. Meredith and Lotrich (1979) used a conceptually similar approach to estimate that the contribution of poorly sampled size classes (< 60 mm) was at least 78% of the total production.

I did not identify cohorts in my data, so the techniques of Valiela *et al.* (1977) and Meredith and Lotrich (1979) cannot be applied to estimate the contribution of poorly sampled small size classes. Tables 1, 2, and 3 show the size categories (j) used in the size-frequency method, and in each case estimates for the smallest size groups are very low. The individual size categories of this method are thought not to represent actual numbers of individuals when life history parameters are poorly known (Menzie 1980). Life history parameters of abundant salt marsh nekton are well described in the literature, however. Menzie (1980) indicates that

if Pe/Pa and 365/CPI are assumed to be accurate, then Nj for each group does meaningfully represent the number of individuals recruited into that size range over the study period. If these assumptions are made, then the population structure between size categories of Tables 1 - 3 can properly be used to generate estimates for the production of the poorly sampled small size classes.

In my study, the population structure between size categories (Tables 1 - 3) indicated that the j = 3 size class was the first well-sampled size group. To estimate the contribution of small size classes of marsh nekton (Tables 1 - 3) I assumed that the j = 3 size classes were well sampled, then used estimates of mortality to back calculate a corrected Nj for each of the previous size classes. Production was recalculated using the new values of Nj. Mortality was arbitrarily assumed to be 75% between the first and second size group, and 50% between the second and third size group (Tables 1 - 3). In reality, mortality may be much higher (Meredith and Lotrich 1979, Kneib 1993) and my corrections may underestimate the production of poorly sampled small individuals.

Interestingly, 78 individual rainwater killifish (*Lucania parva*) between 9 and 19 mm TL were caught in SAV habitats at low tide, but none in this size range were ever captured from any habitat at high tide. For whatever reason, small rainwater killifish were completely unavailable to the sampling gear at high tide. They may have been using the unsampled very shallow water on the marsh surface. Talbot and Able (1984) captured *L. parva* of this size range in ditches and ponds on the high marsh surface, but it is unclear from my data what habitats these size classes were using in my area at high tide. In any case, the correction for poorly sampled size classes of *L. parva* was carried out as described above for other marsh resident nekton.

Correction for gear removal efficiency

The clearing device used to remove creatures from drop rings did not capture every trapped organism, and gear removal efficiency for marsh residents varied from 78% for

palaemonids (mean) to 99% for cyprinodontids and fundulids in unvegetated habitats (Table 1, Chapter 1). Separate production estimates were generated that have been corrected for these removal efficiencies (Tables 4 and 5). The estimates of Table 1, Chapter 1 were used as correction factors.

COHORT-FREE ALLOMETRIC EQUATION METHODS

General explanation

In addition to using size-frequency methods, I also calculated values of production using published allometric equations. The use of these two independent methods to calculate production provides a valuable check for accuracy of the estimates. In addition, allometric equation techniques can be used to estimate production in situations where the size-frequency method (and other methods) would not be appropriate.

Edgar and Shaw (1995a) report an allometric equation that can be used to estimate somatic production of fishes given biomass (ash-free dry weight) and temperature. This equation is:

$P = 0.00051 * B^{0.69} * T^{1.04}$ where:

P is daily somatic production in grams (ash-free dry weight) per day;

B is individual biomass in ash-free dry weight;

T is temperature in degrees C.

The equation is based on a regression calculated from literature obtained for 62 fish species distributed around the world.

Edgar (1990) provides a similarly derived allometric equation for estimating somatic

production of invertebrates, given individual biomass (ash-free dry weight) and temperature. This equation is:

$$P = 0.0049 * B^{0.80} * T^{0.89}$$ where P, B, and T are as above.

Separate equations are also provided for adult animals and juvenile animals:

$$P = 0.0050 * B^{0.78} * T^{0.92}$$ (adults)

$$P = 0.0063 * B^{0.86} * T^{0.80}$$ (juveniles)

Adults are defined as having attained 70% of published maximum body length. Invertebrates which grow to a size much larger than 1 g afdw were not included in the data set upon which the equation is based.

Assumptions

These allometric equation methods assume that the production of somatic tissue per day is dependent primarily on temperature and on size of individual. The methods assume quantitative sampling of the animals present in an area over the time period of interest, but do not assume a closed population. The methods do not account for differences in production between fast growing species and slow growing species, nor do they account for food availability in the environment (Edgar 1990). Specific factors such as local hypoxia, thermal stress, episodic food events, differing inundation of habitats, etc. are also not accounted for. These methods essentially assume that production of the sampled population is similar to the central tendency of all the production studies upon which the allometric equations were based, dependent only on temperature and on body sizes of the individuals in the populations. Further assumptions specific to my study are discussed below.

Allometric equation methods: application to data

I converted my dry weight biomass estimate for each sampled animal to ash-free dry weight using conversion factors in Cummins and Wuycheck (1971), then applied the allometric equation methods to each individual using the mean temperature of each sampled month. Multiplied by the number of days in a month, this provided a monthly estimate of production. The monthly production estimates obtained in this way were summed to provide estimates for the entire sampling period, June - October 1995. Production estimates were converted from ash free dry weight back into dry weight to provide comparability to results obtained using the size-frequency methods.

Data from the primary habitat study were used for these calculations. Although this data was taken as a mean of replicates from two biweekly sampling periods each month, the allometric equation methods are not sensitive to this data structure as are the size-frequency or cohort methods discussed above. Allometric equation techniques consider each individual animal separately, and do not holistically consider the size structure of the population in each sampling period. Therefore, using the higher replication provided by the biweekly collapsing of the data provides a better basis for allometric techniques than would monthly data based on only one biweekly sampling period. In addition, analyzing different subsets of data with the allometric techniques and the size-frequency techniques provides better independence of the two production estimates.

Data are evaluated per hypothetical transect of marsh surface in a manner similar to that used to calculate size-frequency production estimates. Data are reported as production of the population of marsh resident nekton per mean square meter of marsh at mean high tide, in the same way that size-frequency results are presented. Mean high tide is selected as a more relevant descriptor of marsh utilization than spring high tide, and values are converted to this standard. It must be noted, however, that sampling actually took place at spring high tide.

Assumptions used to convert estimates from spring high tide to mean high tide for marsh residents are discussed in the size-frequency section above.

Corrections for poorly sampled small size classes of marsh resident nekton were applied to production estimates generated by allometric methods. This was done using the relationships between uncorrected and corrected size categories of resident nekton in the size-frequency calculations (Tables 1 - 3). The factor that mathematically converted uncorrected Nj to corrected Nj (Tables 1 - 3) was determined for each size category. These factors were then applied to the appropriate size classes in the raw data. Allometric calculations were repeated on the corrected data, and results are reported for both corrected and uncorrected data.

Corrections for gear removal efficiency were also applied to allometric production estimates for resident and transient marsh nekton. The raw data were converted using the removal estimates of Table 1, Chapter 1 as correction factors. Allometric equations were then used to recalculate production from the corrected data set. Gear-corrected results are reported along with uncorrected results (Tables 4 and 5).

Allometric equation methods: special considerations for marsh transient species

Estimating the contribution of the marsh surface to production of marsh transients was also possible using these techniques. Marsh transient species moved into marsh habitats at high tide, where they are assumed to have fed for the duration of time that each habitat was inundated (see Chapter 4). While these species are not permanent occupants of the marsh, the trophic resources of the marsh do contribute to the growth and production of these animals. This contribution was estimated by applying the allometric equations described above. It was assumed that marsh transients fed equally at all stages of tide in all habitats in which they exist. The portion of time spent per day in marsh habitats was then considered to equal the portion of the total daily production that can be attributed to feeding on the marsh. As applied, the allometric equations predicted total production per day for transient animals that were captured in marsh habitats. This total daily production was multiplied by the fraction of

a day that each marsh habitat was inundated (Chapter 4). Monthly estimates of production are obtained, and these estimates are summed to provide a seasonal total from June through October, 1995.

Results of production calculations for transients are reported per average square meter of marsh at mean high tide. The basic assumptions underlying this manner of reporting data are described in the beginning of this chapter, but transients were not assumed to exist in closed populations. Data obtained for transients per square meter of marsh at spring tide were applied to the area of marsh at other tides as well, without compressing populations into a smaller area. Results are also reported per square meter of marsh edge habitat, since this habitat clearly supported the largest part of marsh-derived production in transient species.

Blue crabs, *Callinectes sapidus*, present an added difficulty in the application of these allometric equations. Blue crabs grow larger than the range of animals making up the invertebrate data set used by Edgar (1990) to construct the equations. While Edgar (1990) suggests that the general invertebrate equation might be applied to larger creatures as well, it is possible that out-of-range problems might occur in applying these exponential equations to very large blue crabs. A previous production study of blue crabs in Chesapeake Bay seagrass beds was reported by Fredette *et al.* (1990), who employed size-frequency and instantaneous growth methods. As a test, the allometric equations of Edgar (1990) and Edgar and Shaw (1995) were applied to the blue crab data of Diaz and Fredette (1981), which contains the raw data used in Fredette *et al.* (1990). Results of this test were compared to their production estimates. Allometric equations consistently produced underestimates relative to the instantaneous growth and size-frequency methods. The closest results were obtained by applying the juvenile invertebrate equation to small crabs (< 1 g afdw) and the fish equation to larger crabs. This approach was used in my calculations. Application of these equations assumes that small blue crabs produce somatic tissue similarly to other juvenile invertebrates, while large blue crabs produce somatic tissue at rates similar to fish. This last assumption is supported in Edgar (1990), where differences in taxonomic group were much less important in predicting production

than were differences in individual mean biomass. Large crabs are similar in size to many of the fish used by Edgar and Shaw (1995) to construct their fish production equation. Nonetheless, comparisons to data and results of Diaz and Fredette (1981) and Fredette *et al.* (1990) suggest that the production values I report for blue crabs may still underestimate the true values.

Calculations for production of transient species are based on daytime sampling. The day-night study reported in Chapter 2 suggested differences in diel use of the marsh surface by striped bass (*Morone saxatilis*), and a refuge use by Atlantic silversides (*Menidia menidia*) at night. Since Atlantic silversides did not appear to be feeding at night (Chapter 2), this use of the marsh surface was not considered in the production of silversides. The refuge value of marsh habitat may be of considerable importance to populations of silversides. Secondary production is based on quantifiable changes in biomass, however, so refuge value was not included in these calculations. The results of the night study for actively feeding marsh transients such as striped bass (2 fish captured) were too limited to apply to model calculations. Although night time use of marsh habitats by larger transient species may be greater than day time use (Rountree and Able 1997), data are not available in my region to generate good estimates for this type of night time use.

A further assumption made for marsh transient species was that variation in use of marsh habitat between spring and neap tides is related primarily to the time period for which habitats are inundated. If marsh transients visit the marsh in lower numbers at neap tide, my estimates will overestimate production. On the other hand, if marsh transients feed more actively in marsh habitats at high tide than they do in other habitats at low tide, then my production values will underestimate the marsh contribution to production. This assumption is also made for marsh residents. The entire population of marsh residents is most likely captive to marsh habitats at both spring and neap tides, so the assumption is more accurate for residents.

As should be obvious from the above discussion, estimates for marsh-derived production of transient species should not be interpreted as precise and flawless quantifications. Production calculations for marsh transient species are carried out to provide a first-order evaluation of an ecosystem function that has not previously been well quantified. Nonetheless, it is believed that the overall approach to calculating this production is sound, and that the results provided do approximate the true values.

Table 1. Seasonal Population Production of *Fundulus heteroclitus* and *F. majalis* per 1 m x 23 m of Marsh, June - October 1995

This table shows the size-frequency procedure used to estimate production of *Fundulus heteroclitus* and *F. majalis*. Data are calculated per 1 m x 23 m transect of marsh surface, as discussed in the text. Equations and symbols used are discussed in the text, and in Menzie (1980). Corrections for poor sampling of small size classes are shown in parentheses. Values are provided for production per square meter of marsh area inundated at mean spring high tide and per square meter inundated at mean high tide.

Production of *F. heteroclitus* and *F. majalis* per 1 m x 23 m of Marsh, June - October 1995

j	Size Group (TL)	est. N (inds)	nj (inds)	Wj (gdw)	(Wj*(Wj+1))^0.5 (gdw)	Pe/Pa (ratio)	365/CPI (ratio)	Nj (inds)	Nj-(Nj+1) (inds)	P (gdw)
1	9 - 25 mm	106	21.2	0.021	0.060	1.7	0.42	75.8 (226.4)	32.4 (169.8)	2.0 (10.2)
2	26 - 41 mm	86	17.2	0.174	0.262	1.2	0.42	43.4 (56.6)	15.1 (28.3)	4.0 (7.4)
3	42 - 58 mm	84	16.8	0.394	0.649	0.8	0.42	28.3	20.5	13.3
4	59 - 74 mm	27	5.3	1.068	1.398	0.7	0.42	7.8	6.0	8.4
5	75 - 91 mm	7	1.4	1.829	2.103	0.6	0.42	1.8	1.8	3.7
				(2.417)				(0)		31.4 (43.0)

Mean production per m2 at spring high tide per 150 d = 1.4 gdw (1.9 gdw corrected)
Mean production per m2 at mean high tide per 150 d = 2.0 gdw (2.7 gdw corrected)

Size-frequency method with i = 5, Menzie 1980
Corrections for poorly sampled small size classes shown in parentheses

Table 2. Seasonal Population Production of *Lucania parva* per 1 m x 23 m of Marsh, June - October 1995

Production estimates for *Lucania parva* are shown as determined using size-frequency procedures. Data are calculated for a 1 m x 23 m transect of marsh surface, as described in the text. Equations and symbols used are taken from Menzie (1980) and are discussed in the text. Parentheses are used to indicate corrections for poor sampling of small size classes. Values are provided for production per square meter of marsh area inundated at mean spring high tide and per square meter inundated at mean high tide.

Production of *Lucania parva* per 1 m x 23 m of Marsh, June - October 1995

j	Size Group (TL)	est. N (inds)	nj (inds)	Wj (gdw)	(Wj*(Wj+1))^0.5 (gdw)	Pe/Pa (ratio)	365/CPI (ratio)	Nj (inds)	Nj-(Nj+1) (inds)	P (gdw)
1	9 to 18 mm	0	0.0	0.008	0.022	1.7	0.5	0.0 (92.6)	-3.1 (69.5)	-0.1 (1.5)
2	19 to 28 mm	5	1.0	0.062	0.090	1.2	0.5	3.1 (23.2)	-8.5 (11.6)	-0.8 (1.0)
3	29 to 38 mm	29	5.8	0.132	0.175	0.8	0.5	11.6	11.3	2.0
4	39 to 48 mm	1	0.1	0.233	0.447	0.7	0.5	0.2	0.2	0.1
5	> 48 mm	0	0.1	0.856	0.856	0.6	0.5	0.1	0.1	0.1
				(0.856)				0		1.3 (4.7)

Mean production per m2 at spring high tide per 150 d = 0.1 gdw (0.2 gdw corrected)
Mean production per m2 at mean high tide per 150 d = 0.1 gdw (0.3 gdw corrected)

Size-frequency method with i = 5, Menzie 1980
Corrections for poorly sampled small size classes shown in parentheses

Table 3. Seasonal Population Production of *Palaemonetes pugio* per 1 m x 23 m of Marsh, June - October 1995

This table displays the calculations used to estimate production for *Palaemonetes pugio* (size-frequency method). Data are calculated per 1 m x 23 m transect of marsh surface. The equations and symbols used are discussed in the text and in Menzie (1980). Parentheses are used to show the corrections for poor sampling of small size classes. Values are given for production per square meter of marsh area inundated at mean spring high tide and per square meter inundated at mean high tide.

Production of *Palaemonetes pugio* per 1 m x 23 m of Marsh, June - October 1995

j	Size Group (TL)	est. N (inds)	nj (inds)	Wj (gdw)	(Wj*(Wj+1))^0.5 (gdw)	Pe/Pa (ratio)	365/CPI (ratio)	Nj (inds)	Nj-(Nj+1) (inds)	P (gdw)
1	5 to 12 mm	80	15.9	0.003	0.005	1.8	1	143.5 (3602)	-56.1 (2702)	-0.3 (13.5)
2	13 to 19 mm	181	36.3	0.010	0.016	1.1	1	199.5 (900.6)	-251 (450.3)	-4.0 (7.2)
3	20 to 27 mm	643	128.7	0.027	0.043	0.7	1	450.3	412.9	17.8
4	28 to 34 mm	53	10.7	0.069	0.085	0.7	1	37.4	22.8	1.9
5	35 to 42 mm	21	4.2	0.104	0.130	0.7	1	14.6	14.6	1.9
				(0.163)				(0)		17.3 (42.3)

Mean production per m2 at spring high tide per 150 d = 0.8 gdw (1.8 gdw corrected)
Mean production per m2 at mean high tide per 150 d = 1.1 gdw (2.6 gdw corrected)

Size-frequency method with i = 5, Menzie 1980
Corrections for poorly sampled small size classes shown in parentheses

RESULTS

Size-frequency methods

Production of marsh resident fishes at mean high tide (if corrected for poorly sampled small size classes and for removal efficiency of the gear) was estimated at 3.6 gdw m^{-2} 150 d^{-1}, approximately equivalent to 13.9 gww m^{-2} 150 d^{-1} (Table 4). If uncorrected, production was estimated at 2.1 gdw m^{-2} 150 d^{-1}. Production of *Palaemonetes pugio* was estimated at 3.3 gdw m^{-2} 150 d^{-1} (12.6 gww m^{-2} 150 d^{-1}) with both corrections. The uncorrected estimate was 1.1 gdw m^{-2} 150 d^{-1}. Total corrected marsh resident production is estimated at 6.9 gdw m^{-2} 150 d^{-1} or 26.5 gww m^{-2} 150 d^{-1} (Table 4). The contributions of individual species and groups and the effects of correction factors are shown in Table 4 .

Allometric equation methods

Results of allometric methods to estimate production are presented per square meter of marsh surface at mean high tide over the five month period in Table 4. The results from the allometric and size-frequency methods agreed reasonably well. Total production of marsh resident species, if corrected for small size classes and gear was estimated using allometric equations as 6.3 gdw m^{-2} 150 d^{-1} (24.2 gww m^{-2} 150d^{-1}). If uncorrected, the estimate was 3.8 gdw m^{-2} 150 d^{-1} (14.6 gww m^{-2} 150 d^{-1}).

The allometric technique was also used to estimate marsh-derived production of marsh transient species (Table 4). The gear-corrected production was calculated at 1.1 gdw m^{-2} 150 d^{-1} (4.2 gww m^{-2} 150 d^{-1}). The uncorrected estimate was 0.5 gdw m^{-2} 150 d^{-1} (1.9 gww m^{-2} 150 d^{-1}). Most of the activity by marsh transient species took place at the marsh edge (Chapter 2). Table 5 shows the contribution to production of marsh transient species per square meter of marsh edge over 5 months; a gear-corrected total value of 6.6 gdw m^{-2} (24.8 gww m^{-2}) is estimated. The uncorrected value was exactly half this. Gear correction had a major effect on transient

production in edge habitat because of the large contribution by small blue crabs. These were removed from the rings at an efficiency of only 16% in marsh habitats (Table 1, Chapter 1). As discussed above, production values reported for transients are most likely less accurate than are values for residents. Nonetheless, these estimates represent a reasonable attempt to quantify a relatively unstudied ecosystem function.

Estimates of total production - both techniques

Both production techniques were employed in order to calculate a range of total marsh surface production for all nekton. The corrected value for transient use (which could only be calculated by the allometric equation method) was added to the corrected values estimated using each method for marsh residents, arriving at a range for total somatic production of nekton on the marsh surface of 7.4 - 8.0 gdw m^{-2} 150 d^{-1} (28.4 - 30.7 gww m^{-2} 150 d^{-1}) for the area flooded at mean high tide. If uncorrected for poorly sampled small size classes and gear efficiency, values were about half this (Table 4). A crude estimate for the production of poorly sampled larger transient fishes in marsh edge habitats is provided in the discussion section below.

Table 4. Seasonal Production of Marsh Nekton, June - October 1995

This table shows production of marsh nekton per square meter of marsh inundated at mean high tide. Results from the size-frequency method and the allometric equation method used to estimate production are displayed. The first section of the table shows the total production of populations of resident marsh nekton. The second section, for transient marsh species, shows the portion of production that is estimated to be derived from the marsh surface. As indicated, values in columns are uncorrected, are corrected for poorly sampled size classes of nekton, or are corrected for both poorly sampled size classes and for gear removal efficiency. Totals for the production of various groups are also provided.

Seasonal Production per Square Meter of Marsh Surface (Mean High Tide, June - October 1995)

Species/Group	Size-Frequency * (gdw m-2 150 d-1) data	corr 1	corr 2	Allometric ** (gdw m-2 150 d-1) data	corr 1	corr 2
Population Production						
Fundulus heteroclitus	na	na	na	2.1	2.6	3.1
Fundulus majalis	na	na	na	0.8	1.0	1.2
Both *Fundulus spp*	2.0	2.7	3.2	2.9	3.6	4.3
Lucania parva	0.1	0.3	0.4	0.2	0.4	0.5
Total marsh fishes	2.1	3.0	3.6	3.1	4.0	4.8
Palaemonetes pugio	1.1	2.6	3.3	0.7	1.2	1.5
Total marsh nekton	3.2	5.6	6.9	3.8	5.2	6.3
Habitat-Specific Production						
Callinectes sapidus	na	na	na	0.4	na	1.0
Marsh transient fishes	na	na	na	0.1	na	0.1
Total Production ***	3.7	6.1	8.0	4.3	5.7	7.4

* Method proposed by Hynes, as described in Menzie (1980).

** Methods of Edgar (1990), Edgar and Shaw (1995a).

*** Size-frequency estimate of total production incorporates the allometric equation estimate for *C. sapidus* and transient fishes.

Column "corr 1" is corrected for poorly sampled small size classes

Column "corr 2" is corrected for poorly sampled small size classes and for removal efficiency of the clearing device.

Table 5. Seasonal Production of Marsh Transients,
Marsh Edge Habitats, June - October 1995

This table shows the estimated production of marsh transient nekton per square meter of marsh edge, calculated using the allometric equation method. Only the portions of production for each species that are estimated to have been derived from the marsh edge during periods of inundation are shown. Values corrected for gear removal efficiency are provided in parentheses.

Seasonal Production of Marsh Transient Species per Square Meter of Marsh Edge (June - October 1995)

Species/Group	Allometric Equation Method* (gdw m-2 150 d-1)	
Habitat-Specific Production		
Callinectes sapidus	2.9	(6.0)**
Menidia menidia	0.2	(0.3)
Cynoscion nebulosus	0.1	(0.1)
Bairdiella chrysoura	0.1	(0.1)
Estimated Total Production	3.3	(6.6)

* Methods of Edgar (1990) and Edgar and Shaw (1995a)

** Values in parentheses are corrected for removal efficiencies of the clearing device.

DISCUSSION

Overall comparisons

Kneib (1997a) reports ranges of densities of palaemonids on the marsh surface as between 0.6 and 32 ind m^{-2}, and densities of marsh resident fishes on the marsh surface as between 0.1 and 1.8 ind m^{-2}. The densities reported in my study fall within these ranges. A crude first-order extrapolation from density to production suggests that production values for my marsh should fall within the range of production values for other marshes. At the same time, many marshes in other geographic regions (in particular the Gulf coast) may experience much higher densities of total nekton (see Chapter 2). The marsh I sampled was a narrow open-embayment marsh without tidal creeks. Based on comparisons within the local area (Ayers 1995), this marsh should be less productive than nearby creek marshes. While production in my marsh probably falls within the range of values expected in other marshes, the type of marsh I sampled might also be less productive than some other types of marshes.

Palaemonids

Corrected production of palaemonids was estimated at 1.5 - 3.3 gdw m^{-2} 150 d^{-1}, depending on method (Table 4). The values reported in the literature for production of palaemonids range from 0.56 g afdw m^{-2} yr^{-1} (0.68 gdw m^{-2} yr^{-1}) for *Palaemonetes pugio* on the marsh surface (Sikora 1977) to 1.8 gdw m^{-2} yr^{-1} for *P. vulgaris* in a Virginia seagrass bed (Fredette *et al.* 1990) to 3 - 7.5 gdw m^{-2} for *P. pugio* per month in a shallow embayment (Welsh 1975). The type of habitat and shrimp densities reported by Sikora are much closer to those of my study. Sikora did not correct his estimates for the contribution of poorly sampled size classes, and his value (0.68 gdw m^{-2} yr^{-1}) resembles my uncorrected estimates (0.7 - 1.1 gdw m^{-2} 150 d^{-1}).

Total production of fishes

The corrected estimates for total somatic fish production at my marsh were 3.7 - 4.9 gdw m^{-2} 150 d^{-1} depending on technique (Table 4). Estimates for total production of shallow water fish communities in the geographic region of my study are rare. Adams (1976b) estimated that North Carolina SAV systems produced about 4.6 gdw m^{-2} yr^{-1} of which 78% or 3.6 gdw m^{-2} yr^{-1} occurred in the months of June - October. Adams also reported that marine systems other than seagrass beds typically produce lower values than this. Edgar and Shaw (1995a) estimated production for Australian seagrass areas at 3.82 g afdw (ash-free dry weight) m^{-2} yr^{-1}, and estimated that production was 1.58 g afdw m^{-2} yr^{-1} in unvegetated habitats, and 1.93 g afdw m^{-2} yr^{-1} in mudflat tidal creeks. Pihl and Rosenberg studied shallow bays in Sweden and estimated a total epifaunal production of 3.8 to 5.0 g afdw m^{-2} yr^{-1}, which included crabs, shrimp, and benthic fishes as sampled by drop trap gear. Given that fish dry weight contains about 16% ash (Thayer *et al.* 1973), my estimates are within the range of what is reported in these community studies of shallow water habitats, though some studies of single species production have found considerably higher values. Weinstein *et al.* (1984) estimated production of spot (*Leiostomus xanthurus*) in Virginia salt marsh tidal creeks near my sampling site at 4.6 gdw m^{-2} over a 90 day period. Deegan and Thompson estimated that fish production in the Mississippi delta region for the dominant species *Brevoortia patronus* and *Micropogonias undulatus* was 13 and 23 g m^{-2} yr^{-1} (wet weight) respectively. Based on these comparisons, the values I report for marsh surface fish production in the area I sampled are within the range of values reported for other shallow habitats.

As indicated in the Introduction to this Chapter, it is possible that production by single fish species on the marsh surface is in general lower than has been believed in the past. Several key works that report high production (Wright 1972, Valiela *et al.* 1977, Meredith and Lotrich 1979) cannot properly be applied to the marsh surface (see Introduction). My work suggests that secondary production in marshes may be comparable to secondary production in other shallow water habitats. This should not, however, diminish the perceived importance

of marshes in any way. Most shallow water habitats, including marshes, are very productive. A tremendous body of literature and evidence supports the idea that marshes play an integral and important role in the trophic functioning of the estuary and coastal ocean.

In fact, while marsh surface production of larger adult and sub-adult size classes of mummichogs may be less than has been thought, production of larval and juvenile mummichogs and other marsh residents may be much greater. Growth in these size classes is very rapid (Kneib and Stiven 1978). New techniques have recently been used to quantify the smallest size classes of marsh nekton (Ayers 1995, Kneib 1997b), and densities of juveniles on the marsh surface may be higher than hitherto believed. Kneib (1997b, Table 3) reports an overall mean of 7.2 inds m^{-2} on the marsh surface for *F. heteroclitus*, with higher densities at certain times of year. Ayers (1995) showed high densities of juvenile *F. heteroclitus* in marsh creek habitats in early summer (25 inds m^{-2} in June) though abundances of juveniles in other months and in other habitats was lower. High levels of predation occur in these size classes (Kneib 1987, Kneib 1993) and this mortality in juvenile and larval stages constitutes production which has generally been unaccounted for.

In my study, I conservatively assumed 75% mortality between the first two size categories (Tables 1 - 3) in back-calculating production of poorly sampled small size classes. This is almost certainly an underestimate of mortality (Meredith and Lotrich 1979, Kneib 1993). Likewise, other studies of production on the marsh surface do not account for potentially high mortality of early life stages. Talbot and Able (1984) suggested that the contribution of larval fish populations on the high marsh to secondary production may be substantial. A comprehensive production study which quantitatively samples all size classes of salt marsh nekton is much needed.

Marsh transient species

The contribution of the entire marsh surface to production of transient species (gear-corrected) was estimated at 1.1 gdw m^{-2} 150 d^{-1}, equivalent to 4.2 gww m^{-2} 150 d^{-1} (Table 4) during

the fraction of a day that the marsh was inundated. Most of this production was due to blue crabs, *Callinectes sapidus*, on marsh edges. Corrected for gear efficiency, the marsh edge habitat contributed 6.0 gdw m^{-2} 150 d^{-1} (22.1 gww m^{-2} 150 d^{-1}) to the production of blue crabs and 0.6 gdw m^{-2} 150 d^{-1} (2.6 gww m^{-2} 150 d^{-1}) to the production of transient fishes. These numbers represent only the portion of production obtained in the fraction of a day that marsh edge was inundated.

The production of crabs at the marsh edge (6.0 gdw m^{-2} 150 d^{-1}) is comparable to the 7.7 gdw m^{-2} yr^{-1} size-frequency production estimate of Fredette *et al.* (1990) for blue crabs in a Virginia seagrass bed. Moreover, production at the marsh edge was calculated by assuming that the habitat is submerged only 13.1 out of 24 hours (tidal and elevation survey, Chapter 1). Even given less available time to forage in this habitat, the estimated production of crabs per square meter of marsh edge is similar to production per square meter of nearby SAV habitats. Trophic support for this production is partially derived from unvegetated habitats (Chapter 4) but my data suggest that marsh edge habitat supports the production of a large and commercially important population of blue crabs.

Unsampled marsh transient fishes

Drop ring gear is not effective in the capture of large active fishes (Jacobsen and Kushlan 1987) and no large transients other than American eels (SAV habitats, Table 3, Chapter 1) were captured in my study. For this reason, the contribution of marshes to the production of larger transients may be underestimated by the above numbers. Cicchetti (unpublished 1996 data) conducted a study at the Goodwin Islands between June and September 1996 to sample the erosional marsh edge (Figure 1, Chapter 2) for larger fishes when the tide was at the level of the marsh surface. This project employed a 1.2 m catamaran equipped with a net spool holding 30 m of specially-designed netting. The catamaran was deployed almost silently from the erosional marsh edge, and quickly enclosed 100 m^2 of unvegetated area with the net, that typically included 20 m of erosional marsh edge. Fishes and crabs were raked

along the marsh edge as the net was closed off, forcing nekton into a box-like cod end. Preliminary estimates of removal efficiency were about 50% using mark-recapture techniques.

Cicchetti (unpublished data) found that the abundance and biomass of larger fish species that were absent from drop ring samples was high, with a mean of 0.32 ± 0.07 (SE) inds m^{-2} and 1.52 ± 0.45 (SE) gdw m^{-2} (based on 4 months, 3 replicates per month, corrected for gear removal efficiency of 50%). Biomass-dominant species poorly represented in drop rings were spot (*Leiostomus xanthurus*), bluefish (*Pomatomus saltatrix*), summer flounder (*Paralichthys dentatus*), inshore lizardfish (*Synodus foetens*), and striped bass (*Morone saxatilis*). Spot made up 45% of the 1.52 ± 0.45 gdw m^{-2} reported here. Ten other large benthic or piscivorous species not found in drop ring samples were also captured. This study provides a range for larger fish use of Goodwin Islands marshes.

Cicchetti (unpublished data) collected fish on erosional edge marshes, where larger predatory fishes may be more abundant than on the depositional edge marshes investigated in this dissertation (McIvor and Odum 1988, Hettler 1989a). Results of Cicchetti (unpublished data) therefore cannot be directly applied to the study area used in this dissertation. However, the study does give an indication that use of marshes by larger transient fishes at the Goodwin Islands can be high. If the allometric equation method of Edgar and Shaw (1995) is applied to this data, and if it is assumed that fishes used the habitat for 6 hours out of 24, then the contribution of marsh edge to production in these fishes would be 2.0 gdw m^{-2} 120 d^{-1}. This value represents only those larger species which were not captured in drop rings. If trends in fish use are extrapolated to include October and to cover the 150 day time period of this dissertation study, production would be 2.2 gdw m^{-2} 150 d^{-1}. This value, though not obtained at the sampling sites of this dissertation, provides a rough estimate of the potential marsh edge production of larger fishes that are unavailable to drop ring gear.

Unquantifiable marsh value and secondary production

The vegetated surface of the salt marsh provides an important refuge from predation for small size classes of resident nekton (Kneib 1987a) and for Atlantic silversides at night (Rountree and Able 1993, this study). While production can be directly quantified as addition of tissue, refuge value cannot. Refuge function therefore tends to be overlooked in quantitative production studies. Without refuge protection from predation, however, populations of small nekton (and consequently of larger nekton) may be very drastically reduced. Production therefore depends on refuge, and this critical function of salt marshes should not be minimized.

Salt marshes are also widely available throughout a very large geographic area. In this region at least, marshes are structurally persistent from season to season and from year to year. The resident fauna of marshes are not particularly susceptible to annual variation (Chapter 2). Another unquantifiable value of marshes to estuarine production may be this widespread availability and permanence over several time scales. Marshes may take on even more importance to the estuary in seasons, years, or decades when other vegetated habitats (such as seagrasses) are less abundant. In this way, marshes may function as buffers to estuarine productivity. This buffering function has also been described for marsh production of detritus. These attributes are difficult to quantify, but the importance of marshes to the production of nekton is certainly greater than indicated by numeric estimates of somatic production alone.

CONCLUSIONS

Production studies of marsh surface nekton are rare, and community-level production work does not exist to my knowledge. In this study, two techniques were used to estimate production of dominant nekton on the marsh surface. The results from these techniques agreed closely, even though different subsets of the data were used for each. Total corrected somatic marsh surface production was estimated at 7.4 - 8.0 gdw m^{-2} 150 d^{-1} (28.4 - 30.7 gww m^{-2} 150 d^{-1}) for the area flooded at mean high tide. If uncorrected for poorly sampled small size classes and removal efficiency, production was about half of this. These results are in the range of values reported for other shallow water ecosystems.

Previous very high estimates of single species fish production in marsh habitats may not be fully applicable to the marsh surface. The estimates of Wright (1972) and of Valiela *et al.* (1977) may include a calculation error that overestimates production tenfold. The high estimate of Meredith and Lotrich (1979) was quantified for a lowtide refuge habitat; this study was never intended as an estimate of fish production on the marsh surface. Consequently, production of larger adult and sub-adult size classes of nekton in marsh surface habitats may be lower than has been thought. However, production of juveniles may be higher. As is true of previous marsh production studies, my work did not quantitatively sample the smallest size classes of nekton. Recent quantitative work suggests that these small organisms are very abundant on the marsh surface (Ayers 1995, Kneib 1997b), and experience very high rates of mortality (Meredith and Lotrich 1979, Kneib 1993). This combination of factors indicates high levels of production, as is proposed in Talbot and Able (1984). Standard methods to correct for poor sampling of small size classes cannot account for this combination of factors; a study employing a new quantitative approach similar to that of Kneib (1997b) would be needed to accurately estimate this production.

The contribution of marshes to the production of transient marsh species was estimated at 1.1 gdw m^{-2} 150 d^{-1}, equivalent to 4.2 gww m^{-2} 150 d^{-1} for the entire area flooded at mean high tide. Most transients used marsh edge habitat, and transient production here was estimated at 6.6 gdw m^{-2} 150 d^{-1}, equivalent to 25.2 gww m^{-2} 150 d^{-1}. Part of this production was due to transient fish species (0.6 gdw m^{-2} 150 d^{-1}), but large species may not have been well sampled with the drop ring gear. Production of larger transient fishes unavailable to drop sampling was estimated at erosional marsh edges using different gear at 2.2 gdw m^{-2} 150 d^{-1}, or 8.8 gww m^{-2} 150 d^{-1} (Cicchetti unpublished data). Most transient production was due to the blue crab, *Callinectes sapidus*, in marsh edge habitats. The value calculated for blue crab production per square meter of marsh edge habitat was 6.0 gdw m^{-2} 150 d^{-1}, or 22.1 gww m^{-2} 150 d^{-1}. Comparisons to another Chesapeake Bay study (Fredette *et al.* 1990) suggests that crab production may be roughly similar between marsh edge and SAV bed. Marsh edge contributed significantly to production of transients, especially given that this production was calculated only for the fraction of time that these habitats were inundated.

Production on the marsh surface is high, but the importance of marshes to estuarine function goes beyond this production. The refuge value of the marsh surface also plays a key role in supporting populations of nekton; although this value is not easily quantified it may be of critical importance. The widespread spatial distribution of marshes and their permanence on several time scales also serves an unquantifiable role in estuarine productivity. Marshes and their trophic resources are always available; this feature may be of considerable value to the larger estuary if time scales longer than one year are considered. For a number of reasons, marshes are very important in the trophic functioning of estuaries.

CHAPTER IV. TROPHIC LINKS BETWEEN INVERTEBRATES AND NEKTON, AND EXPORT OF BIOMASS FROM THE SALT MARSH INTO ADJACENT WATERS

ABSTRACT

A dynamic calculation model was constructed to examine the trophic dependencies that link invertebrates and nekton in salt marshes and in adjacent unvegetated habitats. The model evaluates consumption of invertebrate prey by the fishes and crustaceans that use marsh habitats, and is based on the sampling program described in previous chapters. Total consumption of animal prey between June and October (1995) by marsh residents and transients was estimated at 13 gdw m^{-2} 150 d^{-1} for the area of marsh flooded at mean high tide. Consumption on the marsh edge was about three times this. Certain marsh transient species fed heavily on marsh invertebrates, thereby removing marsh biomass as export into deeper water ecosystems. This pathway of trophic export moved 5.6 gdw m^{-2} 150 d^{-1} from the marsh surface to deeper water. Export was highest at the marsh edge, transferring 28.0 gdw m^{-2} 150 d^{-1} into other habitats. Blue crabs were the major transient predator in the sampling area. The most important prey of blue crabs were non-portunid crabs in marsh interior areas, and annelids in marsh edge and unvegetated areas. Blue crabs at marsh edge habitats fed in unvegetated areas as well as in vegetated areas. The value of edge springs from the combination of refuge value and trophic value provided by the juxtaposition of two habitats. I suggest that the vegetated and unvegetated sides of the marsh edge function inseparably together to support high biomass and production of nekton. Biomass export from the unvegetated area was also high, at 8.0 - 11.7 gdw m^{-2} 150 d^{-1}. All sampled habitats were important in the interconnected trophic processes of these shallow water ecosystems.

INTRODUCTION

TROPHIC LINKS ON THE MARSH SURFACE

General patterns of energy flow from primary producers

High levels of primary production on the salt marsh surface provide the potential for considerable secondary production. The pathways by which this production is actually used by consumers can be quite complex, however. *Spartina alterniflora* makes up the major part of standing plant biomass on the flooded marsh surface at the site I sampled (Buzzelli 1996) as well as at many other marshes in the eastern United States. Benthic microalgae are also abundant on the salt marsh surface in the area of this study (Buzzelli 1996). Living tissues of *Spartina* seem not to be extensively used in a direct way by the nekton community (Kneib 1997a), but the live plants may be directly used by the salt marsh insect community (Teal 1962, Marples 1966, Davis and Gray 1966). These insects, in particularly leafhoppers, are in turn fed upon by aquatic organisms; this constitutes a short trophic link between *Spartina* and aquatic ecosystems (Allen *et al.* 1995). On the whole, however, consumption of detrital *Spartina* and of benthic microalgae appears to be a more important link to aquatic food webs than is consumption of live *Spartina* (Kneib 1997a).

Food webs for communities of marsh nekton are characterized by omnivorous feeding on a wide variety of available items. Kneib *et al.* (1980) and Currin *et al.* (1995) showed through stable isotope analyses that both benthic microalgae and detrital *Spartina alterniflora* are important food resources to marsh invertebrates. Hughes and Sherr (1983) similarly showed the importance of vascular plants and benthic algae to consumers in an estuary. Deegan and Garritt (1997) used isotopic analyses to show that consumers in the middle and lower estuary depended on a mixture of benthic microalgae, *Spartina* spp, and phytoplankton for food web support, and suggested that the tidal range of an estuary would have important effects on determining the relative proportions of organic constituents utilized by consumers. Isotope work

by Kwak and Zedler (1997) on the West coast found that macroalgae, microalgae, and *Spartina foliosa* all contributed to the base of the food web. Depending on location and time, it seems that a variable mix of primary production acts to support higher level consumers in marshes.

Trophic links between primary producers and nekton (mostly via detritus and detritus-feeding invertebrates) are clearly very important in the ecological functioning of estuaries and the coastal ocean. Kneib (1997a) suggests that invertebrate decomposers may be the major trophic connection between marsh primary production and most species of marsh nekton. In marshes, organic detritus is often a large component of the diet (Kneib and Stiven 1978, Werme 1981). It is thought, however, that fishes do not gain significant nutritional benefit from this detritus due to an inability to digest it (Prinslow *et al.* 1974, Katz 1975). Peters and Schaaf (1991), however, suggest that detritus derived from vascular plant production (both marsh and SAV) is at least indirectly necessary to support observed yields of fisheries species in coastal waters. The primary production of *Spartina* and of other marsh plants together with that of phytoplankton and algae drive marsh secondary production, but the pathways involved may not be direct.

Benthic invertebrates in marsh habitats

Macroinfauna are the most studied group of salt marsh invertebrates, and together with the epifauna seem to constitute the biggest prey resource for nekton (Kneib and Stiven 1978, Werme 1981). Production studies of salt marsh infaunal communities are rare, however. Cammen (1979) estimated that mean standing stock biomass of infauna at a North Carolina salt marsh ranged from 1.3 to 6.1 g afdw m^{-2}, and estimated annual production at 5.9 g afdw m^{-2} yr^{-1} or 8.3 gdw m^{-2} yr^{-1}. Cammen suggested that these production values for infauna were comparable to expected values for salt marsh epifauna. Standing stocks of infauna at my marsh were similar to this (Diaz *et al.*, unpublished data). The highest production values seen for mobile marsh surface animals are perhaps for fiddler crabs; Cammen *et al.* (1980) report a yearly production for *Uca pugnax* and *U. minax* together at 24 gdw m^{-2} yr^{-1}.

Variability in the distributions of invertebrates on the marsh surface occurs on many scales, just as does variability in the distribution of marsh nekton (Chapter 2). In general, elevation and distance from open water seem to have major structuring effects on macrofaunal communities. Minello *et al.* (1994) found that polychaetes in sampled Texas salt marshes were more abundant in habitats near channel edges than in marsh interior areas. Moy and Levin (1991) reported that total macrofaunal numbers were greatest at lower elevations on the marsh surface. Kneib (1984a) found that infauna in a Georgia salt marsh showed clear zones of distribution along a tidal gradient, but Kneib also points out that these distribution patterns are very complex and are affected by predation, selective larval settlement or mortality, complex (multi-trophic level) interactions, physical factors, and stochastic events (Kneib 1984a).

The species composition of infauna also affects nekton use of marsh resources. Oligochaetes were overall the numerically dominant taxon in marsh habitats at my study area (Diaz *et al.* unpublished data). This dominance of oligochaetes has similarly been shown in other systems as well (Moy and Levin 1991, Levin *et al.* 1998). But Moy and Levin (1991) concluded that oligochaetes were inaccessible as prey to *Fundulus heteroclitus* based on gut content studies; despite being the most abundant infaunal species sampled, oligochaetes were rarely found in guts.

Variation has been found to exist on smaller spatial scales within vegetated marshes as well. Core samples taken to include culms of *Spartina alterniflora* in North Carolina contained significantly higher densities of macrofauna than did cores taken 10 cm or more from culms (Rader 1984). Lana and Guiss (1992) also found evidence of small-scale spatial patterns in that macrofaunal numbers of certain species were related to below-ground *Spartina* biomass. This small scale variation may be very important to feeding dynamics; if prey exist in patches of abundance, then their perceived density to mobile predators may be higher than if these prey were evenly dispersed. Patterns of invertebrate distribution may have significant consequences for nekton feeding in marshes.

Benthic invertebrates in unvegetated habitats

Comparisons of macrofauna between the salt marsh and adjacent mudflat have shown different results in various marsh systems. Levin *et al.* (1998) found similar densities of organisms between a *Spartina foliosa* marsh in California and the adjacent mudflat, but species composition differed. Marsh communities were much more dominated by oligochaetes (81 - 88% of infauna) than were mudflat communities where oligochaetes were 25 - 33% of infauna. Marshes contained proportionally fewer polychaetes, crustaceans and mollusks than did mudflat habitats. Zimmerman *et al.* (1991) found a very clear pattern of greater infaunal abundance in the salt marsh relative to adjacent mudflats. Lana and Guiss (1991) compared densities of macrofauna in *Spartina* habitats and unvegetated habitats, finding that marsh sites contained significantly higher numbers of infauna and higher diversity of infauna as well. These differing results indicate variation in patterns of invertebrate distribution. The marsh I sampled saw patterns similar to those reported by Levin *et al.* (1998) in California. My area was characterized by higher infaunal biomass in the adjacent mudflat than on the marsh surface, though this was not true of infaunal abundance. Marsh habitats were dominated by small, numerous oligochaetes, and total infaunal densities were therefore high. Larger polychaetes were more abundant in the mudflat community, in particular the nereid *Laonereis culveri* (Diaz *et al.*, unpublished data).

Indeed, invertebrate abundance and biomass in unvegetated intertidal habitats can be very high at certain locations. Diaz *et al.* (1982) found an impressive total infaunal biomass in unvegetated habitats at the Guinea marshes (across the York River from the sampling area used in this dissertation). Diaz *et al.* (1982) reported a wet weight biomass of 235.7 g m^{-2} in muddy areas and 185.0 g m^{-2} in sandy areas, of which 67.0 g m^{-2} and 10.1 g m^{-2} were polychaetes (respectively). The literature often reports lower numbers of organisms in unvegetated areas relative to the marsh surface (see above) but it is clear that exceptions do exist, and that unvegetated habitats can support very large invertebrate biomasses in some cases. It is important to note a distinction between the subtidal unvegetated and the intertidal

unvegetated. The high biomass seen by Diaz *et al.* (1982) occurred in the intertidal. Buzzelli (1996) and others report high production of benthic microalgae in this area; high levels of sunlight in these shallow areas and tidal processes are likely responsible for high production on several trophic levels.

Links between invertebrates and nekton in marsh surface habitats

A general pattern that emerges from the literature is that trophic links between predators and prey on the marsh surface are complicated, and depend on many interconnected factors. Different authors focus on various aspects of this complexity. Minello and Zimmerman (1992) state that "the use of prey density as an indicator of food value in a marsh can be misleading unless trophic pathways are well understood and access to the marsh surface is considered". Kneib and Stiven (1982) suggest that trophic relationships between nekton and invertebrates on the marsh surface can be complex, and that intermediate predators such as *Palaemonetes pugio* may play an important role in these processes. Miller and Dunn (1980) remark that juvenile fishes in estuaries are trophic generalists and that little evidence can be found to show a dependence on specific prey populations. Kneib hypothesizes (1984a) that nekton predation may control invertebrate densities in the stable mid-zones of the salt marsh while densities in the high marsh may be controlled by tolerance of dessication and adaptation to terrestrial life, in part because the higher elevation of the high marsh limits foraging time available to predatory nekton (Kneib 1984a).

In spite of the complex nature of nekton/infaunal relationships on the marsh surface, nekton have been clearly shown in several studies to affect abundance or distribution of marsh invertebrates (Vince *et al.* 1976, Kneib and Stiven 1982, Wiltse *et al.* 1984, Walters *et al.* 1996, see also review by Kneib 1997a). Kneib (1984a) also noted that the period of greatest infaunal abundance in many southeast marshes (spring and fall) corresponds to lowest nekton abundance, while the period of lowest infaunal abundance (summer) corresponds to highest nekton abundance. This seasonal pattern of infaunal abundance is also seen in Texas marshes

(Zimmerman *et al.* 1991), North Carolina marshes (Cammen 1979) and Massachusetts marsh creeks (Wiltse *et al.* 1984). Wiltse *et al.* (1984) showed through predator exclusion experimentation that predation by killifishes, green crabs, and grass shrimp was responsible for this mid-summer depression in marsh creek habitats in a Massachusetts marsh. Where patterns of predators eating prey on the marsh surface are strong, they are identifiable despite complicating factors.

SPECIES-SPECIFIC PATTERNS OF NEKTON FEEDING

Mummichogs, *Fundulus heteroclitus*

This species is the most abundant salt marsh fish in many areas of the Atlantic coast. A large body of literature can be found to describe the feeding habits of mummichogs; some of this literature as it might apply to my particular study is discussed below.

Diet of mummichogs. Kneib and Stiven (1978) studied the gut contents of *Fundulus heteroclitus* over an entire year in North Carolina and found evidence of seasonal variation in the diet. The most commonly consumed food items for all seasons were small crustaceans and polychaetes, though larger mummichogs consumed proportionally more crabs and detritus as well. In fact, size-selective predation by mummichogs has been well documented (Werme 1981, Kneib 1986), and several workers have found that larger mummichogs consume larger prey such as *Palaemonetes* shrimp (Schmelz 1964, Nixon and Oviatt 1973, Kneib and Stiven 1982) and fiddler crabs (Schmelz 1964, Kneib and Stiven 1978). The diet of very small mummichogs is often found to be heavily composed of meiofauna (Werme 1981) and in particular of harpacticoid copepods. Kneib (1986) found that harpacticoid copepods were the most frequently occurring prey in guts of larval *F. heteroclitus*, but that tanaids, small polychaetes, and other small prey also occurred frequently. Nixon and Oviatt (1973) list harpacticoid copepods, amphipods, diatoms, and detritus as prey of small mummichogs, in order of abundance. Moy and Levin (1991) noted that meiofauna comprised about half of the animal matter ingested by mummichogs 10 - 20 mm SL, and that harpacticoid copepods were the most

commonly ingested meiofaunal organism. As is true of many other fish species, mummichogs feed differently at the various stages in their life history.

Schmelz (1964) found evidence of seasonal shifts in mummichog feeding between March and June, with diets including more plant matter and more large crustaceans (*Palaemonetes* spp and *Uca pugnax*) towards June. Schmelz did not remark on any shifts in feeding after June, the time period of interest to this dissertation, although Werme (1981) did see these shifts after June. Mummichogs also ingest a considerable quantity of detritus and plant material (Kneib and Stiven 1978). Lab studies by Prinslow *et al.* (1974) and Katz (1975) indicated that mummichogs are unable to use this consumption for maintenance or growth. It is possible that detrital material is ingested incidental to pursuing animal prey (Prinslow and Valiela 1974).

Food limitation in mummichogs. Weisberg and Lotrich (1986) report that mummichogs were apparently food limited in a Delaware marsh system. These authors conducted an enclosure study using mummichogs in the range of 50 - 100 mm TL and concluded that natural populations of mummichogs in the studied marsh may have been regulated by food supply. Kneib and Parker (1991) reported evidence that salt marsh populations of prey were suboptimal to support populations of larval mummichogs in a Georgia marsh. Using enclosure methods and an experimental approach, Kneib (1993) also found evidence of food limitation for larval mummichogs. Werme (1981) used gut content evidence to argue that food was limiting to both *Fundulus heteroclitus* and *F. majalis*. Other species may not be as food limited in marsh habitats: Currin *et al.* (1984) reported that food did not appear to limit production of juvenile spot and croaker using intertidal marsh creek systems, while Werme (1981) reported that guts of transient fishes feeding in marsh areas were generally full of high quality animal prey.

Other marsh resident fishes

Baker-Dittus (1978) showed that feeding of three sympatric killifish (*Fundulus heteroclitus, F. majalis,* and *F. diaphanus*) showed considerable overlap. All three species fed on infaunal and epifaunal prey in about the same proportion, and primary prey items of all

three were small crustaceans and polychaetes. This supports a general conclusion that these fishes are opportunists, making use of whatever food is available. Werme (1981), on the other hand, found evidence of separate feeding styles between *F. heteroclitus* and *F. majalis*. Based on gut content information, morphological observations, and lab experiments, Werme concluded that *F. majalis* fed more on benthic invertebrates than did *F. heteroclitus*. Werme observed a style of feeding in *F. majalis* where the swimming motion of the fish was used to force the snout into the sediment, allowing for the acquisition of deeper dwelling benthic invertebrates. In addition, the diets of *F. heteroclitus* contained more algal matter than did those of *F. majalis*. Also, *F. majalis* did not seem to show a tidal signal to feeding, whereas *F. heteroclitus* did, feeding more heavily at high tide than at low tide (Werme 1981).

Werme (1981) observed that, of the marsh fishes she captured, only the sheepshead minnow (*Cyprinodon variegatus*) is morphologically adapted to herbivory. While other marsh resident fishes (notably *F. heteroclitus*) fed on algae in her study, Werme indicated that this was incidental to feeding on invertebrates living within algal mats. For Atlantic coast marsh fish other than *C. variegatus*, animal prey seem to be the most important source of trophic support.

Marsh transient fishes

Werme (1981) reported that transient fishes feeding in salt marsh habitats consumed higher quality seasonal prey and in general had fuller guts than did marsh resident species. She also documented much faster growth rates in these fishes relative to salt marsh fishes, but noted that transients were much less numerous than residents.

Sciaenids in particular have been shown in other systems to be very important in marsh trophic dynamics. Hodson *et al.* (1981) blocked off intertidal marsh rivulets with weirs and found that postlarval and juvenile spot traveling up these rivulets utilized an important food resource from the marsh surface. Spot guts were more full as they departed the creeks on an ebbing tide than when they entered the creek, and marsh surface invertebrates were found in

the gut contents of departing fish. Sciaenids have been shown to be very important in the local area of my project as well (Weinstein *et al.* 1984) but were rare in my study area in 1995. Interestingly, they were very abundant in a 1998 sampling project in the same habitats and sampling area as my dissertation (Cicchetti, Reay, and Woodin, unpublished data). While sciaenids were not particularly abundant in my study, their importance in marsh areas is well documented elsewhere.

Callinectes sapidus

Laughlin (1982) studied feeding habits of blue crabs in Florida and concluded that crabs consumed whatever food items were available in the area. Laughlin did not find any diel differences in diet or food consumption. Laughlin did find differences in feeding of crabs in different size groups < 30 mm, 31 - 60 mm, and > 60 mm CW. Fitz and Wiegert (1991) reported that large crabs (> 100 mm) feeding on the marsh surface preyed upon non-portunid crabs (43% of diet) and fishes (38% of diet) Shrimp and other crustaceans made up 12% of the diet, while other invertebrates made up only a small proportion of the diet. Ryer (1987) collected crabs at 3 hour intervals over a 24 hour period found significantly greater gut fullness at high tide after crabs had foraged in the *Spartina* at the creek margins than at low tide, when crabs were burrowed into the mud of the creek bottoms. Crabs (60 - 130 mm CW) in Ryer's study fed primarily upon *Spartina*-derived detrital material, with discrete prey items less commonly found. No diel pattern of feeding was evident.

Palaemonids

Palaemonetes pugio, though capable of consuming large amounts of detritus and algal tissue (Welsh 1975) is predatory on small invertebrates as well (Sikora 1977, Kneib 1985). For this reason, palaemonids are included in my calculations of invertebrate consumption on the marsh surface. Nelson (1979) suggests that only larger size classes of palaemonids can capture amphipod prey.

EXPORT OF PRODUCTION FROM MARSHES INTO ADJACENT WATERS

General patterns

A useful manner of evaluating export by marsh nekton is to categorize them into marsh resident species and marsh transient species (Chapter 2). Marsh resident nekton such as fundulids and palaemonid shrimp are well adapted to remain on the marsh surface and in shallow water refugia (Kneib 1997a) and may not export significant marsh energy into deeper water via their own migration (Currin *et al.* 1984). Once recruited, marsh residents essentially never leave the area of the marsh and adjacent low tide refuge; therefore they contribute to other ecosystems only when eaten by a predator from the different ecosystem. These species are important "relay" species of Kneib (1997a), and act as vectors between marsh surface and deeper waters by feeding on marsh surface invertebrates at high tide, then moving off of the marsh at low tide. Away from the refuge of the marsh surface, they may be consumed by larger aquatic and avian predators. This pathway is also suggested by Kneib and Wagner (1994), but is not quantified in my dissertation due to a lack of the proper type of data. Drop rings do not effectively sample larger piscivorous fishes (Jacobsen and Kushlan 1987).

Marsh transients are defined as those species that move between marshes and the open estuary, exporting energy from marsh systems in the process. Note that these marsh transient species as defined here differ from marine or estuarine transients as defined by Peterson and Turner (1994), that migrate between the estuary and the coastal ocean. Marsh transient species use marshes for a portion of their life history. These organisms need not be immediately fed upon in order to contribute to deeper water trophic processes; they may move out of a marsh system never to return, and in doing so bring with them whatever energy they consumed within the marsh ecosystem. Marsh transients may fall to predation within the estuary, and if so they contribute in this way to deeper estuarine food webs. Other transient species may migrate out of the estuary and into the coastal ocean, contributing directly to oceanic food webs. Examples of these ocean-migrating or ocean-spawning species are *Bairdiella chrysoura* (Chao

and Musick 1977), *Leiostomus xanthurus* (Chao and Musick 1977), *Pomatomus saltatrix* (Day *et al.* 1989), *Callinectes sapidus* (Day *et al.* 1989), and *Menidia menidia* (Fay *et al.* 1983). Many of these species are juveniles when using the marsh habitat, and if they reproduce before being preyed upon, then the food and refuge provided by the marsh has contributed to the propagation of that species as well. In my study and in the study of Hettler (1989a) in North Carolina, blue crabs (*Callinectes sapidus*) were the biomass dominant marsh transient species.

Export via transient species predation on permanent marsh resident nekton

As suggested above, predation on permanent marsh residents such as *Fundulus heteroclitus* and *Palaemonetes pugio* may constitute a very important trophic link between marsh habitats and the adjacent deeper water estuarine habitats (Kneib and Wagner 1994, Kneib 1997a). Kneib (1982) found that blue crabs appeared to be important predators on mummichogs in confined pool habitats, and suggests that blue crabs may be very important predators on mummichogs in salt marshes (Kneib 1986). Other studies suggest or document predation on killifishes by a variety of predators (Butner and Brattstrom 1960, Wright 1972, Valiela *et al.* 1977, Yozzo 1994) but this link is very difficult to quantify. Kneib (1986) points out that much of the information about predation on mummichogs is anecdotal, and that "few species at higher trophic levels are known to prey heavily on mummichogs". Rountree and Able (1992b) showed evidence of predation on *Fundulus heteroclitus* and *Palaemonetes vulgaris* by summer flounder in marsh creeks, however. Export of production by bird predation may also be considerable, but note that Kneib (1982) found little effect of wading bird predation on mummichog populations.

Kneib, in a 1997(a) review paper, points out the importance of flooding water and marsh landscape in determining the rates of transfer of energy from the marsh surface to deeper water habitats. Kneib (1997a) indicates that periods of overlap between populations of permanent marsh resident prey and their potential deeper water predators will occur at certain specific points in the tidal cycle. Kneib (1997a) suggests a "trophic relay" in which production

is moved from the marsh surface into deeper waters via predation by progressively larger predators in progressively deeper water. This takes the form of young resident nekton (interior marsh residents, Figure 2, Chapter 2) being preyed on by adult resident nekton (interior marsh users, Figure 2, Chapter 2) who are preyed on by juvenile transient predators (Kneib 1997a). In this way, energy is moved off the marsh in stages.

Export via migration of transient species from marsh habitats

Kneib (1997a) suggests that emigration of transient species from marsh habitats holds the most potential to move production from the marsh surface into deeper estuarine and oceanic waters. Indeed, Deegan (1993) estimated that average export of gulf menhaden (*Brevoortia patronus*) out of a Louisiana estuary was 38 g m^{-2} yr^{-1} (dry weight), calculated per area of marsh habitat. This number was about 5 - 10% of the primary productivity of the area (Deegan 1993) and represents not just an enormous abundance and biomass of fish, but also a tremendous export from the shallow marsh and bay to the ocean.

Peters and Lewis (1984) have indicated that Atlantic menhaden (*Brevoortia tyrannus*) has an ability to digest *Spartina*-derived detritus. If this detritus constitutes a significant part of the nutritional support of these fishes, then the exported value of marsh surface primary production to ocean waters through this pathway has the potential also to be very large. Atlantic menhaden are not only very abundant fishes, they also serve as a direct food source for many estuarine and oceanic predators. Since menhaden feed at a low trophic level, they can very efficiently convert organic matter into fish biomass. Atlantic menhaden may not remain for an entire season in areas associated with marshes to the extent that Gulf menhaden do (Deegan 1993), but occur in high numbers in areas adjacent to marshes for shorter periods of time. Nixon and Oviatt (1973) reported a temporary residence of juvenile Atlantic menhaden in a small Rhode Island marsh embayment as attaining school densities of 40 inds m^{-2} and biomass on the order of 20 g m^{-2} (dry weight) for the entire embayment in the month of August. However, Nixon and Oviatt comment that these menhaden seemed not to be obtaining sufficient

food for growth in this area, but rather appeared to be seeking refuge from the voracious bluefish found in deeper parts of the estuary. Other authors have noted Atlantic menhaden in areas adjacent to marshes as well (Rulifson 1991). It is possible that in some areas the contribution of marshes to the trophic support of *Brevoortia tyrannus* during the time that these fishes feed in waters adjacent to salt marshes may represent a significant export of marsh primary production into open waters and higher trophic levels on the Atlantic coast.

The Atlantic silverside, *Menidia menidia*, may also be a particularly important species in the transfer of energy from marsh and estuarine areas into the coastal ocean. This species spawns in shallow estuarine waters including the marsh surface (Fay *et al.* 1983). Silversides are preyed upon by a variety of predators within estuaries (Fay *et al.* 1983). Silversides also undertake a winter migration into the coastal ocean where they are further preyed upon by oceanic fishes, and experience considerable mortality (Fay *et al.* 1983).

Fitz and Wiegert (1991) suggested that blue crabs, *Callinectes sapidus*, may function as vectors of carbon transport from the marsh surface, though densities of crabs in their study were relatively small (40 - 50 per hectare). These same authors also showed through a tagging study that some of the crabs were returning to the marsh of initial capture: 28 of 107 marked crabs were recaptured at least once in this study. Kneib (1982) suggests that blue crab predation on mummichogs may constitute a significant export of marsh production into deeper water. Indeed, a growing number of studies are showing the importance of a variety of marsh transient species to the export of energy from marshes into deeper waters.

Export from tidal creeks

Salt marsh tidal creeks provide for the export of considerable animal biomass. Weinstein *et al.* (1984) found high densities and production of spot (*Leiostomus xanthurus*) in polyhaline marsh tidal creeks of the York River (Virginia). Production was estimated at 4.6 gdw m^{-2} over a 90 day period between mid June and early September. This study suggested that marsh creek systems may sustained a seasonally resident population of spot. Average residency

was calculated as 86 days; if so, then seasonal export of the production calculated per square meter represents a significant contribution from marsh creeks to deeper water ecosystems as these fish migrate out of the creeks at the end of the season. In a different study, Weinstein *et al.* (1980) found an important link between shallow estuarine habitats and the coastal ocean via export by marine transient species in tidal creeks of the Cape Fear River estuary, and estimated that biomass available for export to the coastal ocean via marine transients from these tidal creeks was about 1.51 grams dry weight per square meter of habitat at low tide.

These patterns are seen in other species as well. Kleypas and Dean (1983) suggested that silver perch moving into tidal creeks and feeding on palaemonids in intertidal creek areas may constitute an important transfer of energy from marsh areas into the deeper estuary. Allen *et al.* (1995) documented a contribution of exported biomass in the form of marsh creek zooplanktivorous fishes. A direct connection to the marsh surface was suggested based on the presence of leafhoppers in guts of rough and Atlantic silversides; leafhoppers are among those insects that graze directly on *Spartina alterniflora*. Bozeman and Dean (1980) showed considerable use of tidal creeks by larval fishes of 16 species, and suggested that the export of biomass from these habitats as fishes matured over a season may be a valuable contribution of export. Rountree and Able (1992a) found a tremendous biomass of nekton moving out of marsh creek areas with each tidal cycle. Rountree and Able (1997) documented a greater use of marsh creeks by certain large juvenile and adult piscivores at night than during the day, suggesting the possibility of greater predation on marsh residents at night. This tremendous preponderance of evidence leaves little doubt that salt marsh tidal creeks are very important conduits for the export of marsh-derived production. The area of marsh which I studied, however, did not contain a tidal creek.

I investigate the pathway of trophic export from the marsh to the estuary via consumption of animal tissue on the marsh surface by marsh transients, who eventually leave the marsh system for the larger estuary. This functional pathway of trophic export has been relatively well investigated in subtidal marsh creeks (see above) but is much less studied on

the marsh surface and at open embayment sites such as my study area. This type of area has also been termed the bay-marsh fringe by Rountree and Able (1992a) and is characterized by a lack of tidal creeks. My study was conducted at a simple creekless site which I feel represents an important baseline marsh system that, paradoxically, has not been intensively studied for export of marsh energy.

METHODS AND MODEL CONSTRUCTION

CONCEPTUAL DESIGN

A dynamic calculation model was constructed to evaluate flows of energy from invertebrates to nekton in shallow water habitats at an open embayment marsh site. The model describes the same sampling area, habitats, and data base that are discussed in the previous Chapters of this dissertation. The model actually is very simple and in reality does only one thing: it quantitatively predicts the consumption of sampled predators on each available prey in each quantified habitat. Figure 1 shows a diagram of the calculations that are carried out to achieve this. In addition to this primary consumption calculation, the model also displays sampling data in such a way as to facilitate ecosystem analyses. The data were collected at the Goodwin Islands (York River, Virginia) in 1995 and 1996 during separate studies for invertebrates and nekton. Monthly data are entered into the model as means of three replicate cores for invertebrates, and as means of five replicate drop samples for nekton. Gut content examinations of nekton are used to evaluate links between groups. The calculations of the model synthesize the data into a trophic picture of the ecosystem, and provide insight as to ecosystem connections.

Figure 1 shows the conceptual basis for the calculations of this model. In practice, the number of simultaneous equations necessary to describe 18 nekton groups x 15 prey categories x 8 habitats x 5 months was so large that several component models were constructed to minimize model run times. The unedited equations of the model are shown in the Appendix.

SAMPLING FOR THE MODEL - INFAUNA

Three habitats were sampled for infauna using 7.3 cm diameter corers at low tide (Diaz, Yozzo, Hinchey, Nestlerode, Wooden, and Cicchetti, unpublished data). Three replicate cores were taken each month. These habitats include the following, with abbreviations in

parentheses referenced to model equations (Appendix): the irregularly flooded high marsh (hm), 5 to 30 m from the marsh-unvegetated border; the vegetated marsh edge (lm), 0 to 2 m from the marsh-unvegetated border (typically from 0 to 1 m from this edge); and the unvegetated intertidal flat (uf) area of unvegetated muddy sand between 1 and 5 m from the marsh-unvegetated border. The model directly compares invertebrates to nekton (and predation) within these three habitats, which were sampled in both invertebrate and nekton projects.

Macro-infauna that were common in the invertebrate study of Diaz, Yozzo, Hinchey, Nestlerode, Wooden, and Cicchetti (unpublished data) included crustaceans, mollusks, worms, insects, spiders, mites, nemerteans, and anemones. Crustaceans included gammaridean amphipods (*Gammarus palustris* and *Orchestia uhleri* were the most common species), isopods (*Cyathura polita, Edotea triloba,* and *Sphaeroma quadridentatus*), the tanaid *Leptochelia savigny,* caprellid amphipods, corophiid amphipods, and cumaceans. Mollusks included *Gemma gemma, Melampus bidentatus,* unspeciated hydrobiids, and *Acteocina canaliculata.* Worms included oligochaetes and polychaetes; polychaetes were primarily composed of *Laonereis culveri, Nereis succinea, Lycastis pontica,* Capitellids, *Streblospio benedicti, Manayunkia aestuarina,* unspeciated syllids, *Asabellides oculata,* orbinids, phyllodocids, *Polydora ligni, Scoloplos fragilis, Eteone heteropoda,* unidentified spionids, and unidentified polychaete larvae. Insect larvae were mostly chironomids, tabanids, ciratulids, and ceratopogonids. Terrestrial animals captured were adult insects (dipterans and leafhoppers), spiders, and mites. Other groups found were nemerteans and anemones (mostly *Edwardsia elegans*). Large animals were not considered to have been quantitatively sampled and the 2 large *Geukensia demissa* and 11 individual crabs (*Sesarma* and *Uca*) captured in the core samples were not included in the analysis.

SAMPLING FOR THE MODEL - NEKTON

Sampling for nekton took place as described in Chapters 1 and 2. A habitat diagram is shown as Figure 5 in Chapter 1. The data incorporated into the model are identical to the data used in the primary habitat study of Chapter 2, and are displayed in their entirety in Table 3 and Figures 3 and 4 of Chapter 2. Since these data are thoroughly described in Chapter 2, the information is not repeated here. Twenty-three species of fishes and four species of crustacean captured during the drop ring study were included in the trophic model as eighteen groups of nekton (Appendix). Gut contents of SAV species were not examined, and seagrass habitat is not directly included in the model, except when marsh residents were captured in seagrass at low tide. Other excellent works describe energy flows in seagrass habitats (Adams 1976 a, b, c; Edgar and Shaw 1995a, b).

MATHEMATICAL DESIGN OF THE MODEL

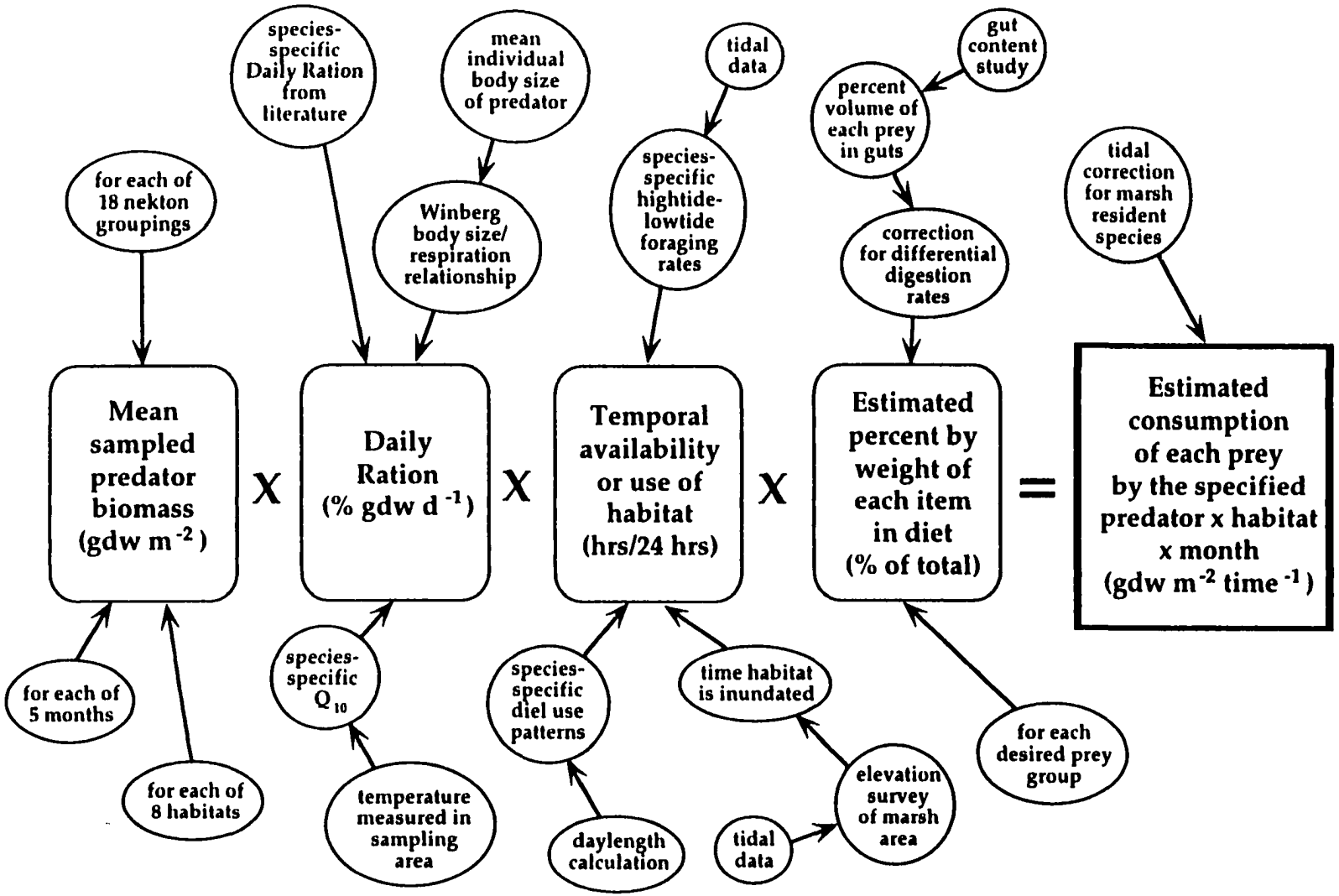
Overview

A series of descriptive equations were written using the software package Madonna (YouSeeSoftware) to summarize and synthesize the results of sampling in this marsh area. These equations are shown in the Appendix. The function of the resulting descriptive model is to incorporate tide, temperature, daylength, predator biomass, and predator diet data into a dynamic mathematical calculation that predicts the consumption of various prey groups by each nekton species in each habitat over time (Figure 1). This calculation was based on the daily ration for each predator, the sampled biomass of the predators, the percent by weight made up of each prey item in the diet, and the time allowed by tidal inundation for feeding in each habitat, with a correction for tidal compression of habitats. Daily rations were taken from the literature and were adjusted to temperature and to predator body size. This was done using Q_{10} values from the literature and using Winberg's k for body size (Winberg 1960). Model forcing functions were temperature (from means measured at the site), tidal height (from correlated NOAA tide data), and daylength (using an algorithm for the region). These forcing

Figure 1. Conceptual Diagram of Model Calculations and Design.

This Figure shows the conceptual basis for the consumption calculation of the trophic model. Other than as necessary to display sampling data, this is the only calculation of the model. The calculation is repeated for each of the possible predator x prey x habitat x month combinations to provide monthly values for each. The monthly values are summed to yield total consumption over the five months of the study.

Diagram of Model Calculations and Design



functions were then applied to the calculation of species-specific consumption. Output of the model for each of the 18 nekton species/size class groups for each of the 5 month x 8 habitatcombinations was grams dry weight consumed of each dietary item per square meter per day. The major assumptions of the model are discussed in more detail below, as are the correction factors that were necessary to apply.

Forcing functions

The forcing functions used in this model are time, expressed in Julian days, tide, temperature, and daylength. In addition to the discussion below, forcing functions are further explained and documented in the model text (Appendix).

Tidal influence is dynamically calculated in the model based on the number of hours per day that each habitat is under water. Tidal data were from the NOAA record for Gloucester Point taken at VIMS pier and correlated to the Goodwin Islands (58 observations, r-squared = 0.95, see Chapter 1). A period of clearly inconsistent NOAA tide data in July and August (broken gauge suspected) was replaced with the mean values for the rest of the year. Data from a marsh surface elevation study at the sampling area in 1996 were used to calculate mean habitat elevations (see Chapter 1). The model assumes that each individual habitat is homogeneous with respect to tidal influence; no correction is made for differential flooding within the horizontal distance that constitutes a single habitat. Flooding differences were accounted for in each habitat through time available in each habitat, not through distance available. A correction factor was applied to model results to adjust for spatial compression of habitats with the tides (see below).

Temperature was measured on the site using a bulb thermometer. Salinity was also included in the model and can be graphically displayed, but salinity is not truly a forcing function as no other calculations are dependent upon it. Salinity data were courtesy of K. Moore (unpublished data), from a station within 200 m of the site; K. Moore also provided ancillary temperature data. These data are shown in Figure 2, Chapter 1.

Daylength, in hours of sunlight per day, was expressed with an equation for the local area taken from the literature. Diel cycle calculations were achieved by combining the tidal signal with the predicted time of daylength. In this way, mean daytime and nighttime high and low tide flooding durations were applied to those nekton which show diel feeding differences in marsh habitats.

Parameters

Certain parameters were derived from the literature in order to complete this model. These can be seen in the last sections of the Appendix, where they are individually documented. Daily rations (Table 1, also Appendix) were taken from the literature, then recalculated to be specific for a 1 gram (wet weight) animal feeding at 20° C. Exceptions to this were the calculation for palaemonids, which applies to an 0.1 gram (wet weight) animal and for large crabs, which applies to a 10.0 gram (wet weight) animal. Wet weights were converted to dry weights and vice versa using values from Cummins and Wuycheck (1971) and other sources. Daily rations in the model are affected directly by temperature (see below) and by predator body size. Winberg's k (an exponent of -0.2, Winberg 1960) was used to adjust daily ration to body size, so that smaller individuals of a species consume more food in proportion to their weight than do larger individuals.

Q_{10} equations for predators were used to adjust the daily ration to temperature, so that food intake increases with temperature. Q_{10} values were taken from the literature to apply to a temperature range of 18° C to 32° C. These were written to produce a value of 1.0 at 20° C. These Q_{10} expressions are documented in the last section of the Appendix. In general, Q_{10} values less than 2.0 were found in the literature. A Q_{10} value of 2.0 was used if literature was not available. The value of 2.0 produces results more comparable to those of Krogh's normal curve for this temperature range. Krogh's normal curve is a mathematical expression, similar to Q_{10}, which is described in Winberg (1960) as a generally applicable description of metabolic changes with temperature in fishes.

Table 1. Daily Rations of Predatory Nekton, Taken from the Literature

This table shows the Daily Rations used in the trophic model, and the literature reference for each. These Rations were converted mathematically for modeling purposes to a standard 1 gram (wet weight) organism at 20 degrees Celsius using Winberg's body size calculation (Winberg 1960) and Q_{10} equations (see Appendix). The Rations are shown in this converted form in the Appendix.

Daily Rations for predators, in percent of body weight consumed per day

Species/group	Daily Ration	Reference
F. heteroclitus	12.89	for 58 - 63 mm fish in summer based on lab studies at 20 degrees C, calculated by Weisberg and Lotrich (1982) using data in Weisberg et al (1981)
L. xanthurus	7.7	for larger juveniles at 22 degrees C, Brooks et al (1982)
Large *C. sapidus*	7.9	for 60 - 130 mm CW crabs at 25 - 32 degrees C, calculated from data in Ryer (1987) using the method of Elliott and Perrson (1978) based on finding of exponential evacuation in Custer (1985)
Small *C. sapidus*	14.2	extrapolated from above to a 1 gww crab using metabolism/size relationship in Laird and Haefner (1976)
P. pugio	21	for 6 - 52 mgdw shrimp at 31.9 degrees C, calculated by Morgan (1980) using data in Wood (1967)
Other fundulids	12.89	value for *F. heteroclitus* used as above
Other sciaenids	7.7	value for *L. xanthurus* used as above
Other palaemonids	21	value for *P. pugio* used as above
Other animals	12	for 1 gww organism at 20 degrees C, mean of all above values when converted to 1 gww at 20 degrees C

Diel feeding cycles for each predator were also described with a parameter, mathematically constructed so that a value of 1.0 indicates equal feeding during day and night (this is explained and documented in the last section of the Appendix). The fraction of time during day or night time that coincides with high tide was calculated (see forcing functions above), and related to the extent that each species uses marshes during the day vs. the night. In practice, since consumption is calculated by the model as a daily ration applied to a period of 24 hours, this calculation is not of great consequence to the final results.

Tidal foraging efficiency was also described as a parameter for each species (see explanation and documentation in the Appendix, last section). Many marsh resident fishes have been shown to feed more actively at high tide than at low tide. Gut fullness data from my gut study was used together with information from the literature to determine the extent of this preference for marsh dependent species.

Gut content information specific to each predator-prey-habitat combination was also entered as a parameter. Tables 2 and 3 show the fraction by volume of the gut content made up of each prey item for each predator by habitat. The model requires fraction by weight of diet (not of gut content) to run accurately, however, and a conversion for differential digestion of soft-bodied versus hard-bodied prey was superimposed on the results of Tables 2 and 3. This is discussed below. Final values of the gut parameter were entered into the last section of the model, as can be seen in the Appendix.

Gut content study - methods

Gut contents of all individual captured fishes > 20 mm and of all blue crabs > 30 mm were quantitatively examined. Gut studies were done on subsamples of palaemonid shrimp and on subsamples of fishes and crabs in size classes smaller than described above. Guts of species found only in SAV beds were not examined, but guts of marsh species captured in SAV habitats were examined.

Table 2. Percent by Volume of each Item in the Guts of Resident Nekton

This table shows the results of the gut content investigation for marsh resident species. Values from all sampling dates are grouped together. Annelids are categorized separately as nereids and as other polychaetes, which does not include nereids. Vegetative matter is distinguished from organic detritus only when clearly recognizable as such. Due to preservation in liquid nitrogen and storage in an ultra-cold freezer, many gut contents were characterized by a thick cloudy mucus which is found in fresh guts but is not found in this form in guts preserved with formalin. This mucus was quantified, but is mathematically removed from the values presented in this Table to provide better comparability to other gut content studies.

***Fundulus heteroclitus* 20-39 mm**
(Habitats LD, LS) n = 31

% Volume	Item
35.7%	organic detritus
19.7%	inorganic matter
16.2%	harpacticoid copepods
11.7%	nereids
5.9%	amphipods
2.9%	isopods
2.5%	unrecognizable animals
2.3%	vegetative matter
1.0%	other crustaceans
0.9%	insects, spiders, mites
0.8%	other polychaetes
0.2%	C. *sapidus*
0.2%	ostracods

***Fundulus heteroclitus* ≥ 40 mm**
(Habitats LD, LS) n = 33

% Volume	Item
35.1%	organic detritus
29.3%	inorganic matter
8.5%	vegetative matter
7.2%	non-portunid crabs
5.9%	amphipods
4.8%	nereids
2.2%	palaemonids
2.1%	insects, spiders, mites
1.4%	gastropods
0.9%	other polychaetes
0.7%	harpacticoid copepods
0.6%	isopods
0.5%	eggs
0.3%	foraminifera
0.3%	oligochaetes
0.1%	mysids

***Fundulus heteroclitus* 20-39 mm**
(Habitat HE) n = 0
(None captured this size)

***Fundulus heteroclitus* ≥ 40 mm**
(Habitat HE) n = 14

% Volume	Item
48.8%	organic detritus
15.5%	inorganic matter
13.3%	vegetative matter
10.0%	non-portunid crabs
2.6%	nereids
2.4%	amphipods
2.0%	insects, spiders, mites
0.8%	harpacticoid copepods
0.8%	tanaids
0.8%	unrecognizable animals
0.8%	foraminifera
0.7%	gastropods
0.7%	other crustaceans
0.3%	insect larvae
0.3%	bivalves
0.1%	other polychaetes

Fundulus heteroclitus 20-39 mm
(Habitat HF) n = 35

% Volume	Item
33.1%	organic detritus
15.8%	insects, spiders, mites
12.9%	nereids
12.0%	vegetative matter
5.6%	tanaids
5.2%	other crustaceans
4.3%	inorganic matter
4.0%	amphipods
3.5%	harpacticoid copepods
1.8%	isopods
0.8%	oligochaetes
0.8%	eggs

Fundulus heteroclitus ≥ 40 mm
(Habitat HF) n = 37

% Volume	Item
45.1%	organic detritus
17.8%	vegetative matter
5.9%	amphipods
5.8%	inorganic matter
5.3%	nereids
4.4%	tanaids
3.8%	insects, spiders, mites
3.0%	oligochaetes
2.5%	other polychaetes
2.2%	insect larvae
1.8%	other crustaceans
1.3%	harpacticoid copepods
0.9%	palaemonids

Fundulus heteroclitus 20-39 mm
(Habitat HI) n = 40

% Volume	Item
23.0%	organic detritus
22.3%	tanaids
16.5%	harpacticoid copepods
9.1%	inorganic matter
6.2%	insects, spiders, mites
5.8%	amphipods
4.9%	unrecognizable animals
2.9%	nereids
2.9%	vegetative matter
1.8%	insect larvae
1.3%	eggs
1.2%	*C. sapidus*
0.6%	ostracods
0.6%	other crustaceans
0.6%	other polychaetes
0.2%	nematodes
0.1%	gastropods

Fundulus heteroclitus ≥ 40 mm
(Habitat HI) n = 20

% Volume	Item
33.0%	organic detritus
17.2%	non-portunid crabs
14.5%	inorganic matter
13.5%	vegetative matter
5.7%	insects, spiders, mites
3.4%	unrecognizable animals
2.8%	amphipods
2.8%	bivalves
2.8%	insect larvae
2.2%	eggs
1.6%	other polychaetes
0.7%	nereids

Fundulus majalis 26-67 mm
(Habitats LD, LS) n = 32

% Volume	Item
32.5%	organic detritus
23.2%	inorganic matter
20.6%	harpacticoid copepods
8.7%	nereids
3.9%	foraminifera
3.0%	insects, spiders, mites
1.9%	nematodes
1.8%	ostracods
1.7%	bivalves
1.1%	unrecognizable animals
0.7%	other crustaceans
0.4%	amphipods
0.4%	tanaids

Fundulus majalis 26-67 mm
(Habitats HE, HF, HI) n = 33

% Volume	Item
36.1%	harpacticoid copepods
27.7%	organic detritus
12.4%	inorganic matter
7.1%	unrecognizable animals
5.6%	oligochaetes
3.2%	nereids
2.2%	other polychaetes
2.0%	non-portunid crabs
0.8%	other crustaceans
0.7%	gastropods
0.6%	bivalves
0.4%	nematodes
0.4%	vegetative matter
0.3%	insect larvae
0.2%	amphipods
0.1%	insects, spiders, mites

Lucania parva
(Habitats HE) n = 27

% Volume	Item
55.7%	organic detritus
28.5%	nereids
7.6%	harpacticoid copepods
2.3%	ostracods
2.1%	other polychaetes
1.4%	insect larvae
0.7%	*C. sapidus*
0.7%	inorganic matter
0.6%	isopods
0.3%	nematodes
0.2%	foraminifera

Lucania parva
(Habitats HF, HI) n = 21

% Volume	Item
21.0%	organic detritus
11.7%	non-portunid crabs
11.2%	other crustaceans
10.7%	harpacticoid copepods
10.5%	amphipods
7.5%	tanaids
5.6%	unrecognizable animals
5.6%	other polychaetes
3.1%	*C. sapidus*
3.1%	oligochaetes
3.0%	nereids
2.6%	insects, spiders, mites
1.9%	ostracods
1.0%	isopods
0.9%	mysids
0.6%	inorganic matter

Palaemonetes pugio
(Habitats LD, LS) n = 25

% Volume	Item
78.0%	organic detritus
10.1%	nereids
8.7%	unrecognizable animals
3.2%	inorganic matter

Palaemonetes pugio
(Habitat HE) n = 20

% Volume	Item
58.1%	organic detritus
12.1%	vegetative matter
10.1%	nereids
9.6%	inorganic matter
3.8%	insects, spiders, mites
3.3%	insect larvae
2.5%	amphipods
0.3%	nematodes
0.2%	other polychaetes

Palaemonetes pugio
(Habitats HF, HI) n = 36

% Volume	Item
82.0%	organic detritus
6.9%	inorganic matter
6.1%	insect larvae
1.5%	vegetative matter
1.0%	other crustaceans
0.9%	harpacticoid copepods
0.7%	nereids
0.5%	other polychaetes
0.3%	tanaids
0.1%	nematodes

Table 3. Percent by Volume of each Item in the Guts of Transient Nekton

Results of the gut content study for transient marsh species are shown for all sampling dates grouped together. Vegetative matter is distinguished from organic detritus only when vegetation was clearly separable from detritus. Annelids are categorized as nereids and as other polychaetes. The "other polychaetes" group does not include nereids. Guts were preserved in liquid nitrogen and stored in an ultra-cold freezer. Because of this preservation, many guts contents were characterized by a thick cloudy mucus, also found in fresh guts. This mucus is not recognizable as such in guts preserved in formalin. The mucus was volumetrically quantified, but is mathematically removed from this Table.

***Callinectes sapidus* ≤ 30 mm**
(Habitats LD, LS) n = 33

% Volume	Item
52.7%	organic detritus
14.5%	vegetative matter
	(0.6% *Spartina*)
9.8%	nereids
9.4%	inorganic matter
2.5%	fish
2.2%	amphipods
2.2%	mysids
2.2%	non-portunid crabs
1.8%	unrecognizable animals
1.0%	bivalves
0.7%	other crustaceans
0.6%	other polychaetes
0.3%	gastropods
0.1%	nematodes

***Callinectes sapidus* > 30 mm**
(Habitats LD, LS) n = 28

% Volume	Item
33.2%	vegetative matter
	(7.9% *Spartina*)
26.5%	organic detritus
15.6%	inorganic matter
7.7%	bivalves
6.3%	unrecognizable animals
5.1%	mysids
2.7%	non-portunid crabs
1.5%	other crustaceans
0.7%	other polychaetes
0.6%	gastropods
0.1%	foraminifera

***Callinectes sapidus* ≤ 30 mm**
(Habitat HU) n = 22

% Volume	Item
51.2%	organic detritus
16.9%	nereids
13.7%	inorganic matter
5.1%	vegetative matter
	(0% *Spartina*)
4.8%	unrecognizable animals
4.6%	amphipods
3.4%	other polychaetes
0.3%	bivalves

***Callinectes sapidus* > 30 mm**
(Habitat HU) n = 9

% Volume	Item
67.6%	organic detritus
11.1%	nereids
8.5%	unrecognizable animals
5.5%	foraminifera
3.6%	other crustaceans
1.6%	inorganic matter
0.6%	other polychaetes

***Callinectes sapidus* ≤ 30 mm**
(Habitat HE) n = 14

% Volume	Item
67.6%	organic detritus
11.1%	nereids
8.5%	unrecognizable animals
5.5%	foraminifera
3.6%	other crustaceans
1.6%	inorganic matter
1.6%	vegetative matter (0% *Spartina)*
0.6%	other polychaetes

***Callinectes sapidus* > 30 mm**
(Habitat HE) n = 25

% Volume	Item
24.6%	vegetative matter (20.1% *Spartina)*
22.0%	non-portunid crabs
15.7%	organic detritus
14.0%	bivalves
10.8%	inorganic matter
7.4%	*C. sapidus*
1.7%	other polychaetes
1.5%	unrecognizable animals
1.4%	gastropods
1.0%	nereids

***Callinectes sapidus* ≤ 30 mm**
(Habitats HF, HI) n = 16

% Volume	Item
38.4%	organic detritus
29.4%	vegetative matter (21.4% *Spartina)*
16.0%	unrecognizable animals
6.0%	other crustaceans
4.7%	nereids
2.3%	amphipods
1.7%	bivalves
0.5%	other polychaetes
0.3%	inorganic matter
0.3%	insect larvae
0.3%	oligochaetes

***Callinectes sapidus* > 30 mm**
(Habitats HF, HI) n = 19

% Volume	Item
48.5%	non-portunid crabs
15.2%	*C. sapidus*
9.6%	organic detritus
9.6%	vegetative matter (6.6% *Spartina)*
7.7%	bivalves
3.9%	inorganic matter
2.5%	other polychaetes
1.9%	nereids
0.9%	unrecognizable animals
0.2%	gastropods

Bairdiella chrysoura
(All Habitats) n = 7

% Volume	Item
51.6%	mysids
30.5%	nereids
14.4%	palaemonids
1.8%	organic detritus
1.1%	inorganic matter
0.7%	amphipods

Cynoscion nebulosus
(All Habitats) n = 5

% Volume	Item
40.6%	palaemonids
31.8%	fish
23.4%	mysids
1.9%	amphipods
1.1%	organic detritus
1.1%	other polychaetes
0.2%	foraminifera

***Gobiesoma bosc* and similar gobies**
(All Habitats) n = 15

% Volume	Item
53.2%	nereids
28.7%	organic detritus
7.6%	inorganic matter
5.4%	other polychaetes
2.6%	mysids
1.7%	oligochaetes
0.4%	other crustaceans
0.2%	harpacticoid copepods
0.2%	insect larvae

Gobiesox strumosus
(All Habitats) n = 6

% Volume	Item
31.1%	amphipods
26.0%	*C. sapidus*
20.8%	organic detritus
14.4%	isopods
4.3%	other crustaceans
2.9%	mysids
1.4%	unrecognizable animals

Leiostomus xanthurus
(All Habitats) n = 10

% Volume	Item
36.4%	mysids
24.2%	oligochaetes
8.1%	organic detritus
7.5%	harpacticoid copepods
7.3%	inorganic matter
6.0%	unrecognizable animals
3.4%	other polychaetes
3.3%	palaemonids
1.6%	amphipods
1.6%	nereids
0.5%	ostracods

Menidia menidia
(Habitat HU) n = 6

% Volume	Item
33.3%	organic detritus
25.0%	nereids
11.0%	inorganic matter
10.1%	amphipods
7.9%	*C. sapidus*
7.9%	isopods
2.8%	eggs
2.1%	harpacticoid copepods

Menidia menidia
(Habitats HE, HF, HI) n = 26

% Volume	Item
45.2%	organic detritus
13.0%	unrecognizable animals
12.6%	insects, spiders, mites
12.2%	nereids
7.1%	eggs
4.3%	harpacticoid copepods
3.5%	other polychaetes
1.0%	inorganic matter
0.7%	other crustaceans
0.3%	gastropods
0.2%	insect larvae

Symphurus plagiusa
(Habitat HU, HE) n = 7

% Volume	Item
38.3%	nereids
19.8%	organic detritus
13.2%	eggs
12.3%	inorganic matter
10.8%	other polychaetes
3.8%	*C. sapidus*
1.9%	harpacticoid copepods

Symphurus plagiusa
(Habitat LD) n = 10

% Volume	Item
51.6%	nereids
22.0%	inorganic matter
16.7%	organic detritus
7.7%	other polychaetes
1.0%	amphipods
0.6%	isopods
0.3%	foraminifera
0.1%	eggs

The contents of the stomach were examined for fish species that have distinct stomachs. Fundulids, however, have no distinct stomach; for these species the content of the corresponding Section I of the gut (Babkin and Bowie 1928) was examined. For crustaceans, the content of the cardiac stomach ("gastric mill") was examined. Percent composition by volume of dietary items in the guts was estimated indirectly (Hyslop 1980) using a grid on the stage of a dissecting microscope (Odum 1970).

Percent composition data from the gut content study is reported as percent volume of items in the gut content upon examination (Table 2). This does not necessarily reflect the desired descriptor, which is the percent by weight of items that are actually eaten in the diet. The conversion from percent of volume to percent by weight was made by assuming that all items in the gut had approximately the same specific gravity, i.e., that all items were slightly heavier than water. Precedent for this can be found in Swedberg and Walburg (1970). This does introduce some inaccuracy, in comparison to directly weighing each item in a gut, but it is felt that the inaccuracy resulting from this is not a major concern. Certainly the savings in time resulting from this method are very significant.

Samples were preserved in the field using liquid nitrogen, and were transferred to an ultracold (-80° C) freezer for storage. This method assured that digestion was stopped completely within minutes after capture, and simplified the processing of these samples. Relative to preservation in formalin, preservation by freezing maintains the gut in a loose, liquid state (as the gut is found in life). The gut content in certain fish species was often suspended in a matrix of thick cloudy mucus, which is not found as such in guts preserved in formalin. The mucus is most likely a mixture of digestive secretions, partially digested foods, and prey body fluids. Although I have not tested for this, I believe that this mucus appears in formalin-preserved guts as a solidified, flaky, amorphous matter without texture. It is possible that workers with formalin-preserved guts have included the amorphous matter as unrecognizable organic material, or alternatively, have ignored it. The mucus, when present in guts I examined, was quantified in my study as an estimated percent of the volume of the gut. In

my reporting of gut data (Table 1), this mucus has been mathematically removed from the percent volume of gut contents shown for each prey; this was done to facilitate comparisons with other studies. The estimated percent of mucus is included in the modeling of consumption, however; regardless of origin, mucus is an item that occupies volume and has to be passed through the foreguts of predators. If mucus were to be eliminated from the percent-of-gut data applied to the model, then the predicted percents-of-gut of all other prey items would increase accordingly, by a value of 20 - 30% for species whose guts regularly contained mucus.

The analysis of gut information in my study was collapsed with regard to season so as to provide more detail and better replication in examining patterns of habitat use and feeding. Guts obtained throughout the study are grouped into a mean for June through October. This was necessary in order to provide enough guts for a meaningful analysis. It should be noted that other authors have shown seasonal shifts in feeding (Schmelz 1964, Werme 1981, Mansour 1992); these shifts are lost in my analysis. For this reason, my results are generally reported as values for the entire 150 days of the study. Although the total consumption is robust to seasonal shifts in dietary composition, attempting to compare the consumption of various prey items between different months might be less meaningful due to this collapsing of the data.

Quantification of differential digestion in fishes

Differential digestion is a concern with this study, as for any study that tries to estimate feeding from gut contents. If various prey items are digested at different rates, then gut contents will tend to underestimate the importance of rapidly-digested items. Hyslop (1980) remarks that the error induced by differential digestion is minimized by sampling as close to the period of peak feeding as possible, as in the high tide sampling periods of this project. It is also thought that immediate preservation in the field with liquid nitrogen eliminated digestion after capture in this study, but digestion before capture is of course still a concern.

The dominant fish studied, *Fundulus heteroclitus*, does not possess a distinct stomach, but rather a tubular digestive tract that can be divided into 3 segments, I - III (Babkin and Bowie 1928). Mummichogs feature an alkaline digestive system (Nicholls 1931) and digestion is reported to be minimal in the first hour following feeding (Nicholls 1931, Weisberg and Lotrich 1982a). Given the short time period of access to marsh habitats, food items consumed on the marsh surface were generally well preserved and easily identified. The question of differential digestion of the gut content, however, is not addressed by this.

In my study, only items in segment I were removed from fundulids for analysis. Weisberg *et al.* (1981) examined evacuation rates and found that evacuation from segment I into section II took 1 to 2 hours. Since food moves rapidly out of gut segment I (the only segment examined in my dissertation), it is hoped that differential digestion does not dramatically affect these results for mummichogs. A partial correction based on the available literature is offered nonetheless, for mummichogs and all fishes. Results were not dramatically different in model runs with and without gut content corrections; although the values generated differed, similar trends were seen in both cases.

A review of the published literature on differential digestion in fishes shows that several studies have been carried out, but on a wide variety of fish species. Three studies were found which quantified rates of digestion of small, easily digestible particles versus larger and harder food items. Graphs in Kionka and Windell (1972) show that the background matter of easily digestible particles in rainbow trout was processed up to 1.5 times faster than were large chitinous invertebrate parts. Swenson and Smith (1973) found that small minnow prey in walleye guts were digested about 2 times faster than were larger minnows at the same temperature (mean from data points if regressions are plotted). Lankford and Targett (1997) found that mysid shrimp were evacuated 1.8 times faster than larger, thicker shelled *Crangon* shrimp in juvenile *Cynoscion regalis* (weakfish). Although these studies employed different predators, different prey, and different methodology, they all seem to provide similar results. Therefore the mean value of these studies, 1.8, is used as a correction factor to account for slower

digestion of large hard food items in all fishes. It should be noted that the study results were presented as rates, whereas my correction was applied as a single factor. Fish guts in nature contain a mixture of food that has been ingested over a period of time; in this situation a single correction factor can perhaps be appropriately applied.

Another trend which surfaces in the literature is that rates of digestion seem similar between different items that are not large, hard-shelled, or bony. Weisberg *et al.* (1981) examined evacuation rates in mummichogs using trout chow pellets and chopped *Palaemonetes* spp at 20° C. They found that rates of digestion were similar for both food types tested, and that both items had passed through in 1 to 2 hours. Kionka and Windell (1972) found that smaller chitinous parts were passed through the gut at about the same rate as "digestible organic matter" and that large size of chitinous particles played a bigger role in impeding progress than did hardness alone. Kennedy (1969) reported that oligochaetes were rapidly digested by dace, but did not compare rates to digestion of other matter since oligochaetes were the only food offered to the experimental fish. In fact, oligochaetes remained identifiable in the stomachs of dace until they passed to the intestine 2 to 3 hours after ingestion. Parts of cuticle remained identifiable for up to 24 hours in the intestines of dace, and were recognizable for as long as they remained in the fish (Kennedy 1969). It is certainly possible to interpret Kennedy's results to indicate that oligochaetes are not digested so rapidly as to constitute a differential rate problem in gut content studies. Because of the results of these studies I conclude that there is insufficient evidence to warrant applying a correction factor to account for more rapid digestion of very soft prey relative to the general background of "digestible organic matter" (*sensu* Kionka and Windell 1972).

The only correction for differential digestion in fishes, then, was to divide percents of gut content for large, hard shelled prey such as crabs and mussels by 1.8 relative to other prey so as to approximate the actual percent of diet. Following this correction, all percents of gut content were then readjusted by the factor necessary to bring the total back to 100%.

Quantification of differential digestion in crustaceans

Digestion in crustaceans may differ from digestion in fishes. A primary reason to explain this in the case of the blue crab and certain other crustaceans is the presence of a toothed, muscular gastric mill ("grinding stomach"). Differential digestion in blue crabs (*Callinectes sapidus*) was studied by Custer (1985). Interestingly, for small and medium sized crabs (mean carapace width 35 and 51 mm), Custer found no significant differences in rates of digestion of mussels (eaten with shell), shrimp (*Penaeus*), or fish (whole small *Bairdiella chrysoura*). A significant difference was found, however, for large crabs (mean carapace width 84 mm) in that mussel and shrimp prey were cleared from guts more rapidly than were fish. Fish bones often remained in stomachs of large crabs 12 hours after feeding, while mussel and shrimp food was cleared within 6 hours. Custer used fish prey that were sized appropriately to each crab size class, and it is possible that the slower digestion of fish in large crabs vs. small and medium crabs results from her use of larger fish prey (with larger bones) for the larger crabs. Custer noted that mussel shells were regurgitated by the crab within 2 - 6 hours from feeding, and that this accounted for the unexpected rapid removal of these hard items from the stomach.

Even though no statistical differences were found, a slight trend in rates, with mussels being removed fastest, then shrimp, then fish is evident from the regression lines presented in Custer's Figures 2 through 5 for crabs of all sizes combined and individually. Also, it should be noted that Custer found that soft fleshy tissue was always digested within two hours. The purpose of Custer's study was to compare digestion of mussels, shrimp, and fish; but it can also be inferred from her results that digestion of soft organic tissue was perhaps 3 times as rapid as was digestion of shell, carapace, and bone. This conclusion results from her findings, for small and medium sized crabs, that flesh is cleared within two hours while harder parts are cleared within 6 hours. Consequently, although Custer's study reported minimal differences in digestive rate for the tested prey items, a difference is implied for rates of digestion between the tested items and soft tissue. Based on the work of Custer, a correction is made for

digestion of very soft prey in crabs (annelids) but not for digestion of any hard bodied creatures. It is assumed that soft unshelled organisms pass through crabs 3 times faster than do shelled organisms or the general matrix of refractory material that typified crab gut contents. This factor was applied in the same way that the correction for fishes was applied, with the same caveat regarding rates vs. single factors. Again based on Custer, no correction is made for differences in rates of digestion between types of hard-shelled organisms or between these organisms and the general matrix of crab stomach content. The slight (not statistically significant) trends in rates seen among prey types in Custer do not suggest that corrections are necessary between types of hard bodied prey to obtain reasonable results in predicting diet.

Palaemonid shrimp also consume invertebrates (Sikora 1977, Morgan 1980, Kneib 1985), but no information could be found dealing with differential digestion in these crustaceans. McTigue and Feller (1989) suggest that differential digestion probably takes place in penaid shrimp, and point out that the gastric mill of penaids is less calcified than in other decapods; this seems true of palaemonid guts upon examination as well. The palaemonid shrimp I studied did not show a tremendous variety of food size and hardness in their diets. Most gut material was decaying organic detritus, at times mixed with algae or other vegetative matter. Common prey items were nereids and insect larvae (Table 2). No hard parts of larger prey were seen. Based on the uniform appearance of the gut content of these animals, and on the lack of information in the literature, no correction factor for differential digestion in palaemonid shrimp is offered.

Tidal correction for marsh resident species

Marsh resident fishes live in habitats that expand and contract with the level of tide. As tide levels fall from slack high water, densities of marsh resident fish increase per square meter of still-available marsh surface. Drop samples I took in the marsh fringe habitat when the tide had fallen significantly from slack high generally contained extremely high abundances of marsh resident nekton (no samples taken at such tides were included in the data

set used in this dissertation). This tidal concentration of marsh resident populations complicates the analysis of nekton consumption per square meter of marsh.

Unfortunately, little quantitative information exists to describe differences in feeding on the marsh surface within the cycle of high tide. It is not known to what extent nekton are actively feeding when they are compressed by tides into edge habitats. If an assumption is made that feeding is uniform at all stages of the tide, then consumption in habitats near the edge is calculated to be very high due to this tidal population compression. It may be loosely implied from the data of Kneib and Wagner (1994) that larger marsh resident nekton might feed more actively and efficiently in high marsh habitats when these habitats are flooded near slack high tide, but this is not described quantitatively in the literature.

In my mathematical model, consumption is calculated based on nekton populations that were sampled at slack high tide. The basic model allows the sampled population to feed in each habitat for the time period that the habitat is inundated, but does not mathematically compress populations into marsh edge areas with the falling tides. Mathematically, this compression would lead to unrealistically high estimates of consumption at the marsh edge, and it is obvious from this type of calculation that feeding cannot be uniform through the entire tidal cycle as residents are concentrated by falling tides.

In order to deal with this problem, I applied "tidal correction factors" to marsh resident use of the entire marsh surface. The correction factors are applied uniformly to all high tide habitats to adjust daily ration. First, the uncorrected total consumption of each marsh resident species is estimated from the basic (uncorrected) model. The uncorrected consumption figure results from model assumptions of: population densities as determined at slack high tide, equal feeding efficiency in each habitat for the time period that each habitat is inundated, and no tidal compression of populations when tides differ from slack high. This results in an underestimate of consumption, because the model only considers animals in high marsh habitats to exist during the time period of high marsh inundation.

Next, a second consumption estimate is derived for the entire population as sampled at slack high tide, had all animals remained on the marsh for the entire time period that any marsh habitat was inundated. This second estimate predicts what the sampled population should consume during the entire time period that the marsh is flooded. Both of these estimates are generated in an identical manner, using the published daily rations that are incorporated into the mathematical model described above (with corrections for low-tide feeding). The "tidal correction factor" is taken as the ratio between these two estimates. This is done on the mean results of the entire five month study to achieve a single correction factor for each species.

In use, results of the uncorrected model for each habitat are multiplied by the correction factor so that resident nekton actually consume their entire daily ration. If no correction is applied, then marsh resident nekton populations consume considerably less than their expected daily ration, which is clearly an unacceptable situation. The correction factor was remarkably similar for all species of fundulid at about 3.0. The correction factor for palaemonid shrimp was smaller, at 1.8. Another correction factor was applied similarly to estimates of low tide consumption by marsh resident fishes, so that the complete daily ration of the estimated populations of residents were met. The population of larger mummichogs and striped killifishes was not well sampled at low tide. This is thought to be due to gear avoidance of the throw-sampler when used in shallow unvegetated areas (see Chapter 1). Kneib (1997a) suggests that adult fishes do not use the marsh surface as a primary low tide refuge. In any case, the low tide estimates of adult mummichog population numbers are about 5.3 times less than the high tide estimates if the area available to the population is considered in each case. This value was applied as a correction factor to the low tide population estimates, again to maintain the daily ration of the population and to avoid underestimating consumption at low tide.

These correction factors are based on several assumptions, the first of which is that the population of each species of marsh residents in this area is adequately described by slack high

tide sampling. Once an estimate of the total population is obtained, then this population is assumed to be closed within a tidal cycle; the entire group feeds on the marsh surface at high tide, and the entire group feeds in the subtidal at low tide (note that an adjustment is made for use of marsh surface microhabitat as low tide refuge by small nekton, however). The correction factors are then applied to provide the population with the appropriate daily ration over the entire tidal cycle.

A high tide correction factor of 3 implies that nekton consumption increases three-fold in low marsh habitats due to tidal compression of populations, and increases three fold in the high marsh due to increased foraging activity here. It should be noted that some kind of correction factor is necessary to maintain a realistic daily ration. Model results that describe entire marsh populations are robust to these factors, but results that compare use of different habitats are more affected. In practice, the application of correction factors does not dramatically change between-habitat relationships of consumption in corrected vs. uncorrected models, because factors apply to habitats evenly. However, results obtained for individual habitats must be interpreted with these corrections in mind. If the relationship between habitat compression and differential feeding with tide stage is not actually as assumed here, then relationships between use of habitats by resident nekton will likewise differ from model predictions.

The assumptions described above do not hold for marsh transient species, which are not captive to the marsh area within a tidal cycle. Transient species may arrive and depart from marsh habitats in a more or less random manner when these habitats are flooded. It is assumed that my samples at slack high tide represent a snapshot of transient use which can be applied over the entire period of marsh inundation. Unlike residents, transients may leave the marsh surface entirely rather than concentrate in edge habitats as the tide recedes. No correction factors are applied to transient species. They are assumed to feed efficiently in all marsh habitats (at the density sampled at slack high tide) for the time period that each habitat is submerged, without concentrating with the tides at the marsh edge.

While the application of "correction factors" is generally not desirable, they are felt to be necessary in this case for resident nekton. Both transient and resident marsh nekton were sampled as a snapshot at slack high tide; this allows a valid estimate of nekton populations per square meter at that time. If the total area available of each habitat is known, then an estimate of the total population can also be made, as was done here. Resident nekton live in expanding and contracting habitats, however, which causes the number of individuals in a square meter to change despite assumed stable total population sizes. Added to this complexity, rates of feeding may differ between stages of the cycle and between habitats. In order to maintain predicted daily rations for resident populations, some adjustment had to be made. The approach taken minimizes assumptions, maintains predicted daily rations, does not hide any information, and allows the presentation of results that are derived as much as possible from actual sampling.

Corrections for removal efficiency

Results of the model have been corrected for removal efficiencies of the clearing device used to empty the drop rings. These efficiencies ranged from 16% for juvenile blue crabs in *Spartina alterniflora* habitat to 99% for cyprinodontids and fundulids in unvegetated habitats (Table 1, Chapter 1). Efficiencies estimated for marsh resident fishes were applied to all fishes. Efficiencies for large crabs was assumed to be 86% in all habitats, though large crabs were tested for efficiency only in *Spartina alterniflora* habitat (Table 1, Chapter 1). Juvenile crabs were not tested for removal efficiency in unvegetated habitat. This efficiency is assumed to be higher than the 39% and 16% estimates for juvenile crabs in SAV and marsh habitats (Table 1, Chapter 1). In unvegetated habitats, the clearing device was used to scrape a large quantity of mud and associated organisms into the cod end of the device; in vegetated habitats the root mass prevented this. Because of this uncertainty, a range of values was generated from the model based on the assumption that this efficiency was between 40% and 100%. All model calculations involving juvenile crabs in unvegetated habitats incorporate this range of

estimates. All results described in this Chapter have been corrected for the removal efficiency of the gear. This provides a more accurate picture of energy flow in the sampled habitats.

Corrections for poorly sampled size classes of resident nekton

As discussed in Chapters 1, 2, and 3, the gear used in this project did not effectively sample very shallow marsh surface habitats thought to be inhabited by the smallest size classes of marsh nekton. Population size structure was analyzed in Chapter 3, and corrections for poor sampling of larval and juvenile nekton were applied to marsh production estimates. These same corrections are incorporated in the results of the trophic model as well. For trophic calculations, the unsampled population of larvae and early juveniles predicted from production data (Tables 1 -3, Chapter 3) was assumed to use marsh interior habitats.

The unsampled population of marsh resident fishes was estimated at a mean of 5.0 inds m^{-2} and 0.14 gdw m^{-2} over the five months of the study. This is consistent with Kneib (1997b, Table 3) who reports an overall mean of 7.2 inds m^{-2} on the marsh surface for *F. heteroclitus*, with higher densities at certain times of year. It should be noted that Ayers (1995) did not capture juvenile mummichogs in a Goodwin Islands marsh similar to mine, but Ayers sampled only in marsh edge habitats, and did not investigate marsh interior areas. Gut content examinations of captured early juvenile fishes in my study showed a diet consisting primarily of meiofauna; this is also incorporated into these corrections. Juvenile palaemonids were assumed not to feed on animal prey (Nelson 1979) and a correction for this group is not included in the model. In all cases, results for the marsh interior habitat report a range of values; from the estimate which does not include the predicted population of poorly sampled larvae and juveniles, to the estimate which does include them.

Model construction: further information

Model equations are provided in the Appendix to this dissertation. These equations are explained and documented in this Appendix as well. Corrections for tidal habitat compression,

poorly sampled small size classes, and clearing device removal efficiency are not intrinsic to the model and are not shown in the Appendix. The Appendix is intended as a more detailed description of model construction to clarify aspects which are not dealt with thoroughly above.

Types of model output

The models will graphically display monthly means of collected data for each species in numbers of individuals per square meter, or in grams dry weight of that taxa per square meter. This model calculates consumption in each habitat due to any individual predator or combination of predators. The model displays consumption in two ways: predation in grams dry weight removed per day, and as an integration of total grams dry weight removed over time. The model can be run for any sampled time interval to calculate total predation over the specified length of time for any predator/prey combination.

ASSUMPTIONS

It is important to bear in mind that any model involves certain assumptions, which must be considered as model results are evaluated. The following are among the assumptions and caveats incorporated into this model:

1 - Populations are adequately described by the sampling program as modified by correction factors for removal efficiency and for poorly sampled small size classes.

2 - The same nekton access the marsh surface at neap tides (or intermediate tides) and at sampled spring tides, the only difference being the amount of time available for nekton to access a habitat at each tide, due to different durations of flooding.

3 - The entire area within each defined habitat floods for the same length of time; the model does not adjust nekton use within a habitat by area available with tide, but rather by time available with tide.

4 - The gut contents of predators reflect feeding in the habitats where they were captured. This may not be true for individual predators. The assumption becomes more accurate on larger sampling scales, when means of gut information from many predators are considered.

5 - The proportion of each prey item in the diet over the 5 month period of the study can be described by a single value that represents the mean of all months.

6 - Corrections for differential digestion and for tidal population compression (as discussed above) are applied properly.

In spite of these assumptions, model output can be interpreted in a meaningful and informative way. The strength of this model is in the prediction of total consumption over the 150 day sampling period. Comparisons between prey type and habitat type within one month are more subject to error. For this reason, results are generally presented as total values for the entire five months of the study.

RESULTS AND DISCUSSION

SPECIES-SPECIFIC PATTERNS OF DIET AND ENERGY FLOW

Mummichogs

Peracarid crustaceans (amphipods, isopods, and tanaids) constituted a large part of the diet of mummichogs in all habitats at this marsh (Figure 2 and Table 2). Annelids were also an important prey, especially for fish feeding in the unvegetated at low tide. Non-portunid crabs were found in guts of larger fishes (Table 2), and larval and adult insects were an important component of the mummichog diet as well. These results are very similar to those reported by Kneib and Stiven (1978) for a North Carolina salt marsh. If nothing else, my study reinforces the results and general applicability of the study by Kneib and Stiven for mummichog diets in this region.

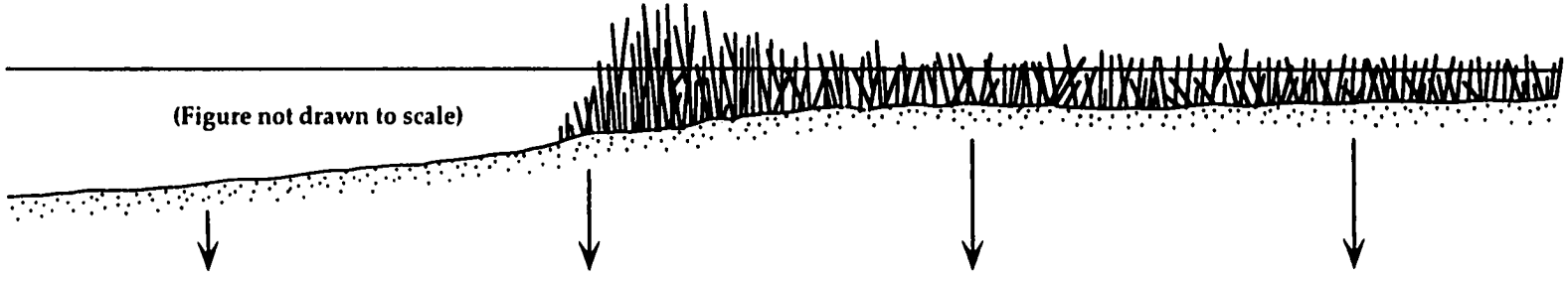
Rainwater killifish, *Lucania parva*.

Hettler (1989b) found that rainwater killifish were the most common fish prey species encountered in guts of juvenile spotted seatrout (*Cynoscion nebulosus*) in Florida seagrass, channel, and mangrove systems. Seatrout were captured more frequently in seagrass systems than in the other habitats in Hettler's study. In my study, rainwater killifish were captured both on the marsh surface at high tide and in SAV beds at low tides (Chapter 2). Unlike other marsh resident fishes, the entire population of *Lucania parva* in my study seemed to migrate between the marsh surface at high tide and the SAV habitat at low tide (Table 3, Chapter 2). These fish, by obtaining part of their energy needs on the marsh surface and then moving into seagrass beds at low tide, may function to transfer energy between these two habitats. This would be particularly important if rainwater killifish were preyed upon in the seagrass beds at low tide. In fact, juvenile spotted seatrout were also found in SAV habitats at low tide in my study (Table 3, Chapter 2). If *Lucania parva* is extensively preyed upon in Virginia seagrass

Figure 2. Estimated Consumption of Various Prey by Mummichogs, June - October 1995.

Estimates for the consumption of each major prey group by mummichogs are provided in this Figure. Values are for total consumption over the five months of the study, except for the marsh fringe habitat which was not sampled in June. The terrestrial group includes insect larvae, insect adults, spiders, and mites. Vegetative matter is distinguished from organic detritus only when vegetation was clearly recognizable as such. Separately quantified inorganic matter (sand, mud) is not shown in the Table, although the organic detritus component no doubt contains inorganic matter that is visually indistinguishable from organic matter. Calculations for the unvegetated habitat are a tidal composite of habitats sampled at high and low tide; the composite is driven by tidal and elevation data for the sampling area. The range of values in marsh interior habitat shows the potential contributions of poorly sampled small size classes of mummichogs.

Consumption of Various Prey by Mummichogs, June - October 1995



Unvegetated Habitat
Mean Inundation 21.3/24 hrs

- 0.6 gdw annelids
  - (0.5 gdw nereids)
- 0.6 gdw peracarids
- 0.4 gdw meiofauna
- 0.2 gdw terrestrial
- 0.2 gdw non-portunid crabs
- 0.1 gdw palaemonids
- 0.1 gdw mollusks
- 2.3 gdw total animals
- 2.9 gdw organic detritus
- 0.6 gdw vegetative matter

Marsh Edge Habitat
Mean Inundation 13.1/24 hrs

- 2.2 gdw non-portunid crabs
- 1.3 gdw peracarids
- 0.9 gdw annelids
  - (0.9 gdw nereids)
- 0.9 gdw terrestrial
- 0.9 gdw unrecog. animals
- 0.4 gdw meiofauna
- 6.7 gdw total animals
- 19.2 gdw organic detritus
- 5.4 gdw vegetative matter

Marsh Fringe Habitat
Mean Inundation 7.6/24 hrs

- 2.3 gdw peracarids
- 2.0 gdw annelids
  - (1.3 gdw nereids)
- 1.5 gdw terrestrial
- 0.3 gdw meiofauna
- 0.1 gdw palaemonids
- 6.3 gdw total animals
- 7.1 gdw organic detritus
- 2.7 gdw vegetative matter

Marsh Interior Habitat
Mean Inundation 3.7/24 hrs

- 0.9 gdw peracarids
- 0.8 gdw terrestrial
- 0.6 gdw non-portunid crabs
- 0.5 - 1.3 gdw meiofauna
- 0.4 gdw unrecog. animals
- 0.3 gdw annelids
  - (0.2 gdw nereids)
- 0.1 gdw mollusks
- 0.04 gdw *C. sapidus*
- 3.6 gdw total animals
- 2.7 gdw organic detritus
- 2.7 - 3.0 gdw vegetative matter

All values are in grams dry weight removed per square meter per 5 months (150 days) except the Marsh Fringe habitat which is per 4 months. Marsh Fringe habitat was not sampled in June.

beds by spotted seatrout as in Florida, then this particular seagrass - marsh link may be of some importance. Unfortunately, the scale of my sampling in SAV beds was too small to properly evaluate use of these habitats by seatrout, and fishes in the guts of those seatrout I captured were not identifiable.

Rainwater killifish in marsh interior areas were found to eat primarily small crustaceans (Table 2), including newly settled non-portunid crabs. These crabs had a carapace width of about 2 mm. This was perhaps the largest prey item that *Lucania parva* could handle; each 2 mm crab occupied about 50% of the volume of the guts which contained this prey. *L. parva* probably lack the gape necessary to handle larger crabs. In marsh edge habitats, *L. parva* consumed proportionally more nereids, which indicates that they may have been feeding on the unvegetated side of the marsh edge, where these nereids are much more abundant (Diaz *et al.*, unpublished data).

Blue crabs, *Callinectes sapidus*

The biomass of crabs seen in my study at the marsh edge (uncorrected sampling mean 4.1 grams dry weight per square meter, approximately equivalent to 16 grams wet weight per square meter) is high in comparison to what has been reported for other marsh studies where blue crabs were the biomass dominants (Hettler 1989a, Rozas and Reed 1993). Other studies have not separately quantified crabs at the edge. Several authors (Kneib 1982, Fitz and Wiegert 1991) have suggested that blue crabs, *Callinectes sapidus*, may function to transfer trophic energy from the marsh surface. In these studies, crab densities were fairly low (40 - 50 per hectare in Fitz and Wiegert, less than 0.7 per 100 m^{-2} in Kneib 1982). In the system I sampled, the density of crabs is at least two orders of magnitude higher. Therefore, crabs may be expected to play a correspondingly greater role in energy transfer in my system, particularly from marsh edge areas.

Blue crabs are opportunistic feeders. Trophic patterns in blue crab use of marsh habitat are summarized by Laughlin (1982) who examined over 4000 guts and concluded that the

feeding habit of crabs was mostly dependent on whatever foods were locally available. My study also found crabs to take advantage of the abundant items as food.

Interestingly, blue crabs feeding in marsh areas showed a considerable amount of chopped *Spartina alterniflora* in stomach contents (Table 3). In guts, the stems of this plant were found snipped into small cylinders from 2 - 5 mm in length. Chopped *Spartina* occurred in 22 of 99 crabs taken from the marsh surface, with a mean volume of 46% in guts where it was present. In unvegetated habitats, this food occurred in 5 of 93 crabs, with a mean volume of 40% in these 5 individual guts. The mean size of crabs feeding on *Spartina* material was 57 mm CW. In Figure 3, only chopped *Spartina* is specifically identified; much of the organic detritus category was also probably derived from *Spartina*.

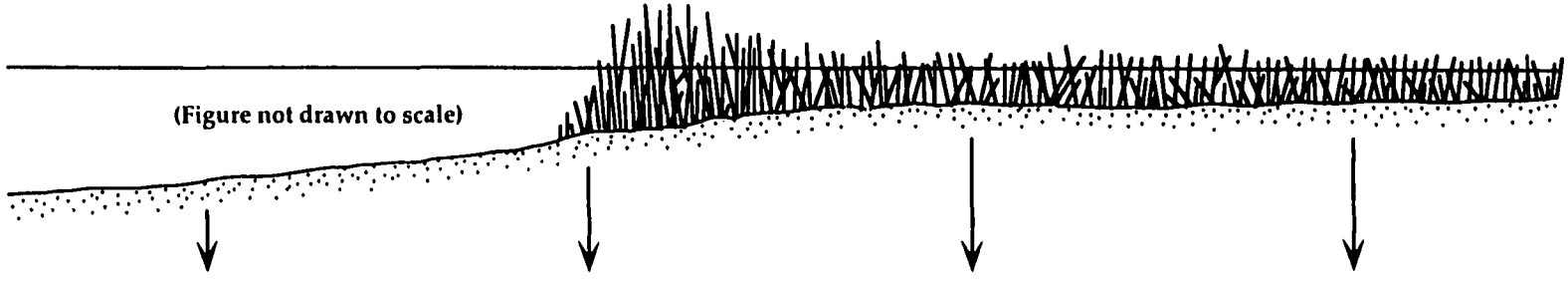
McClintock *et al.* (1991) showed via biochemical analyses that blue crabs may have an ability to digest the starch present in vascular plant matter. Ryer (1987) reported *Spartina*-derived detrital material as the major component of the diet in larger marsh creek blue crabs. These results and my results indicate that blue crabs derive energy directly from *Spartina*. Figure 3 shows that the contribution of *Spartina* material to crabs is less than that of animal prey. Nonetheless, direct use of *Spartina* may be temporally important if crabs are unable to capture animal prey. If so, this implies a very direct transfer of energy from the marsh surface into deeper waters.

The major animal prey of blue crabs feeding in marsh interior areas were the marsh resident crabs *Uca pugnax* and *Sesarma reticulatum* (Figure 3). This is also reported by Fitz and Wiegert (1991); marsh resident crabs made up the largest fraction (43%) of crab gut contents in their study as well. While quantitative data on these non-portunid crabs is not available in my sampling area, they have been quantified in other studies. Teal (1962) found summertime low marsh biomass values for these crabs of 17.6 to 92.42 g m^{-2} (wet weight) depending on location on the marsh surface, and estimated that their production on the marsh surface was on the order of 35 kcal m^{-2} yr^{-1}, equivalent to 12 g m^{-2} yr^{-1} (dry weight) if the conversion of Cummins and Wuycheck (1971) for *U. pugnax* is used. Cammen *et al.* (1980) report a range of mean

Figure 3. Estimated Consumption of Various Prey by Blue Crabs, June - October 1995.

This Figure shows estimates of the consumption of each major prey group by blue crabs. Total consumption over the five months of the study is reported, but the marsh fringe habitat was not sampled in June. The terrestrial group includes insect larvae, insect adults, spiders, and mites. Vegetative matter is distinguished from organic detritus only when vegetation was clearly recognizable. Inorganic matter (sand, mud) is not shown, although the organic detritus component also contains visually indistinguishable inorganic matter. Calculations for the unvegetated habitat are a tidal composite of habitats sampled at high and low tide as driven by tidal and elevation data for the sampling area. The spread of values in the unvegetated habitat is based on a 40% - 100% range of efficiencies for the clearing device in removing small blue crabs from drop rings.

Consumption of Various Prey by Blue Crabs, June - October 1995



Unvegetated Habitat
Mean Inundation 21.3/24 hrs

5.0 - 7.9 gdw annelids
(2.8 - 5.3 gdw nereids)
0.5 - 0.5 gdw mollusks
0.3 - 0.5 gdw unrecog. animals
0.4 - 0.4 gdw non-portunid crabs
0.2 - 0.4 gdw peracarids
0.2 - 0.3 gdw mysids
0.1 - 0.1 gdw *C. sapidus*
6.6 - 10.3 gdw total animals
5.0 - 8.4 gdw organic detritus
1.8 - 2.4 gdw vegetative matter
(0.6 - 0.6 gdw *Spartina*)

Marsh Edge Habitat
Mean Inundation 13.1/24 hrs

12.7 gdw annelids
(11.5 gdw nereids)
3.6 gdw non-portunid crabs
2.8 gdw mollusks
2.5 gdw unrecog. animals
1.7 gdw meiofauna
1.3 gdw peracarids
1.1 gdw *C. sapidus*
25.9 gdw total animals
24.3 gdw organic detritus
4.3 gdw vegetative matter
(3.3 gdw *Spartina*)

Marsh Fringe Habitat
Mean Inundation 7.6/24 hrs

1.9 gdw non-portunid crabs
1.5 gdw annelids
(1.0 gdw nereids)
0.9 gdw unrecog. animals
0.6 gdw *C. sapidus*
0.5 gdw peracarids
0.4 gdw mollusks
0.1 gdw terrestrial
5.9 gdw total animals
2.6 gdw organic detritus
2.1 gdw vegetative matter
(1.5 gdw *Spartina*)

Marsh Interior Habitat
Mean Inundation 3.7/24 hrs

1.0 gdw non-portunid crabs
0.6 gdw annelids
(0.4 gdw nereids)
0.3 gdw unrecog. animals
0.3 gdw *C. sapidus*
0.2 gdw mollusks
0.1 gdw peracarids
2.5 gdw total animals
0.9 gdw organic detritus
0.7 gdw vegetative matter
(0.5 gdw *Spartina*)

All values are in grams dry weight removed per square meter per 5 months (150 days) except the Marsh Fringe habitat which is per 4 months. Marsh Fringe habitat was not sampled in June.

biomass estimates from various studies as between 5.8 gdw m^{-2} and 29.6 gdw m^{-2} if a conversion of 2.671 kcal g^{-1} dw is used (Cammen *et al.* 1980). Grimes *et al.* (1989) report a range of densities for *U. pugnax* as between 27 - 152 inds m^{-2}. These marsh resident crabs feed on diatoms, fungi, and detritus (Grimes *et al.* 1989); their high abundance and biomass on the marsh surface may in part be due to their low position on the food chain. If so, then blue crabs are gaining energy through a fairly direct pathway to the high primary production of the marsh surface. Large blue crabs were particularly effective in feeding on non-portunid crabs in the marsh interior; high percentages of these prey were found in their guts in comparison to percentages of indigestible and refractory material. This ratio of high:low quality food in guts of blue crabs was greater in marsh interior habitats than in other habitats (Table 3). Other important prey of blue crabs on the marsh surface were annelids, mollusks, and other blue crabs.

As was noted by Laughlin (1982) crabs are opportunists that take advantage of whatever food items are locally available. If *Sesarma* and *Uca* are abundant and obtainable on the marsh surface, then *C. sapidus* will feed on them. Crab predation in marsh edge and unvegetated areas was predominantly on nereids and other annelids. Patterns of crab feeding in these habitats are more complex, however, and are discussed in the sections below.

Palaemonids

Detritus was the primary component in the diet of *Palaemonetes pugio* in my study , as was reported by Welsh (1975). Other workers have reported *P. pugio* to be primarily carnivorous (Sikora 1977), or partly carnivorous (Kneib 1985). In my study, infauna made up around 10% of the gut contents (Table 2). *P. pugio* is characterized as an omnivore in my study. Predation by *P. pugio* is estimated to account for between 3 and 8% of total predation on animal prey in marsh habitats (Figure 6). This does not include consumption by the poorly sampled small size classes of shrimp, which were assumed to feed entirely on detritus. If these small shrimp were significant predators, *P. pugio* would account for a greater percentage of the total consumption of invertebrate prey.

Oligochaetes

Overall, oligochaetes were the numerically dominant taxon in the invertebrate coring study at this marsh (Diaz *et al.* unpublished data). The dominance of oligochaetes has been seen in other marsh areas as well (Moy and Levin 1991, Levin *et al.* 1998). Oligochaetes were found only very rarely in guts of predators, however. Since I preserved specimens immediately in the field using liquid nitrogen, digestion of soft-bodied oligochaetes subsequent to capture is not a problem in my study. In addition, oligochaetes were recognizable in the guts when they did occur, and Kennedy (1969) found that tubificids were recognizable in guts of dace for several hours after feeding. Moy and Levin (1991) concluded that oligochaetes were inaccessible to *Fundulus heteroclitus* based on their own gut content studies; my study supports these conclusions. Oligochaetes were rarely found in guts of any predator, despite being the most abundant infaunal group sampled.

HABITAT RELATED PATTERNS OF ENERGY FLOW

Qualitative patterns

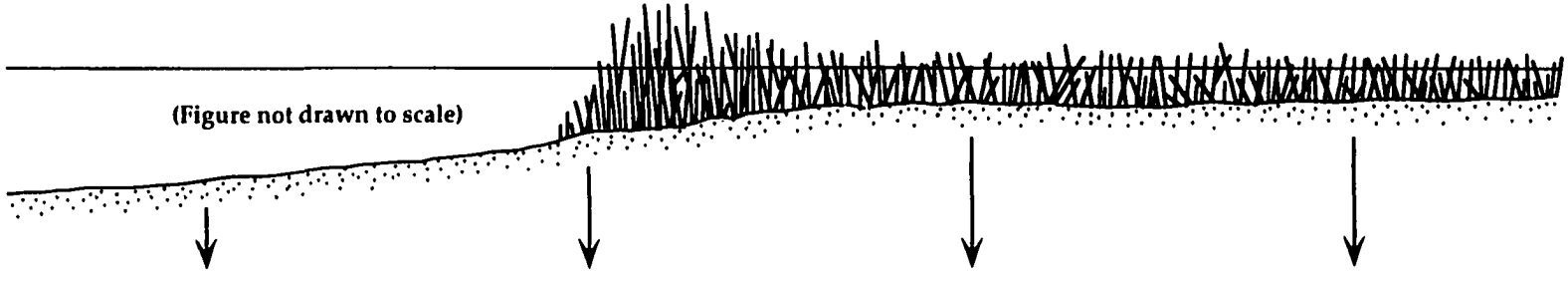
Consumption in the unvegetated habitat (a tidal composite of two low tide habitats and one high tide habitat) was predominantly on annelids, and in particular on nereids (Figure 4). This is also apparent from the raw gut data of Tables 2 and 3 for most species, and is seen in Figures 2 and 3 as model output for mummichogs and blue crabs. The nereid *Laonereis culveri* was especially prevalent in infaunal cores in this habitat (Diaz *et al.* unpublished data) and was often identified in guts as well, though most nereids were unidentifiable to species in the guts. Annelids were clearly the most important prey in unvegetated habitats, as would be expected given their abundance in infaunal cores (Diaz *et al.* unpublished data).

On the marsh surface, annelids, non-portunid crabs (mostly *Sesarma* and *Uca*), peracarid crustaceans (isopods, amphipods, and tanaids) and meiofauna (mostly harpacticoid

Figure 4. Estimated Consumption of Various Prey by Nekton, June - October 1995.

The estimated total consumption of each major prey group by the sum of all nekton predators is displayed in this Figure. Values show total consumption between June and October, except that the marsh fringe habitat was not sampled in June. The terrestrial group includes insect larvae, insect adults, spiders, and mites. Vegetative matter is distinguished from organic detritus only when vegetation was clearly recognizable as such. Sand, mud, and other inorganic matter is not shown, although the organic detritus component no doubt contains inorganic matter as well. Calculations for the unvegetated habitat are a tidal composite of habitats sampled at high and low tide. Ranges in unvegetated habitats and marsh interior habitats (respectively) are *for removal efficiencies on small blue crabs and for contributions of poorly sampled small* nekton.

Consumption of Various Prey by Nekton, June - October 1995



Unvegetated Habitat	Marsh Edge Habitat	Marsh Fringe Habitat	Marsh Interior Habitat
Mean Inundation 21.3/24 hrs	Mean Inundation 13.1/24 hrs	Mean Inundation 7.6/24 hrs	Mean Inundation 3.7/24 hrs
7.1 - 10.1 gdw annelids	18.8 gdw annelids	3.9 gdw annelids	1.8 - 3.2 gdw meiofauna
(4.7 - 7.2 gdw nereids)	(16.9 gdw nereids)	(2.5 gdw nereids)	1.7 gdw non-portunid crabs
1.7 - 1.7 gdw meiofauna	5.9 gdw non-portunid crabs	3.0 gdw peracarids	1.3 gdw peracarids
1.1 - 1.4 gdw unrecog. animals	5.3 gdw meiofauna	1.9 gdw non-portunid crabs	1.3 gdw annelids
1.0 - 1.2 gdw peracarids	3.5 gdw unrecog. animals	1.8 gdw terrestrial	(0.7 gdw nereids)
0.6 - 0.6 gdw mollusks	3.2 gdw peracarids	1.5 gdw meiofauna	0.9 gdw terrestrial
0.5 - 0.6 gdw non-portunid crabs	2.9 gdw mollusks	1.5 gdw *C. sapidus*	0.9 gdw unrecog. animals
0.2 - 0.3 gdw mysids	2.5 gdw terrestrial	0.4 gdw mollusks	0.3 gdw *C. sapidus*
0.3 - 0.3 gdw terrestrial	1.1 gdw *C. sapidus*	0.4 gdw unrecog. animals	0.3 gdw mollusks
0.2 - 0.2 gdw *C. sapidus*	0.4 gdw mysids	0.2 gdw palaemonids	0.04 gdw mysids
0.1 - 0.1 gdw palaemonids	0.4 gdw palaemonids	0.01 gdw mysids	0.01 gdw palaemonids
13.3 - 17.0 gdw total animals	44.2 gdw total animals	14.3 gdw total animals	8.1 - 9.9 gdw total animals
12.1 - 15.4 gdw organic detritus	60.4 gdw organic detritus	14.7 gdw organic detritus	5.5 - 6.0 gdw organic detritus
2.2 - 2.8 gdw vegetative matter	11.8 gdw vegetative matter	4.9 gdw vegetative matter	1.6 gdw vegetative matter

All values are in grams dry weight removed per square meter per 5 months (150 days) except the Marsh Fringe habitat which is per 4 months. Marsh Fringe habitat was not sampled in June.

copepods) were consumed in quantity (Figure 4). A decrease in the importance of annelids with marsh elevation is consistent with results of the invertebrate coring study as well; polychaete abundance decreased with distance into the marsh, while abundances of other phyla increased (Diaz *et al.* unpublished data). Non-portunid crabs were not quantified on this marsh, but are clearly an important prey in this area.

In marsh interior areas, meiofauna were the primary prey consumed (Figure 4). This is due in large part to intensive feeding by *Fundulus majalis* and by small mummichogs. Table 2 shows that harpacticoid copepods were the most important prey to striped killifishes in marsh habitats, and most striped killifish were found in marsh interior areas at high tide (Chapter 2). Meiofauna were the dominant prey item in marsh interior habitat even if the corrections for poorly sampled small size classes of marsh resident fishes are not applied (Figure 4, range of values provided).

A comparison of results from marsh edge, marsh fringe and marsh interior areas shows that predation differs qualitatively between areas of the marsh surface. This is potentially very important in understanding the dynamics and distributions of populations of marsh surface invertebrates. Kneib (1984a) points out that the factors underlying invertebrate distributions on the marsh surface are very complex; my data supports this view as well.

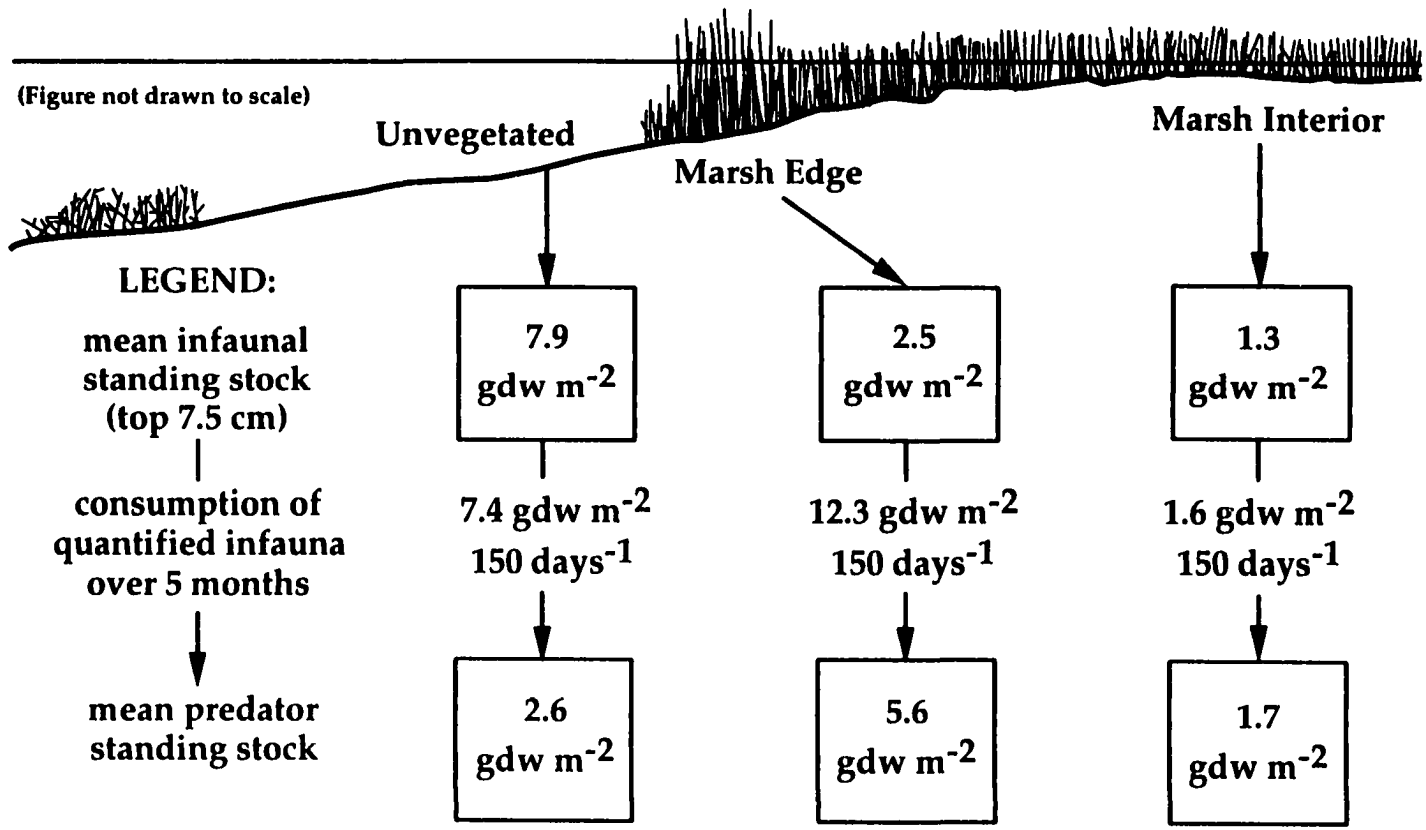
Consumption of infauna by nekton

Figure 5 shows relationships between standing stocks of infauna and predators and the predicted consumption on these infauna. Predicted consumption of infauna is lowest in marsh interior areas. This is mathematically driven in the model by the limited time period of inundation during which nekton could feed here, and by the large proportion of meiofauna, non-portunid crabs, and other unquantified groups in the diets of animals that fed here. Infaunal prey abundances in interior areas of this marsh may be structured more by physical factors such as inundation regime and dessication than by predation, as is suggested in Kneib (1984a).

Figure 5. Estimated Total Nekton Predation on Infauna in Three Intertidal Habitats (Dynamic Calculations for June - October)

This table shows the standing stock biomass of infauna and nekton, calculated as means of the sampled monthly values between June and October. Estimated consumption of quantified infauna by these nekton in each habitat is also shown. Epifauna and other groups are not included in this Figure. Infauna were not sampled at the hightide Marsh Fringe habitat, and no data are provided here. Predation and predator biomass in the unvegetated area are calculated as a tidal composite of habitats sampled at high and low tide. Ranges are provided for gear efficiency (unvegetated habitat) and for poor sampling of small nekton (marsh interior habitat).

Total Nekton Predation on Quantified Infauna in Three Intertidal Habitats (Dynamic Calculations for June - October)



Infaunal prey in unvegetated and marsh interior areas (Figure 5) should be able to maintain stable populations given these levels of predation. If we assume an annual P:B ratio for infauna of 4.9 as is reported for polychaetes in Chesapeake Bay by Diaz and Schaffner (1990), then an estimated 27% and 50% of the available yearly production is consumed by predators in unvegetated and marsh interior habitats. If this P:B is applied to marsh edge infauna, the model estimates that 260% of the available production was consumed, and an imbalance clearly exists. Small blue crabs are the major predators on infauna in marsh edge habitat, and can explain this imbalance, as is discussed below.

Small blue crab use of marsh edge and unvegetated habitats

Nereids were the primary prey consumed by small blue crabs in both marsh edge and unvegetated areas (Table 3). Nereids were the biomass dominant in unvegetated areas, but were much less common in vegetated marsh edge habitats (Diaz *et al.* unpublished data). This suggests that crabs captured on the marsh edge had in fact been foraging on nereids in unvegetated areas. Nereids were found in guts of other nekton captured on the marsh edge as well, particularly *Lucania parva* (Table 2). If consumption of nereids (16.9 gdw m^{-2} 150 d^{-1}, Figure 4) is subtracted from marsh edge predation in Figure 5, the remaining 8.7 gdw m^{-2} 150 d^{-1} would remove 89% of the available yearly infaunal production, and the imbalance noted above is mostly resolved.

In fact, marsh edge and unvegetated areas may function together to support crab populations at my site. Deep unvegetated areas subject small crabs to high levels of cannibalism (Ruiz *et al.* 1993, Heck and Thoman 1981) and the unvegetated areas with abundant nereid prey may expose small crabs to predation by larger conspecifics at high tide. Small blue crabs ($\leq$ 30 mm CW) were abundant in marsh edge habitat at high tide, perhaps as a refuge from predation by larger crabs. Although large crabs were found at the marsh edge as well, foraging efficiency of the larger crabs and cannibalism is no doubt hampered by the stem

structure of *Spartina*. At low tide, small blue crabs are afforded a refuge by shallow water depths (Ruiz *et al.* 1993, Dittel *et al.* 1995) and may forage more heavily in unvegetated areas. In my study, small blue crabs were more abundant in unvegetated areas at low tide than at high tide (Table 3, Chapter 1), but this was not statistically significant (Table 4A, Chapter 1). The Lowtide Shallow habitat (0 - 10 cm deep) was frequented by very small blue crabs; of 104 crabs captured here, only 3 were greater than 35 mm CW. This size distribution also suggests a shallow water refuge from predation at low tide here, given the scarcity of larger crabs. The structure provided by aquatic vegetation also acts as a refuge to blue crabs (Heck and Thoman 1981). The marsh edge may function as an important high-tide refuge for small blue crabs that feed on nereids in the adjacent unvegetated at other stages of tide.

I suggest that the adjacent marsh edge and unvegetated intertidal habitats provide a productive combination of food and structural refuge for small blue crabs. This also appears to be true for *Lucania parva*. I therefore consider that these areas are inextricably linked, and do not attempt to separate the contribution of marsh edge and unvegetated areas based on refuge value or feeding opportunity. Consumption and export from the marsh edge (discussed below) is driven by blue crabs feeding on nereids, and this area may be thought of functionally as a marsh edge/unvegetated complex. Drop ring samples taken at the marsh edge included half vegetated area and half unvegetated area. Although the term "marsh edge" is used in the discussion that follows, the unvegetated side of this interface is just as important as the vegetated side. In fact, it is the combination of attributes from both habitats that make edges so valuable.

Quantitative patterns of energy flow

On a per-square-meter basis, predation is greatest at the marsh edge (44.2 gdw m^{-2} 150 d^{-1} animal prey consumed, Figure 6). This is due to the high abundance and biomass of nekton sampled in this habitat (Chapter 2) and to the longer period of inundation relative to other

marsh habitats. It is also due to the consumption of nereids from the unvegetated side of this interface (16.9 gdw m^{-2} 150 d^{-1}, or 38%) as noted above.

Predation in the unvegetated area not immediately adjacent to marsh edge is calculated as a tidal composite of three habitats (Lowtide Shallow, Lowtide Deep, and Hightide Unvegetated), as driven by tidal information. Consumption of animal prey (13.3 - 17.0 gdw m^{-2} 150 d^{-1}) and particularly of annelids (Figure 4) is considerable in the unvegetated habitat, with blue crabs removing more biomass than other predators. As discussed above, this intertidal unvegetated region is characterized by high standing stocks of infauna and by high production of benthic microalgae (Buzzelli 1996).

Predation on the marsh surface away from the marsh edge is lower than predation on the edge (Figure 6), in part due to shorter inundation times. Predation per square meter in the marsh fringe habitat (14.3 gdw m^{-2} 150 d^{-1}) is similar to predation in unvegetated habitats, due mostly to high consumption by marsh resident fishes. Predation is lowest in marsh interior habitats away from the edge (8.1 - 9.9 gdw m^{-2} 150 d^{-1}), despite the application of correction factors which effectively increased the efficiency of predators feeding here (see above). This is due both to the shorter periods of inundation here and to the generally lower biomass of predators in this habitat.

An estimate of the total area provided by each habitat is useful in evaluating the contributions of these shallow water regions. Figure 7 shows a hypothetical mean transect of marsh, as described in Chapter 3. Tidal and marsh elevation data showed that the sampling area flooded to an average horizontal distance of 16 m during mean high tides within the time period of sampling. Values determined per m^2 in Figure 6 are multiplied by the available area of each habitat at mean high tide in Figure 7. This analysis shows that all habitats are important in providing prey to nekton, with 324 - 385 gdw removed over 5 months (150 days) from the entire 26 m^2 transect, 191 - 215 gdw 150 d^{-1} of which are removed from the 16 m^2 of marsh surface. Activity is most intense at the marsh edge, but the larger area of the unvegetated and the marsh interior gives these habitats a greater overall importance. The

Figure 6. Estimated Flows of Trophic Energy from Marsh and Unvegetated Habitats, June - October 1995.

This table shows the estimated consumption of animal prey by the four major groups of nekton in each habitat, as estimated by the trophic model. Numbers to the right of each nekton box represent grams dry weight of animal prey consumed per square meter over 150 days by that predator group. Nekton are grouped as residents and transients; consumption by transients is considered to be export. Consumption by residents is assumed not to leave the marsh (note that this is not entirely true) and is shown with a downwards pointing arrow. The marsh Fringe habitat was not sampled in June; values here represent a 120 day period. Ranges indicate estimated removal efficiency in the unvegetated habitat and poor sampling of small nekton in the marsh interior habitat.

Estimated Flow of Trophic Energy from Intertidal Habitats

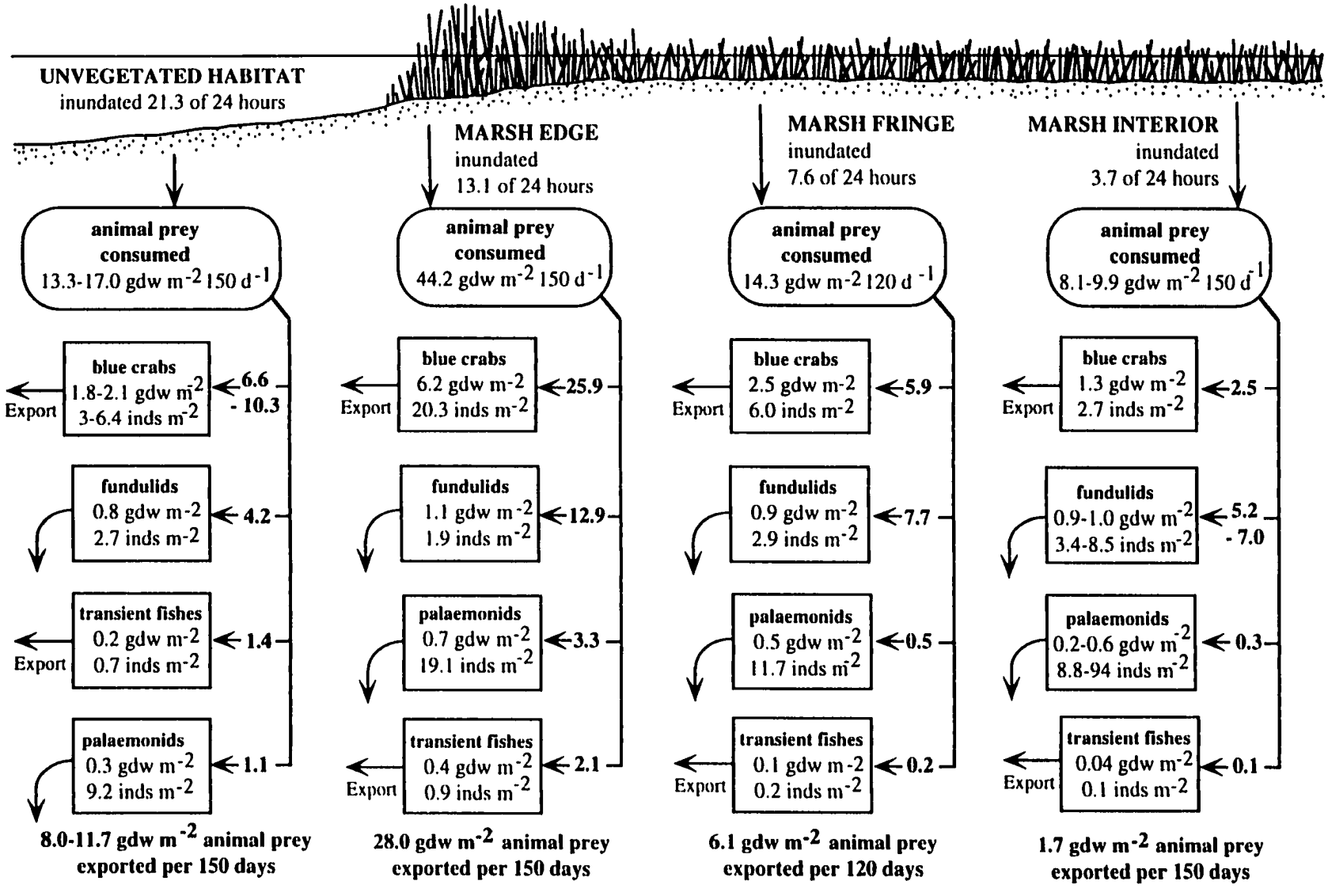
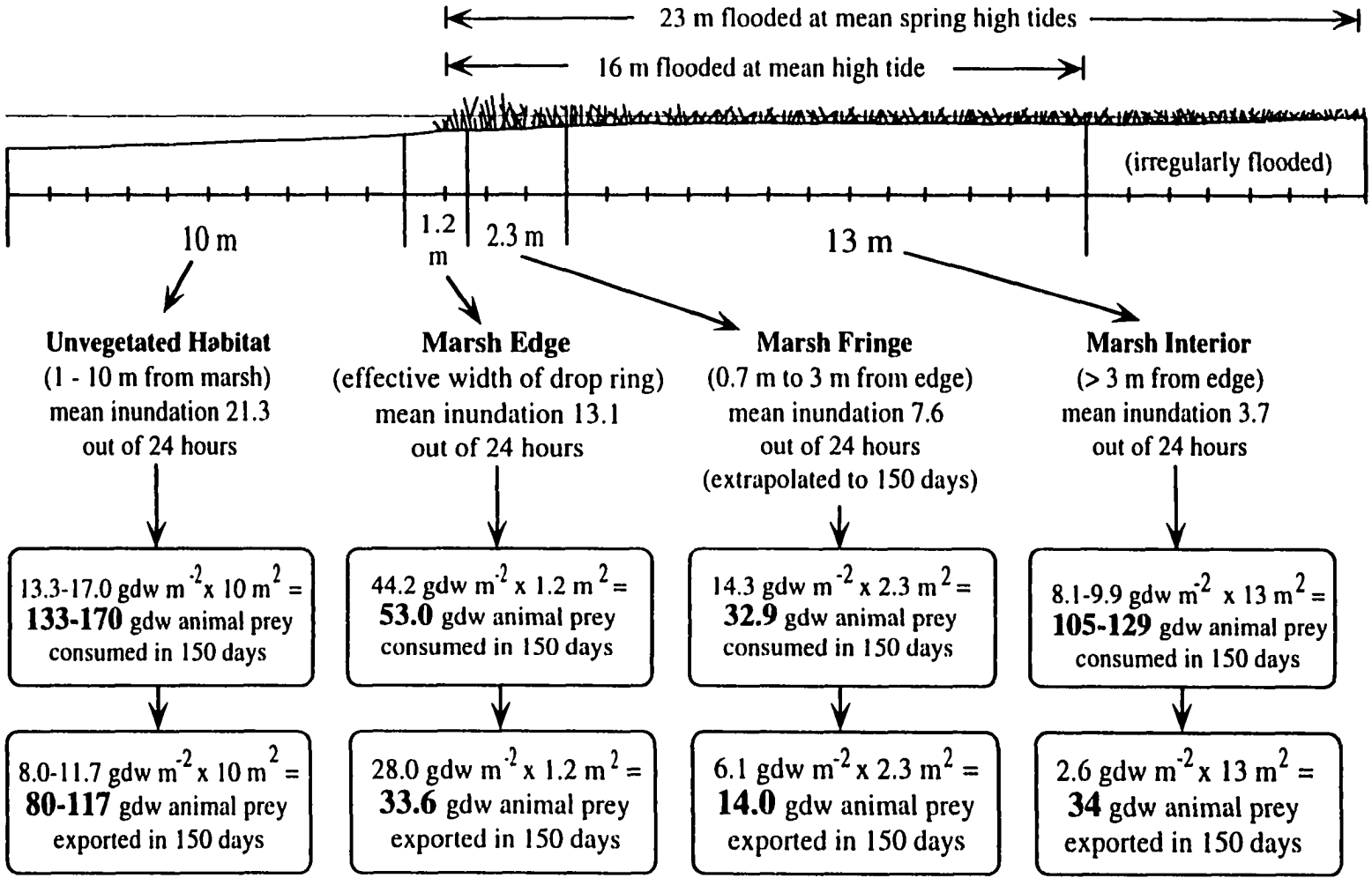


Figure 7. Estimated Export via Predation on Invertebrates by Marsh Transient Species along a 1 m wide Transect of Habitat.

This figure applies values shown in Figure 6 to an average transect of marsh flooded at mean high tide (16 m). The marsh transect was developed using tidal and elevation data for the sampling area. Estimates are provided for the total area encompassed by each habitat quantified in Figure 6. Values for the marsh Fringe habitat are extrapolated from 120 to 150 days to provide an accurate total for the entire transect. The extrapolation was based on changes in nekton biomass seen between months in other habitats. Ranges indicate estimates for gear removal efficiencies (unvegetated habitat) and corrections for poorly sampled small size classes (marsh interior habitat).

Export via Predation on Invertebrates along a 1 m wide Transect of Habitat



unvegetated intertidal clearly plays a major role in the trophic support of shallow water nekton in my sampling area. This is due in part to the use of this area as a low tide refuge by marsh residents, in part to the longer time period for which this habitat is inundated and available, and in part to the large biomass of infaunal prey available here (Diaz *et al.*, unpublished data).

The interior marsh surface is submerged and accessible to predation for a short period (mean 3.7 hours out of 24 hours), but actually sees a rapid removal of animal prey during this time. Figure 6 shows an estimated 8.1 - 9.9 grams dry weight removed per 2.4 - 2.9 gdw of predator per square meter per 3.7 hours x 150 days (Figure 7). This can be expressed as a mean removal rate of 0.0061 gdw per gdw of predator per square meter of marsh per hour of inundation. These rates are similar when calculated for other marsh habitats as well, and are high even if the tidal compression correction factor that provides increased foraging efficiency in the marsh interior is removed (uncorrected, 0.0030 gdw m^{-2} hr^{-1} $pred^{-1}$ for the marsh interior). In contrast, the unvegetated area is submerged for 21.3 hours per 24 hours on average and sees an estimated 13.3 - 17.0 grams dry weight consumed per 3.1- 3.4 gdw of predator per square meter per 21.3 hours x 150 days, or about 0.0015 gdw of animal prey consumed per gdw of predator per square meter per hour of inundation (rates are only slightly higher if just low tide use of the unvegetated is considered). The model predicts a rate of consumption per gdw of predator per hour for the marsh interior that is 2 to 4 times higher than in the unvegetated area.

This phenomenon is due in part to the generally larger percentages of animal prey in guts of animals captured in the marsh interior. While infauna are more abundant in unvegetated areas, their extraction from the sediment may entail consumption of substrate and detritus. The marsh surface is relatively clean, and prey in guts are generally not associated with quantities of detritus. This was not true of large mummichogs, but these were more abundant at marsh edge habitat than in the interior. In terms of importance to the populations of nekton inhabiting these areas, the rate at which high-quality prey can be obtained may be of great importance. Lankford and Targett (1997) demonstrate that energy intake and growth

rate in estuarine fish can be regulated by food quality, and several authors have found that marsh resident fish are food limited (Werme 1981, Weisberg and Lotrich 1986, Kneib 1993). An area such as the marsh interior may be very important as an opportunity to feed rapidly, even if for only a short while (Weisberg and Lotrich 1982b). Marsh habitats are very complex. As Peterson and Turner (1994) point out, it can be misleading to attempt to assign values to habitats given an incomplete understanding of marsh function. It is clear from my data that the unvegetated intertidal area plays an important role in the energy dynamics of this salt marsh; it should not be inferred, however, that marsh interior areas do not.

EXPORT VIA PREDATION ON RESIDENT NEKTON BY TRANSIENTS

Little evidence of direct predation on permanent marsh resident fishes was found in this sampling area during my study. The only potential predator captured in large enough numbers to suggest the possibility of impacting populations of marsh fish was *Callinectes sapidus*. Very few fish were found in crab guts. This is in contrast to studies by Laughlin 1982 and Kneib 1982, who found evidence of predation by *C. sapidus* on fishes in other systems. Predation on marsh resident fishes has been shown in other systems (Rountree and Able 1992b, but see Kneib 1997a). In this dissertation study, palaemonid shrimp were found in the guts of spotted seatrout and silver perch feeding in marsh habitats (Table 3). Silver perch and spotted seatrout were captured in low numbers, however (Table 3, Chapter 2).

It is possible that the choice of gear used to sample these marshes affected my sampling of larger transient predators. Enclosure traps such as I used tend in particular to underestimate densities of large fishes (Jacobsen and Kushlan 1987). It is unclear whether the low abundance of larger fishes in my study is a real result or an artifact of the drop trap gear used in sampling. Cicchetti (unpublished 1996 data) collected piscivorous fishes in a study of erosional marsh edges at the Goodwin Islands in 1996. The methods and results of this project are described in Chapter 3 above. Cicchetti (unpublished data) found that the mean abundance and biomass of larger piscivorous fish species between June and September 1996 was 0.09 ± 0.02

inds m^{-2} and 0.92 ± 0.27 (SE) gdw m^{-2}. The biomass-dominant piscivores were bluefish (*Pomatomus saltatrix*), summer flounder (*Paralichthys dentatus*), inshore lizardfish (*Synodus foetens*), and striped bass (*Morone saxatilis*). Gut examinations showed some evidence of feeding on mummichogs.

Erosional marsh edges may be used more than depositional marsh edges by larger predatory fishes (McIvor and Odum 1988, Hettler 1989a) and results of Cicchetti (unpublished data) therefore cannot be directly applied to this dissertation. However, the study does indicate that larger piscivores use marshes at the Goodwin Islands. Assuming a 6% daily ration at 20° C, 75% of the diet being animal prey, 6 hours to feed at the marsh per 24 hour period, and a Q_{10} of 2.0, then 2.4 gdw m^{-2} 150 d^{-1} of animal prey would have been consumed by these piscivores at the marsh edge. Predation and export by larger transient piscivores does occur in marsh habitats, but is very difficult to quantify. The value of 2.4 gdw m^{-2} 150 d^{-1} is offered as a first order estimate of this predation at an erosion edge site.

EXPORT VIA MIGRATION OF TRANSIENT SPECIES FROM MARSH HABITATS

Captured nekton were divided into two categories, marsh residents and marsh transients, in order to evaluate trophic export from the marsh surface. Figures 6 and 7 estimate export by transient marsh fauna such as blue crabs and non-resident fishes as they migrate on seasonal or shorter time scales into deeper waters. Trophic connections between habitats also occurs via marsh residents and the "trophic relay" hypothesis of Kneib 1997a (see Introduction), where marsh surface production is ultimately consumed by larger aquatic and avian predators in deeper waters. The erosional-edge piscivorous fish predation estimate of 2.4 gdw m^{-2} 150 d^{-1} (above) attempts to quantify these processes, and could be applied to these calculations as a first-order approach. Figures 6 and 7 are based on drop ring data, and do not attempt to describe predation on resident nekton. In Figures 6 and 7, consumption by resident fundulids and palaemonids is assumed to remain in marsh habitats and is represented by a downward-pointing arrow. All consumption by transient fishes and crabs is considered export.

Figure 6 shows that, on a per square meter basis, the marsh edge was the region of greatest foraging activity and trophic export (28.0 gdw m^{-2} 150 d^{-1}). Most of the export from marsh edge habitat was due to blue crabs, *Callinectes sapidus*, with about 8% due to transient marsh fishes. In fact, blue crabs were the major exporter of animal prey from every habitat described. In marsh fringe and interior areas, the most important exported prey were non-portunid crabs (Figure 3). In unvegetated habitats and on the marsh edge, the most important exported prey were annelids (Figure 3).

The marsh edge may provide the greatest export of animal prey per square meter but represents the smallest area of any sampled habitat. Figure 7 shows export from the 1 m wide by 16 m long transect that would be flooded at mean high tide. This Figure predicts a total of 48 gdw m^{-2} 150 d^{-1} exported from the inner 15 m^2 of marsh. Of this, 17.4 gdw m^{-2} 150 d^{-1} or about 36% was non-portunid crab biomass exported via blue crabs. At the marsh edge, 33.6 gdw m^{-2} 150 d^{-1} was exported from the approximate 1.2 m^2 of transect effectively sampled by the drop ring. The marsh edge was an area of very high export relative to total export from the marsh interior. The narrow fringing nature of this marsh did not provide an extensive interior area, and biomass of blue crabs was very large at the marsh edge. The biomass exported from both the edge and from the interior of this marsh represent a clear contribution to deeper ecosystems.

The sampled unvegetated area contributes another 80 - 117 grams of export per 10 m x 1 m (Figure 7). It is of interest that estimates for export from the unvegetated area were so high. Many previous studies of marshes have found nekton to be more abundant in marsh surface habitats than in adjacent unvegetated areas (Zimmerman and Minello 1984, Baltz *et al.* 1993, Rozas and Minello 1998 in press) and this was true of my marsh at high tide as well (Table 4, Chapter 2). The importance of unvegetated areas was evident only when the entire tidal cycle is considered.

In particular, the lowtide use of unvegetated habitat I report may be a function of the tidal regime in the mid-Atlantic. In some Gulf of Mexico marshes, both marsh and unvegetated habitats may be continuously submerged for long periods of time (Rozas and Minello 1998 in

press). Lowtide use of the unvegetated is probably very different between these areas and my area. The unvegetated habitat adjacent to the marsh is not regularly intertidal if inundation periods are long, and may be inherently different for this reason. In addition, if the marsh surface remains submerged for the entire tidal cycle, then the adjacent unvegetated area would not function as a low tide refuge for marsh residents. Regions with different tidal regimes offer habitats that may appear similar at high tide, but provide nekton with very different opportunities for feeding and refuge throughout the entire tidal cycle.

As mentioned above, calculated consumption of animal matter per square meter of marsh edge habitat was considerably larger than was consumption in unvegetated areas (44.2 gdw m^{-2} 150 d^{-1} versus 13.3 - 17.0 gdw m^{-2} 150 d^{-1}, Figure 7), and was more than three times the average consumption per square meter of marsh overall (44.2 gdw m^{-2} 150 d^{-1} versus ~ 13 gdw m^{-2} 150 d^{-1}, Figure 7). Nereids taken by predators captured in edge habitats (particularly blue crabs and rainwater killifish) were probably consumed in unvegetated areas, however. Even if the 18.8 gdw m^{-2} 150 d^{-1} of annelid consumption are subtracted, consumption at the edge is still greater than in other habitats at 25.4 gdw m^{-2} 150 d^{-1}. Export via predation by marsh transients was similarly highest per square meter of edge habitat, even if export of annelids is subtracted from the edge figures.

These trends in consumption and export from the marsh are driven by trends in nekton abundance and biomass, which follow the same pattern of highest values at the marsh edge. Many previous studies have also shown that the edges of tidal marshes support a higher biomass and diversity of fishes and crustaceans than do areas in the marsh interior (Minello and Zimmerman 1992, Baltz *et al.* 1993, Minello *et al.* 1994, Peterson and Turner 1994). Rozas (1993) concluded that marsh edge was selected for by estuarine transients, including species of commercial value. My study adds to this body of evidence, and extends the geographic regions in which these studies have been conducted.

Much of the previous work with salt marsh edges has been in Gulf and south Atlantic marshes. These marshes function differently than mid-Atlantic marshes, in part because of the

very different tidal regimes in each area (Rozas 1993, Kneib 1997a). Nonetheless, some broad conclusions regarding relationships between marsh surface and marsh edge apply similarly in different regions. My study examines a marsh transect in more spatial and temporal detail than have many previous works, quantifying nekton and estimating consumption in 5 habitats at high tide and 3 habitats at low tide over a 5 month period. This consumption and export analysis lends further support to the notion that edges are extremely valuable areas for salt marsh function. In my marsh, the importance of edge was clearly dependent on the adjacent unvegetated area. This may be true in other regions as well. Edges by definition include two habitat types, and it is this combination of habitats that make edges valuable.

Indeed, it is generally in agreement that marshes with more edge habitat support higher densities of estuarine nekton, and that created marshes should attempt to maximize edge by incorporating reticulation into marsh design (Minello and Zimmerman 1992, Peterson and Turner 1994). My study supports these findings, given especially that the adjacent unvegetated intertidal was very important to trophic processes in my sampling area. If a productive intertidal unvegetated site in my sampling area were replaced with a featureless high elevation mitigation marsh, the net benefit to the ecosystem might not be as planned. However, since marsh edge is utilized to a greater extent than is either unvegetated intertidal or marsh interior, restoration that includes the creation of an extensive marsh edge system may well lead to a net improvement of ecosystem function as trophic support for deeper ecosystems.

In the tidal regime of this area (and quite possibly in other tidal regimes) it appears that the unvegetated, the marsh edge, and the marsh surface function together and are all of considerable importance to communities of shallow water nekton. Efforts to restore damaged estuarine areas should recognize the unique importance of every intertidal habitat, as well as their combined importance. These habitats clearly work together in support of the larger ecosystem.

CONCLUSIONS

Several of my findings are consistent with patterns reported from other marshes. Feeding by mummichogs was similar to that reported in Kneib and Stiven (1978) for a North Carolina marsh. Blue crab guts from interior marsh habitats contained large amounts of non-portunid crab prey (as was found by Fitz and Wiegert 1991) and substantial quantities of *Spartina alterniflora* (as was reported by Ryer 1987). Oligochaetes were the most abundant infaunal group on the marsh surface, but were rarely found in gut contents; this was also reported from a North Carolina marsh by Moy and Levin (1991). Marsh edges were characterized by higher abundance and biomass of nekton than were marsh interior or unvegetated areas, as has been described in Zimmerman and Minello (1984), Minello and Zimmerman (1992), Baltz *et al.* (1993), Minello *et al.* (1994), Peterson and Turner (1994) and Rozas and Minello (1998 in press). These and other aspects of predation by nekton may apply similarly to the marsh I studied and to various other systems.

Other aspects of predation by nekton are novel or differ from that reported in other systems, particularly on a community and habitat level. Predation in unvegetated areas was primarily on annelids, which were prevalent in this habitat (Diaz *et al.* unpublished data). In marsh surface habitats, a much greater diversity of prey was exploited, including annelids but also including peracarid crustaceans, various crabs, insect larvae and adults, and meiofauna. The marsh edge was the area of greatest predation and transfer per square meter. In marsh interior habitats, meiofauna were predicted to be the most important prey group (by biomass), due in large part to selective feeding by striped killifishes and small mummichogs, which were most abundant in these habitats. Palaemonid shrimp were primarily detritivores, yet their predation in all areas was estimated to be at least 3 - 8% of the total consumption of animals by all nekton. Most of these results are not contrary to information seen in other studies; they are generally unreported only because consumption is rarely estimated on a community-wide basis.

My study represents one of the few attempts in this region to quantify the removal and export of living animal tissue from the marsh surface. I examined predation by small resident and transient predators on invertebrates. Total consumption of animals on the marsh surface was high, with about 13 grams dry weight of animal matter removed per square meter over a 5 month period (Figure 7). Consumption on the marsh edge was about three times this on a per square meter basis; these high rates were supported by contributions of both the vegetated and the unvegetated sides of the marsh edge. Trophic export in the marsh I studied constituted a significant flux to deeper waters, with 81.6 grams dry weight of animal matter being exported per 1 m x 16 m transect of marsh over five months (Figure 7). Blue crabs were the major predator contributing to this export, and blue crab predation on non-portunid crabs constituted about 36% of total quantified export from the marsh interior. The unvegetated intertidal was also a major source of biomass export to deeper waters, with blue crab and transient fish predation (primarily on annelids) contributing 8.0 - 11.7 gdw m^{-2} as export over five months.

My results indicate a significant contribution of the intertidal unvegetated area and of the marsh surface to deeper waters. Rozas (1993) concluded that densities of nekton on Gulf coast marshes are at least an order of magnitude greater than on Atlantic coast marshes. Therefore, I would expect that marshes from certain other geographic regions would contribute at least as much production to deeper waters as this one does.

This trophic study emphasizes the interconnectedness and importance of all sampled shallow water habitats. Both vegetated and unvegetated habitats at the marsh edge function together to provide food and refuge to support high biomass, consumption, and export. Marsh interior areas are host to a different community of marsh animals, and allow for very efficient removal of invertebrate prey - - this may be of particular importance if marsh residents are food-limited. The unvegetated intertidal is quite productive, especially if analyzed over a 24 hour period, and acts as a necessary low-tide refuge for marsh residents. All habitats contributed importantly - and differently - to the trophic workings of this shallow water

ecosystem. All habitats were linked by nekton that follow the tides seeking food and refuge and, in doing so, move energy from shallow waters to deeper waters.

SUMMARY DISCUSSION: THE SALT MARSH SURFACE AND ADJACENT WATERS

REVIEW OF MAJOR FINDINGS

This study was composed of three major parts, linked in that the same sampling program (Chapter 1) and the same data were used throughout. Chapter 2 describes nekton use of the sampled shallow water habitats between June and October 1995. In Chapter 3, production of these organisms over the same time period is estimated. Chapter 4 analyzes predator-prey relationships over the 5 month time period. Predation calculations were based on mathematical considerations of predator biomass, daily ration, and gut content data, as affected by body size, temperature, tidal effects, and diel effects. All Chapters evaluate different aspects of the same shallow water nekton community, and can therefore be considered together.

In Chapter 2, the community of nekton inhabiting the sampled shallow water habitats was described as diverse (32 captured species) and rich in numbers of individuals, with a mean of 28.6 inds m^{-2} for all samples and habitats. Biomass was also high, with an overall mean of 3.8 gdw m^{-2}. Quantifications provided in Chapter 2 are not corrected for removal efficiency of the sampling gear, and actual values are certainly higher (Chapters 3 and 4 do correct for removal efficiency). Crustaceans were the most prevalent taxon: blue crabs, *Callinectes sapidus*, were the biomass dominant, while palaemonid shrimp were the numeric dominant. Fishes made up three quarters of the numbers of species, however. Fundulids dominated marsh habitats while *Gobiosoma bosc* was the most abundant fish in seagrass areas. In general, seagrass and marsh edge habitats saw greater numbers and biomass of nekton than did marsh interior and unvegetated areas, though these patterns varied considerably for different species. Patterns of habitat use by *Fundulus heteroclitus*, *Lucania parva*, *G. bosc*, *F. majalis*, and *Palaemonetes intermedius* were different from what has been described in other geographic areas. This was interpreted as flexibility in use of SAV, marsh, and unvegetated habitats between regions.

Some of the patterns described in Chapter 2 have been well documented in the literature, while others have not. The marsh edge is suggested as a potentially very important

habitat for blue crab recruitment and trophic support; these values have previously been ascribed to seagrass beds, but not to marsh habitats in Chesapeake Bay. Significant year-to-year variation was shown for recruitment to the edge in blue crabs as well. Significant diel differences in use of the marsh were also documented for Atlantic silversides (*Menidia menidia*). It was also shown in Chapter 2 that the majority of individuals and biomass were of species that used all three habitat types (SAV, unvegetated, and marsh) at one stage of tide or another. Given this finding, I suggest that all three habitats are linked by the tidal migrations of these mobile creatures.

Chapter 3 considers production of marsh resident and marsh transient species. Values of production for single species in these habitats may not be as dramatically high as has been thought. Concerns with previous studies are pointed out, and production at my area fell within the range of values presented in the literature for other shallow water habitats. Nonetheless, production of nekton is considerable in these areas. Although marsh surface production may not be significantly higher than is production in other shallow water areas, this should not detract from the perceived value of marshes. Production was still high, the marsh provided trophic support for a diversity of species, and production of blue crabs on the marsh edge was seen to be high, comparable to what has been seen in local SAV beds. In addition, the unquantifiable value of marshes to estuarine production must be considered. Marshes offer refuge; they also offer permanence on several time scales. These attributes are not quantifiable, but should not be overlooked. I sampled an open embayment marsh with no creeks and only limited horizontal flooding. This type of marsh may represent the low end of the range of productivity in healthy marshes, and secondary production may well increase with marsh complexity, tidal creeks, and submergence.

Chapter 4 estimates the consumption of nekton in marsh and unvegetated habitats using a mathematical model. This chapter first describes feeding patterns of individual nekton species, then summarizes findings per square meter on the community level. Finally, findings

are extrapolated from a square meter of habitat to provide estimates for the entire transect of habitats that made up the sampled area.

Findings for consumption by individual species were generally similar to what has been documented for these species in other marsh areas. On the community and habitat level, major distinctions were seen between habitats. Predation in unvegetated areas was high on the abundant infaunal annelids. Predation in marsh habitats was low on the infaunal dominant (oligochaetes) but predators made considerable use of a wide variety of available prey from infaunal, epifaunal, and terrestrial groups. Export via predation by marine transients was also examined; the largest pathway for export from the marsh interior was seen to be blue crabs feeding on marsh resident crabs *Uca* and *Sesarma* (36% of the quantified prey removed). It is also suggested that *Spartina* material itself may be fed upon directly by blue crabs and used as nutritional support; a study by McClintock *et al.* (1991) provides biochemical evidence for this trophic link.

Consumption and export from marsh edge areas was high. Both the vegetated and the unvegetated habitats which define the marsh edge are considered critically important in supporting large populations of nekton here, especially small blue crabs. The unvegetated intertidal was very important if analyzed over an entire tidal cycle. Perhaps the most important conclusion of Chapter 4, in fact, is the implication that all investigated habitats contribute significantly to the trophic support of shallow water nekton in my area.

SUMMARY

The patterns of use described in Chapter 2 drive the trophic patterns seen in Chapter 4, and these trophic pathways form the ecological basis for the secondary productivity estimates of Chapter 3. Water drains completely off the marsh surface at most low tides in this area. At this time, the larger marsh nekton take refuge in the shallow unvegetated areas and SAV beds. Marsh residents were seen to feed actively in these areas at low tide. At high tide, water floods the marsh, and residents feed even more intensely on the marsh surface. Blue crabs and

transient fishes also move into marsh areas at high tide, in particular exploiting the resources of the marsh edge. The unvegetated area was found to be of major importance to trophic processes as well. In this sampling area, the marsh surface, unvegetated, and SAV habitats are linked by their close spatial proximity. Though SAV-specific predators were not investigated for trophic patterns, it is evident that certain species of nekton are using all three habitats within a single tidal cycle. The entire area, including all three habitat types, is clearly of great value in supporting the abundance and diversity of marine life seen in these shallow waters. In this pristine area, adjacent habitats are linked as the tidal water moves up and down a gradual incline of intertidal substrate, covering and uncovering one habitat after another. These habitats are also linked by the movements of the mobile aquatic creatures that follow these tidal flows.

APPENDIX: TEXT AND EQUATIONS OF THE TROPHIC MODEL

GOODWIN ISLANDS TROPHIC MODEL 1995-1996 Version 6-20-1998

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ABSTRACT:
This dynamic calculation model examines the trophic dependencies that link invertebrates and nekton in salt marshes and in adjacent habitats. The model is based on field work carried out in 1995, 1996, and 1997 at the Goodwin Islands, part of the Chesapeake Bay National Estuarine Research Reserve. The basic paradigm investigated is one where invertebrate secondary production on the salt marsh surface is consumed directly by a suite of marsh resident and transient fishes and crustaceans at high tide. Consumption by transients is considered export. In order to investigate these pathways, we quantitatively sampled three habitats on the marsh surface and adjacent unvegetated for infauna, five habitats on a transect from marsh surface to unvegetated to SAV for small vector nekton at high and low tide. The calculations of this model synthesize the data gathered through these studies into a dynamic description of trophic flows on the salt marsh surface and in adjacent shallow water habitats.

The model as written here does not offer corrections for tidal habitat compression, for removal efficiency of the gear, or for poorly sampled small size classes. These corrections can be subsequently applied and the model re-run, as discussed in the text of this dissertation.

RUN METHOD EULER
TIME STEP = 1 DAY
DT = 0.25 DAY
GRAPH: Julian_Day (Time) 152 - 304, 5 divisions

TABLE OF CONTENTS

3 - Diel feeding
4 - Foraging efficiency at high vs. low tides
5 - Percent of predator diet that is each prey
PREY A, PREY B, PREY C, PREY D

XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
PART I - GENERAL EXPLANATIONS
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

I - OVERALL DESCRIPTION OF PROJECT
This model describes data collected at the Goodwin Islands (York River, Virginia) in 1995 and 1996 during three separate studies. An invertebrate coring study (Diaz, Yozzo, Wooden, Hinchey, Nestlerode, and Cicchetti) collected replicated 7.3 cm diameter cores every two weeks at three habitats from April 1995 to November 1995. A nekton dropring study (Cicchetti) collected replicated 1.48 m diameter samples at eight habitats every two weeks from June 1995 to November 1995 and from April 1996 to June 1996. Monthly data are reported here based on means of three replicate cores for invertebrates and on means of five replicate drop samples for nekton.

II - ASSUMPTIONS and CAVEATS.
The following are among the assumptions and caveats incorporated into this model:

1 - Populations are adequately described by the sampling program.

2 - The same nekton access the marsh surface at neap tides (or intermediate tides) and at sampled spring tides, the only difference being the amount of time available for nekton to access a habitat at each tide due to different durations of flooding.

3 - The entire area within each defined habitat floods for the same length of time.

4 - The model as written here does not offer corrections for tidal habitat compression, for removal efficiency of the gear, or for poorly sampled small size classes. These corrections can be subsequently applied and the model re-run, as discussed in the text of this dissertation.

5- The gut content of a predator reflects feeding in the habitat in which the predator was captured.

6 - The model needs percent of diet data for each predator/prey combination to run accurately. Differential digestion of hard and soft bodied prey items is accounted for using correction factors that are incorporated into the gut information entered into the last section of the model.

III - STUDY SITE
The Goodwin Islands, York River, VA are uninhabited islands maintained by VIMS and the National Estuarine Research Reserve in Virginia. The island is at the low end of the polyhaline salinity range. The marsh site selected is a narrow (5 - 20 m regularly inundated) fringing marsh in a small bay on the East side of the Island. This site is directly exposed to wave action from Chesapeake Bay.

IV - RUNNING THE MODEL
This model runs on Madonna. From the screen you are in right now, apple-e ("edit equations") brings up the run menu. Double clicking on the middle of the displayed graph (or apple-d, "choose data") brings up lists of what you can select to graph. Apple-r (run model) will then calculate equations. "Edit equations", "choose data" and "run model" can also be accessed from the menu bar at the top of the screen. Other features of Madonna are available in this menu bar and on the graph itself and can easily be tryed out.

V - FORMATS, UNITS, AND ABBREVIATIONS USED IN THE MODEL.
All units are per square meter. Calculations for taxonomic groups are arranged in the order habitat-taxon-unit, so that hm_Laoc_dw is high marsh, Laonereis culveri, dry weight per square meter.

Note that in order to compare nekton and invertebrates within a habitat, the following pairs

should be used (see below):

HI_ or H_ (nekton) and H_ (invertebrates) represent the same habitat - marsh interior
HE_ or L_ (nekton) and L_ (invertebrates) represent the same habitat - marsh edge
UF_ or U_ (nekton) and U_ (invertebrates) represent the same habitat - unvegetated area, which is a composite of habitats LD and LS for nekton as tides move over the flat.

A - INVERTEBRATE HABITAT ABBREVIATIONS:

hm_ = H_ = High Marsh (hm): mean of three 7.3 cm x 2.5 cm cores taken each month in mixed Spartina patens and Distichlis spicata in the infrequently flooded high marsh, 5 to 30 m from the marsh-unvegetated border.

lm_ = L_ = Low Marsh (lm): mean of three 7.3 cm x 2.5 cm cores taken each month in tall-form Spartina alterniflora on the regularly flooded marsh surface from 0 to 2 m from the marsh-unvegetated border, typically from 0 to 1 m.

uf_ = U_ = Mud Flat (uf): mean of three 7.3 cm x 2.5 cm cores taken each month in unvegetated intertidal muddy sand from 1 to 5 m from the marsh-unvegetated border.

A_ = all_ = All: a mean value of H, L, and M for invertebrates.

B - NEKTON HABITAT ABBREVIATIONS:

HI_ = H_ = Hightide Interior: Mean of five 1.75 m2 drop ring samples taken each month in marsh interior, 3 to 20 m from the marsh-unvegetated border.

HF_ = Hightide Fringe: Mean of five 1.75 m2 drop ring samples taken each month in Spartina alterniflora, 1 to 3 m from the marsh-unvegetated border.

HE_ = L_ = Hightide Edge: Mean of five 1.75 m2 drop ring samples taken each month where ring is dropped half on and half off a depositional marsh-unvegetated border.

HU_ = Hightide Unvegetated: Mean of five 1.75 m2 drop ring samples taken each month in unvegetated mud or sand, 1 to 10 m from the marsh edge.

HV_ = Hightide Vegetated: Mean of five 1.75 m2 drop ring samples taken each month in Ruppia maritima, typically 10 to 20 m from the marsh edge.

LS_ = Lowtide Shallow: Mean of five 1.75 m2 drop ring samples taken each month in unvegetated mud or sand, 0 to 10 cm deep, at the water's edge.

LD_ = Lowtide Deep: Mean of five 1.75 m2 drop ring samples taken each month in unvegetated mud or sand, 10 to 30 cm deep, 3 to 10 m from the water's edge.

LV_ = Lowtide Vegetated: Mean of five 1.75 m2 drop ring samples taken each month in R. maritima from 10 to 30 cm deep, 5 to 15 m from the water's edge.

U_ = a tidally-driven composite of habitats HU, LD and LS with time dry to reflect time nekton can forage on an area of the mudflat.

C - INVERTEBRATE TAXON ABBREVIATIONS:

Gamm = gammarids
Isop = isopods, Cyathura polita, Edotea triloba, and Sphaeroma quadridentatus
Leps = Leptochelia savigny
oCrs = caprellid and corophiid amphipods and cumaceans.
crust = all four of the above crustacean groups.
Ggem = Gemma gemma
Melb = Melampus bidentatus
oGas = other gastropods: mostly unspeciated Hydrobiids
molls = all three of the above mollusk groups
Olig = all oligochaetes
Laoc = Laonereis culveri
oNer = other nereids: Nereis succinea and Lycastis pontica
oPol = all other polychaetes collected.
polyc = all three of the above polychaete groups
worms = all polychaetes (_polyc_) and all oligochaetes collected
Larv = insect larvae, including chironomids, tabanids, ciratulids, and ceratopogonids
Terr = terrestrial groups: adult insects, spiders, and mites
Othr = other groups: mostly nemerteans and anemones (Edwardsia elegans)
other = all three above groups (_Larv_, _Terr_, and _Othr_) combined
infauna = all infauna collected (except crabs and large Geukensia demissa)

D - NEKTON TAXON ABBREVIATIONS

FLT = Flatfishes: Symphurus plagiusa and Paralichthyes dentatus
gbo = Gobiosoma bosc
str = Gobiesox strumosus
Shet = Fundulus heteroclitus < 40 mm TL

Lhet = Fundulus heteroclitus ≥ 40 mm TL
het = all Fundulus heteroclitus
luc = Lucania parva
maj = Fundulus majalis
men = Menidia menidia
bai = Bairdiella chrysoura
cyn = Cynoscion nebulosus
lei = Leiostomus xanthurus
SCI = all Sciaenids (_bai_ + _cyn_ + _lei_)
SIF = Small Infrequent Fishes. 9 rarer species including bay anchovies, sticklebacks, mullet, spadefish, and various blennies and gobies
fish = all above fishes
Scal = Callinectes sapidus ≤ 30 mm carapace width (point-to-point)
Lcal = Callinectes sapidus > 30 mm carapace width (point-to-point)
cal = all Callinectes sapidus
cra = Crangon septemspinosa
hyp = Hypolyte spp. (mostly H. pleurocantha)
PAL = Palaemonids.
MCR = Miscellaneous Crustaceans: Pagurus longicarpus, xanthid crabs, alpheid shrimps
PEN = Penaid shrimps (P. aztecus and P. duorarum)
CRST = all above crustaceans
NEKT = all above fishes and crustaceans
SCRST = all above crustaceans except for large C. sapidus (_Lcal_)
SNEKT = all above fishes and crustaceans except for large C. sapidus (_Lcal_)

E - UNITS
_no = number of individuals per square meter. For infaunal invertebrates, this is not incorporated into this model - - see "Descriptive Model".
_dw = grams dry weight of that taxa per square meter
_ge = mean grams dry weight each (per individual) for infauna. This is not incorporated into this model - - see "Descriptive Model".
_mm = mean mm length or width of specified measurement, for nekton. Total length and fork length are used for fishes, carapace width is used for crabs (spine to spine), and total length is used for shrimps (tip of rostrum to end of telson). This is not incorporated into this model - - see "Descriptive Model".
_sp = somatic production. The allometric equations of Edgar 1990 and Edgar and Shaw1995 were used to estimate secondary production of somatic tissue in grams dry weight per meter squared per day for infauna and nekton. This is not incorporated into this model - - see "Descriptive Model".

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PART II - FORCING FUNCTIONS
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The forcing functions used in this model are time, expressed in julian days, daylength, tide, and temperature, expressed in degrees Celsius. Salinity is also included in this section and can be graphically displayed, but salinity is not truly a forcing function as no other calculations are dependent upon it.} X=GRAPH(Julian_Day) (1, 0)

__FORCING_FXNS_=X

Julian_Day = (((TIME/365) - (INT(TIME/365))) * 365) {Time counter, resets to 1 on January 1 of each model year. For quick reference use the table below:

January 1 = JD 1	July 1 = JD 182
February 1 = JD 32	August 1 = JD 213
March 1 = JD 60	September 1 = JD 244
April 1 = JD 91	October 1 = JD 274
May 1 = JD 121	November 1 = JD 305
June 1 = JD 152	December 1 = JD 335}

Temp = GRAPH (Time) (155, 24.9) (187, 27.3) (194, 30.7) (213, 31.9) (227, 28.8) (242, 26.8) (255, 25.0) (269, 22.8) (284, 20.8) (298, 18.5) (459, 14.9) (473, 16.6) (488, 20.8) (503, 21.6) (520, 23.0) (530, 25.0)

DayLength = (11.75 - (2.25*COS((2*PI*TIME)/365))) {Hours of light per day, range 10 to 14 hours of sunlight per day, depending on season.}

Sal = GRAPH (Time) (143, 20.20) (160, 19.93) (171, 18.80) (187, 15.10) (199, 12.70) (213, 18.17) (227, 14.17) (241, 19.23) (255, 16.40) (269, 15.20) (283, 20.93) (297, 19.83) (325, 19.70) (438, 14.0) (466, 15.6) (506, 16.8) (521, 14.4) (535, 17.7) (548, 16.4)
{Salinity from Moore unpubl. data, sampled within 200 m of site}

{TIDAL CALCULATIONS. Hrs_HAB is the number of hours per day that each habitat is under water. HAB_SubTime is the fraction of a day that each habitat is under water. Data are from the NOAA record for Gloucester Point (taken at VIMS pier and correlated to the Goodwin Islands (58 observations, r2 = .95). A period of clearly inconsistent NOAA tide data in July and August was replaced with the mean values for the rest of the year. Data from a marsh surface elevation study at the site were used to calculate mean habitat elevations. The model assumes that each individual habitat is homogeneous with respect to tidal influence; no correction is made for differential flooding within the horizontal distance that constitutes a single habitat. Day_ and Nite_ calculations are used to combine the tidal signal with the diel cycle so that mean daytime and nighttime high and low tide flooding durations can be applied to those nekton which show diel feeding differences in marsh habitats.}

Hrs_HE = GRAPH (Time) (152, 6.50) (154, 6.00) (156, 8.50) (158, 13.00) (160, 12.50) (162, 10.50) (164, 12.00) (166, 11.00) (168, 7.50) (170, 7.50) (172, 5.00)(174, 13.00) (176, 11.00) (178, 11.50) (180, 14.00) (182, 10.50) (184, 10.50) (186, 11.50) (188, 6.00) (190, 10.96) (192, 10.96) (194, 10.96)(218, 10.96) (220, 10.96) (222, 10.96) (224, 10.96) (226, 10.96) (228, 10.96) (230, 10.96) (232, 10.96) (234, 10.96) (236, 10.96) (238, 11.50)(240, 15.00) (242, 14.00) (244, 10.00) (246, 13.50) (248, 12.00) (250, 11.50) (252, 13.00) (254, 12.00) (256, 8.00) (258, 10.00) (260, 14.00)(262, 15.00) (264, 12.50) (266, 13.00) (268, 14.50) (270, 13.00) (272, 14.00) (274, 15.50) (276, 13.00) (278, 13.50) (280, 11.50) (282, 13.00)(284, 13.50) (286, 8.00) (288, 10.00) (290, 0) (292, 8.00) (294, 14.50) (296, 9.00) (298, 10.00) (300, 11.00) (302, 8.00) (304, 2.00)

Hrs_HF = GRAPH (Time) (152, 1.00) (154, 1.50) (156, 2.50) (158, 8.50) (160, 9.00) (162, 7.50) (164, 10.00) (166, 8.00) (168, 5.00) (170, 2.00) (172, 3.00)(174, 9.00) (176, 7.50) (178, 9.00) (180, 10.50) (182, 8.50) (184, 7.00) (186, 8.50) (188, 1.00) (190, 7.56) (192, 7.56) (194, 7.56)(218, 7.56) (220, 7.56) (222, 7.56) (224, 7.56) (226, 7.56) (228, 7.56) (230, 7.56) (232, 7.56) (234, 7.56) (236, 7.56) (238, 9.00)(240, 12.50) (242, 11.00) (244, 7.00) (246, 11.00) (248, 8.50) (250, 10.00) (252, 11.00) (254, 9.50) (256, 5.00) (258, 4.00) (260, 10.00)(262, 10.50) (264, 9.00) (266, 10.50) (268, 12.00) (270, 10.50) (272, 10.50) (274, 12.00) (276, 9.50) (278, 10.50) (280, 9.50) (282, 9.50)(284, 10.00) (286, 5.50) (288, 6.50) (290, 0) (292, 1.50) (294, 10.50) (296, 6.00) (298, 7.50) (300, 8.00) (302, 4.50) (304, 0)

Hrs_HI = GRAPH (Time) (152, 0) (154, 0) (156, 0) (158, 3.00) (160, 3.50) (162, 3.50) (164, 7.50) (166, 4.50) (168, 0) (170, 0) (172, 0)(174, 2.50) (176, 2.00) (178, 5.50) (180, 6.50) (182, 2.50) (184, 1.00) (186, 2.00) (188, 0) (190, 3.72) (192, 3.72) (194, 3.72) (218, 3.72) (220, 3.72) (222, 3.72) (224, 3.72) (226, 3.72) (228, 3.72) (230, 3.72) (232, 3.72) (234, 3.72) (236, 3.72) (238, 6.00) (240, 9.50) (242, 7.00) (244, 3.00) (246, 5.50) (248, 4.00) (250, 6.50) (252, 8.00) (254, 4.50) (256, 0) (258, 0) (260, 2.50) (262, 3.00) (264, 4.50) (266, 5.50) (268, 8.50) (270, 7.50) (272, 7.00) (274, 8.00) (276, 5.00) (278, 6.50) (280, 7.00) (282, 6.50) (284, 5.50) (286, 0) (288, 0.50) (290, 0) (292, 0) (294, 5.00) (296, 0) (298, 4.00) (300, 4.00) (302, 0) (304, 0)

Hrs_LD = GRAPH (Time) (152, 2.50) (154, 2.50) (156, 3.50) (158, 2.50) (160, 3.50) (162, 2.00) (164, 2.50) (166, 2.00) (168, 2.00) (170, 2.00) (172, 3.50) (174, 5.00) (176, 4.50) (178, 4.00) (180, 3.00) (182, 3.50) (184, 3.50) (186, 3.00) (188, 6.50) (190, 3.18) (192, 3.18) (194, 3.18) (218, 3.18) (220, 3.18) (222, 3.18) (224, 3.18) (226, 3.18) (228, 3.18) (230, 3.18) (232, 3.18) (234, 3.18) (236, 3.18) (238, 3.00) (240, 2.00) (242, 4.00) (244, 3.00) (246, 5.00) (248, 4.00) (250, 2.00) (252, 2.50) (254, 2.50) (256, 3.00) (258, 5.00) (260, 3.00) (262, 1.00) (264, 4.50) (266, 4.50) (268, 5.00) (270, 3.50) (272, 2.00) (274, 4.50) (276, 3.50) (278, 3.00) (280, 2.00) (282, 3.50) (284, 5.00) (286, 3.50) (288, 3.00) (290, 4.50) (292, 3.50) (294, 4.50) (296, 2.00) (298, 2.50) (300, 2.50) (302, 2.50) (304, 3.50)

Hrs_LS = GRAPH (Time) (152, 3.00) (154, 3.50) (156, 4.50) (158, 4.00) (160, 4.50) (162, 1.50) (164, 2.50) (166, 2.00) (168, 2.00) (170, 2.50) (172, 3.00) (174, 1.50) (176, 3.00) (178, 2.50) (180, 0) (182, 5.00) (184, 5.00) (186, 6.00) (188, 3.00) (190, 2.85) (192, 2.85) (194, 2.85) (218, 2.85) (220, 2.85) (222, 2.85) (224, 2.85) (226, 2.85) (228, 2.85) (230, 2.85) (232, 2.85) (234, 2.85) (236, 2.85) (238, 4.00) (240, 1.50) (242, 1.00) (244, 2.00) (246, 0.50) (248, 4.50) (250, 3.00) (252, 4.00) (254,

4.50) (256, 4.00) (258, 2.50) (260, 0) (262, 0) (264, 1.50) (266, 3.00) (268, 0.50) (270, 3.50) (272, 1.50) (274, 0) (276, 4.00) (278, 4.00) (280, 5.00) (282, 4.50) (284, 1.00) (286, 4.50) (288, 4.00) (290, 4.00) (292, 5.50) (294, 1.50) (296, 3.00) (298, 1.50) (300, 3.50) (302, 3.00) (304, 2.00)

Day_HT = GRAPH (Time) (152, 5.50) (154, 5.50) (156, 7.00) (158, 10.00) (160, 10.00) (162, 8.50) (164, 8.00) (166, 6.50) (168, 6.00) (170, 6.50) (172, 7.00) (174, 10.00) (176, 10.00) (178, 11.00) (180, 11.00) (182, 8.00) (184, 8.50) (186, 9.00) (188, 5.50) (190, 8.25) (192, 8.25) (194, 8.25) (218, 8.25) (220, 8.25) (222, 8.25) (224, 8.25) (226, 8.25) (228, 8.25) (230, 8.25) (232, 8.25) (234, 8.25) (236, 8.25) (238, 9.00) (240, 12.00) (242, 10.00) (244, 7.00) (246, 9.50) (248, 8.00) (250, 7.50) (252, 9.50) (254, 8.50) (256, 7.00) (258, 8.00) (260, 11.50) (262, 12.50) (264, 9.00) (266, 8.00) (268, 10.00) (270, 9.50) (272, 9.50) (274, 10.00) (276, 7.50) (278, 7.50) (280, 7.50) (282, 8.50) (284, 9.50) (286, 7.00) (288, 9.50) (290, 3.00) (292, 6.00) (294, 8.50) (296, 6.50) (298, 7.50) (300, 8.00) (302, 6.50) (304, 3.50)

Hrs_Dry = GRAPH (Time) (152, 7.00) (154, 7.00) (156, 3.00) (158, 0) (160, 0) (162, 7.50) (164, 4.50) (166, 7.00) (168, 9.00) (170, 8.00) (172, 6.50) (174, 0) (176, 0) (178, 0) (180, 0) (182, 0) (184, 0) (186, 0) (188, 5.00) (190, 2.60) (192, 2.60) (194, 2.60) (218, 2.60) (220, 2.60) (222, 2.60) (224, 2.60) (226, 2.60) (228, 2.60) (230, 2.60) (232, 2.60) (234, 2.60) (236, 2.60) (238, 1.00) (240, 0) (242, 0) (244, 4.50) (246, 0) (248, 0) (250, 5.00) (252, 0.50) (254, 1.00) (256, 5.00) (258, 0) (260, 0) (262, 0) (264, 0) (266, 0) (268, 0) (270, 0) (272, 0) (274, 0) (276, 0) (278, 0) (280, 2.00) (282, 0) (284, 0) (286, 3.50) (288, 0) (290, 10.00) (292, 1.50) (294, 0) (296, 7.50) (298, 7.00) (300, 4.00) (302, 7.50) (304, 11.00)

Hrs_Edge = GRAPH (Time) (152, 11.50) (154, 11.00) (156, 13.00) (158, 17.50) (160, 16.00) (162, 13.00) (164, 14.50) (166, 13.00) (168, 11.00) (170, 11.50) (172, 11.00) (174, 17.50) (176, 16.50) (178, 17.50) (180, 21.00) (182, 15.50) (184, 15.50) (186, 15.00) (188, 9.50) (190, 15.37) (192, 15.37) (194, 15.37) (218, 15.37) (220, 15.37) (222, 15.37) (224, 15.37) (226, 15.37) (228, 15.37) (230, 15.37) (232, 15.37) (234, 15.37) (236, 15.37) (238, 16.00) (240, 20.50) (242, 19.00) (244, 14.50) (246, 18.50) (248, 15.50) (250, 14.00) (252, 17.00) (254, 16.00) (256, 12.00) (258, 16.50) (260, 21.00) (262, 23.00) (264, 18.00) (266, 16.50) (268, 18.50) (270, 17.00) (272, 20.50) (274, 19.50) (276, 16.50) (278, 17.00) (280, 15.00) (282, 16.00) (284, 18.00) (286, 12.50) (288, 17.00) (290, 5.50) (292, 13.50) (294, 18.00) (296, 11.50) (298, 13.00) (300, 14.00) (302, 11.00) (304, 7.50)

HU_SubTime = HE_SubTime
HE_SubTime = ((Hrs_HE +(.5*(Hrs_Edge - Hrs_HE)))/24)
HF_SubTime = (Hrs_HF/24)
HI_SubTime = (Hrs_HI/24)
HV_SubTime = HU_SubTime
LV_SubTime = (1.0-HV_SubTime)
LD_SubTime = ((Hrs_LD+((.5*(Hrs_Edge - Hrs_HE))))/24)
LS_SubTime = (Hrs_LS/24)

Nite_Ht = (Hrs_Edge-Day_HT)+.01
Day_LT = MAX((DayLength - Day_HT), .001)
Nite_LT = ((24 - Daylength) - Nite_HT)+.01

{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
PART III - ANIMAL SUMMARIES, ARRANGED BY HABITATS
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

I- HABITATS: TOTALS CALCULATIONS.
This section shows total grams dry weight for each taxonomic group and appears first in the variable list provided in the graphing menu. Note that few calculations are offered here; this section is mostly a regrouping, so that often-used summaries can be found quickly in Madonna's "choose data" menu.}

I__HABITAT_TOTS___=X

hm_infauna_dw = hm_crust_dw + hm_molls_dw + hm_worms_dw + hm_other_dw
lm_infauna_dw = lm_crust_dw + lm_molls_dw + lm_worms_dw + lm_other_dw
uf_infauna_dw = uf_crust_dw + uf_molls_dw + uf_worms_dw + uf_other_dw
a_infauna_dw = (hm_infauna_dw + lm_infauna_dw + uf_infauna_dw)/3

A__HIGHMARSH_TB_=X
H_incrust_dw = hm_crust_dw
H_molls_dw = hm_molls_dw
H_olig_dw = hm_Olig_dw
H_poly_dw = hm_polyc_dw
H_other_dw = hm_other_dw
H_infauna_dw = hm_infauna_dw
H_preyinf_dw = hm_infauna_dw - H_molls_dw - H_olig_dw
H_fish_dw = HI_FISH_dw
H_necrust_dw = HI_CRST_dw
H_nekton_dw = HI_NEKT_dw

B__LOWMARSH_TB__=X
L_incrust_dw = lm_crust_dw
L_molls_dw = lm_molls_dw
L_olig_dw = lm_Olig_dw
L_poly_dw = lm_polyc_dw
L_other_dw = lm_other_dw
L_infauna_dw = lm_infauna_dw
L_preyinf_dw = L_infauna_dw - L_olig_dw
L_fish_dw = HE_FISH_dw
L_necrust_dw = HE_CRST_dw
L_nekton_dw = HE_NEKT_dw

C__MUDFLAT_TB___=X
U_incrust_dw = uf_crust_dw
U_molls_dw = uf_molls_dw
U_olig_dw = uf_Olig_dw
U_poly_dw = uf_polyc_dw
U_other_dw = uf_other_dw
U_infauna_dw = uf_infauna_dw
U_preyinf_dw = uf_infauna_dw - uf_Olig_dw

D__All_HABS_TB___=X
all_incrust_dw = uf_crust_dw
all_molls_dw = uf_molls_dw
all_olig_dw = uf_Olig_dw
all_poly_dw = uf_polyc_dw
all_other_dw = uf_other_dw
all_infauna_dw = uf_infauna_dw
all_fishes_dw = ALL_FISH_dw
all_necrust_dw = ALL_CRST_dw
all_nekton_dw = ALL_NEKT_dw

{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
PART IV - INFAUNA, ARRANGED BY TAXA
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

IV - 1995 INFAUNAL DATA, ARRANGED BY TAXA. Each grouping is arranged alphabetically, with totals and summaries at the end. A_ calculates a mean value per square meter over all three sampled habitats, even if the group in question is not found in certain habitats.}
IV__INFAUN_TAXA=X

A__CRUSTACEANS_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
{Sesarma and Uca were not considered to have been quantitatively sampled and the 11 individuals captured are not included in this analysis.

1- Gammaridean amphipods. Gammarus palustris and Orchestia uhleri were the most common species.}

```
hm_Gamm_dw  =  GRAPH (Time) (168, 0.00478) (198, 0) (225, 0) (258, 0) (286, 0.00478)
lm_Gamm_dw  =  GRAPH (Time) (168, 0.00239) (198, 0.02363) (225, 0) (258, 0.46590) (286, 0.62440)
uf_Gamm_dw  =  GRAPH (Time) (168, 0.00239) (198, 0.00239) (225, 0) (258, 0) (286, 0.00478)
a_Gamm_dw = (hm_Gamm_dw + lm_Gamm_dw + uf_Gamm_dw)/3

{2- Isopods included Cyathura polita, Edotea triloba, and Sphaeroma quadridentatus.}

hm_Isop_dw  =  GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0) (286, 0.00346)
lm_Isop_dw  =  GRAPH (Time) (168, 0) (198, 0.09316) (225, 0.01956) (258, 0.13200) (286, 0.06017)
uf_Isop_dw  =  GRAPH (Time) (168, 0.09316) (198, 0.00319) (225, 0.09958) (258, 0.00637) (286,
    0.09316)
a_Isop_dw = (hm_Isop_dw + lm_Isop_dw + uf_Isop_dw)/3

{3 - Leptochelia savigny was found in considerable abundance in stomachs of fish captured
on the marsh surface, but was not particularly abundant in the Infaunal cores.  This suggests that
it may be more of an epifaunal creature on Spartina stems, or was unavailable to corers for another reason.}

hm_Leps_dw  =  GRAPH (Time) (168, 0) (198, 0.00720) (225, 0) (258, 0) (286, 0)
lm_Leps_dw  =  GRAPH (Time) (168, 0) (198, 0.17199) (225, 0.00720) (258, 0.02862) (286, 0.02151)
uf_Leps_dw  =  GRAPH (Time) (168, 0.02151) (198, 0.00720) (225, 0) (258, 0) (286, 0)
a_Leps_dw = (hm_Leps_dw + lm_Leps_dw + uf_Leps_dw)/3

{4- Other crustaceans include caprellid amphipods, corophiid amphipods, and cumaceans.}

hm_oCrs_dw  =  GRAPH (Time) (168, 0.00252) (198, 0.00953) (225, 0) (258, 0) (286, 0.06012)
lm_oCrs_dw  =  GRAPH (Time) (168, 0.00369) (198, 0.05601) (225, 0) (258, 0) (286, 0.03147)
uf_oCrs_dw  =  GRAPH (Time) (168, 0.00382) (198, 0) (225, 0) (258, 0.00739) (286, 0.06944)
a_oCrs_dw = (hm_oCrs_dw + lm_oCrs_dw + uf_oCrs_dw)/3

{5- Crustacean summaries}

hm_crust_dw = hm_Gamm_dw + hm_Isop_dw +  hm_Leps_dw + hm_oCrs_dw
lm_crust_dw = lm_Gamm_dw + lm_Isop_dw +  lm_Leps_dw + lm_oCrs_dw
uf_crust_dw = uf_Gamm_dw + uf_Isop_dw +  uf_Leps_dw + uf_oCrs_dw
a_crust_dw = (hm_crust_dw + lm_crust_dw + uf_crust_dw)/3

B__MOLLUSKS___=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Large Geukensia demissa were not considered to have been quantitatively sampled and the
2 large individuals captured are not included in this analysis.}

{1 - Gemma gemma.  Only two small bivalves other than G. gemma were captured in the study
(unspeciated newly settled mussels); they are included in the "other" grouping.}

hm_Ggem_dw  =  GRAPH (Time) (168, 0.01100) (198, 0.03385) (225, 0.00282) (258, 0.17286) (286,
    0.09003)
lm_Ggem_dw  =  GRAPH (Time) (168, 0.01088) (198, 0.06483) (225, 0.00587) (258, 0.00198) (286,
    0.00518)
uf_Ggem_dw  =  GRAPH (Time) (168, 0.61602) (198, 0.40389) (225, 0.28178) (258, 0.05005) (286,
    0.11220)
a_Ggem_dw = (hm_Ggem_dw + lm_Ggem_dw + uf_Ggem_dw)/3

{2 - Melampus bidentatus}

hm_Melb_dw  =  GRAPH (Time) (168, 1.05472) (198, 1.39458) (225, 0.39674) (258, 0.20488) (286,
    0.50560)
lm_Melb_dw  =  GRAPH (Time) (168, 0.21410) (198, 0) (225, 0.07706) (258, 0.02458) (286, 0)
uf_Melb_dw  =  GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0) (286, 0)
a_Melb_dw = (hm_Melb_dw + lm_Melb_dw + uf_Melb_dw)/3

{3 - Other gastropods are mostly unspeciated Hydrobids, with one individual Acteocina
canaliculata as well.}

hm_oGas_dw  =  GRAPH (Time) (168, 0) (198, 0.00122) (225, 0.03655) (258, 0) (286, 0.00122)
lm_oGas_dw  =  GRAPH (Time) (168, 0) (198, 0) (225, 0.00122) (258, 0.37890) (286, 0)
```

uf_oGas_dw = GRAPH (Time) (168, 0.00487) (198, 0.01706) (225, 0) (258, 0.00366) (286, 0.00731)
a_oGas_dw = (hm_oGas_dw + lm_oGas_dw + uf_oGas_dw)/3

{4- Mollusk summaries}

hm_molls_dw = hm_Ggem_dw + hm_Melb_dw + hm_oGas_dw
lm_molls_dw = lm_Ggem_dw + lm_Melb_dw + lm_oGas_dw
uf_molls_dw = uf_Ggem_dw + uf_Melb_dw + uf_oGas_dw
a_molls_dw = (hm_molls_dw + lm_molls_dw + uf_molls_dw)/3

C__WORMS________=XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

1- Oligochaetes}

hm_Olig_dw = GRAPH (Time) (168, 0.18364) (198, 0.17179) (225, 0.03258) (258, 0.13477) (286, 0.14365)
lm_Olig_dw = GRAPH (Time) (168, 0.75379) (198, 0.18808) (225, 0.21177) (258, 1.10478) (286, 0.87967)
uf_Olig_dw = GRAPH (Time) (168, 0.05628) (198, 0.10515) (225, 0.26213) (258, 0.01777) (286, 0.06664)
a_Olig_dw = (hm_Olig_dw + lm_Olig_dw + uf_Olig_dw)/3

{2- Polychaetes}

{2a - Laonereis culveri. This was the biomass dominant in the mudflat (uf) habitat.}

hm_Laoc_dw = GRAPH (Time) (168, 0) (198, 0) (225, 0.00065) (258, 0) (286, 0.07422)
lm_Laoc_dw = GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0.00382) (286, 0.00911)
uf_Laoc_dw = GRAPH (Time) (168, 0.41306) (198, 3.66139) (225, 3.22885) (258, 1.25360) (286, 5.02648)
a_Laoc_dw = (hm_Laoc_dw + lm_Laoc_dw + uf_Laoc_dw)/3

{2b- Other nereids. This includes Nereis succinea and Lycastis pontica as well as unidentifiable nereids.}

hm_oNer_dw = GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0.06087) (286, 0)
lm_oNer_dw = GRAPH (Time) (168, 0) (198, 0.01698) (225, 0.18754) (258, 0.10482) (286, 0.76098)
uf_oNer_dw = GRAPH (Time) (168, 0.01133) (198, 0.01829) (225, 0.21969) (258, 0.04699) (286, 0.11659)
a_oNer_dw = (hm_oNer_dw + lm_oNer_dw + uf_oNer_dw)/3

{2c- Other polychaetes include Capitellids, Streblospio benedicti, Manayunkia aestuarina, unidentified syllids, Asabellides oculata, unidentified orbinids, unidentified phyllodocids, Polydora ligni, Scoloplos fragilis, Eteone heteropoda, unidentified spionids, and unidentified polychaete larvae.}

hm_oPol_dw = GRAPH (Time) (168, 0.23116) (198, 0.16338) (225, 0.10834) (258, 0.20523) (286, 0.21056)
lm_oPol_dw = GRAPH (Time) (168, 0.05918) (198, 0.37397) (225, 0.41385) (258, 0.16737) (286, 0.16232)
uf_oPol_dw = GRAPH (Time) (168, 0.15513) (198, 0.12522) (225, 0.92229) (258, 0.11449) (286, 0.35892)
a_oPol_dw = (hm_oPol_dw + lm_oPol_dw + uf_oPol_dw)/3

{2d- Polychaete summaries.}
hm_polyc_dw = hm_Laoc_dw + hm_oNer_dw + hm_oPol_dw
lm_polyc_dw = lm_Laoc_dw + lm_oNer_dw + lm_oPol_dw
uf_polyc_dw = uf_Laoc_dw + uf_oNer_dw + uf_oPol_dw
a_polyc_dw = (hm_polyc_dw + lm_polyc_dw + uf_polyc_dw)/3

{3- Worm summaries}

hm_worms_dw = hm_Olig_dw + hm_polyc_dw
lm_worms_dw = lm_Olig_dw + lm_polyc_dw

```
uf_worms_dw = uf_Olig_dw + uf_polyc_dw
a_worms_dw = (hm_worms_dw + lm_worms_dw + uf_worms_dw)/3


D__OTHER_____=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

1 - "Ins_lar" are insect larvae, mostly chironomids, tabanids, ciratulids, and ceratopogonids.}

hm_Larv_dw  =  GRAPH (Time) (168, 0.00239) (198, 0) (225, 0) (258, 0.00876) (286, 0)
lm_Larv_dw  =  GRAPH (Time) (168, 0.06210) (198, 0.01194) (225, 0.00199) (258, 0) (286, 0.01155)
uf_Larv_dw  =  GRAPH (Time) (168, 0.11147) (198, 0) (225, 0.00239) (258, 0) (286, 0)
a_Larv_dw = (hm_Larv_dw + lm_Larv_dw + uf_Larv_dw)/3

{2 - Terrestrial animals captured were adult insects, spiders, and mites.}

hm_Terr_dw  =  GRAPH (Time) (168, 0.07166) (198, 0.00239) (225, 0.05573) (258, 0.12739) (286, 0)
lm_Terr_dw  =  GRAPH (Time) (168, 0.00717) (198, 0.05573) (225, 0.06051) (258, 0.00478) (286,
    0.01911)
uf_Terr_dw  =  GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0) (286, 0)
a_Terr_dw = (hm_Terr_dw + lm_Terr_dw + uf_Terr_dw)/3

{3- Other groups are nemerteans and anemones (mostly Edwardsia elegans).}

hm_Othr_dw  =  GRAPH (Time) (168, 0) (198, 0) (225, 0) (258, 0.00823) (286, 0.00106)
lm_Othr_dw  =  GRAPH (Time) (168, 0) (198, 0.00717) (225, 0.00717) (258, 0.01314) (286, 0.13629)
uf_Othr_dw  =  GRAPH (Time) (168, 0.00717) (198, 0.00717) (225, 0.02866) (258, 0) (286, 0)
a_Othr_dw = (hm_Othr_dw + lm_Othr_dw + uf_Othr_dw)/3

{4- Summaries of other groups}

hm_other_dw = hm_Larv_dw + hm_Terr_dw +  hm_Othr_dw
lm_other_dw = lm_Larv_dw + lm_Terr_dw +  lm_Othr_dw
uf_other_dw = uf_Larv_dw + uf_Terr_dw +  uf_Othr_dw
a_other_dw = (hm_other_dw + lm_other_dw + uf_other_dw)/3


E__SUMMARIES___=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}

hm_infauna_dw = hm_crust_dw + hm_molls_dw +  hm_worms_dw + hm_other_dw
lm_infauna_dw = lm_crust_dw + lm_molls_dw +  lm_worms_dw + lm_other_dw
uf_infauna_dw = uf_crust_dw + uf_molls_dw +  uf_worms_dw + uf_other_dw
a_infauna_dw = (hm_infauna_dw + lm_infauna_dw + uf_infauna_dw)/3


{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
                    PART V - NEKTON DATA, ARRANGED BY TAXA
XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

Each grouping is arranged alphabetically, with totals and summaries at the end.

V__NEKTON_TAXA=X

A_fishes_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}
{23 species of fishes were captured during the study.}

{1- American eel, anguilla rostrata.  Larger eels (~200 mm) migrated through SAV habitats in the
fall; elvers used these habitats in the spring.}

{See Goodwin Islands Descriptive Model for SAV habitat information.}

{2- Flatfishes.  Blackcheek tonguefish (Symphurus plagiusa) and summer flounder
(Paralichthyes dentatus) primarily used unvegetated and SAV habitats.}
```

HU_FLT_no = GRAPH (Time) (192, 0) (224, 0.23) (261, 0.69) (290, 0) (504, 0) (520, 0.19) (555, 0.19) (560, 0)
HU_FLT_dw = GRAPH (Time) (192, 0) (224, 0.0115) (261, 0.1572) (290, 0) (504, 0) (520, 0.3720) (555, 0.3720) (560, 0)

HE_FLT_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0)
HE_FLT_dw = GRAPH (Time) (224, 0) (261, 0.0373) (290, 0)

LD_FLT_no = GRAPH (Time) (140, 0) (145, 0.23) (161, 0.23) (192, 0) (224, 0.23) (261, 0.46) (290, 0.57) (310, 0.57) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0.29) (504, 0)
LD_FLT_dw = GRAPH (Time) (140, 0) (145, 0.1399) (161, 0.1399) (192, 0) (224, 0.0047) (261, 0.1283) (290, 0.2125) (310, 0.2125) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0.0397) (504, 0)

{3- Naked gobies (_gbo_, Gobiosoma bosc) and skilletfish (_str_, Gobiesox strumosus) were the most common goby species captured. Other gobies (less than 5 inds captured) are included in the Small Infrequent Fish category (SIF) below. }

HU_gbo_no = GRAPH (Time) (224, 0) (261, 0.34) (290, 0.11) (310, 0.11) (315, 0)
HU_gbo_dw = GRAPH (Time) (224, 0) (261, 0.0136) (290, 0.0247) (310, 0.0247) (315, 0)

HE_gbo_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.11) (290, 0.11) (310, 0.11) (315, 0)
HE_gbo_dw = GRAPH (Time) (192, 0) (224, 0.0054) (261, 0.0078) (290, 0.0187) (310, 0.0187) (315, 0)

LD_gbo_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.91) (290, 0.57) (310, 0.57) (315, 0)
LD_gbo_dw = GRAPH (Time) (192, 0) (224, 0.0009) (261, 0.0756) (290, 0.0880) (310, 0.0880) (315, 0)

LS_gbo_no = GRAPH (Time) (192, 0) (224, 0.34) (261, 0) (310, 0) (315, 0)
LS_gbo_dw = GRAPH (Time) (192, 0) (224, 0.0079) (261, 0) (310, 0) (315, 0)

HE_str_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0) (290, 0.11) (310, 0.11) (315, 0)
HE_str_dw = GRAPH (Time) (192, 0) (224, 0.0506) (261, 0) (290, 0.0319) (310, 0.0319) (315, 0)

LD_str_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0.14) (310, 0.14) (315, 0)
LD_str_dw = GRAPH (Time) (224, 0) (261, 0.0656) (290, 0.0349) (310, 0.0349) (315, 0)

LS_str_no = GRAPH (Time) (224, 0) (261, 0.23) (290, 0)
LS_str_dw = GRAPH (Time) (224, 0) (261, 0.0380) (290, 0)

{4 - Mummichogs (Fundulus heteroclitus) were the most abundant fishes caught and were also the fish biomass dominants. At high tide these fish foraged almost exclusively in marsh habitats, with only one adult fish caught in a non-marsh habitat at high tide. They are divided into a small group (Shet), TL < 40 mm and a large group (Lhet) with TL ≥ 40 mm.}

HU_Shet_no = GRAPH (Time) (161, 0) (192, 0.11) (224, 0)
HU_Shet_dw = GRAPH (Time) (161, 0) (192, 0.0203) (224, 0)

HE_Shet_no = GRAPH (Time) (140, 0) (145, 0.38) (161, 0.38) (192, 0)
HE_Shet_dw = GRAPH (Time) (140, 0) (145, 0.0255) (161, 0.0255) (192, 0)

HF_Shet_no = GRAPH (Time) (161, 0) (192, 2.17) (224, 0.91) (261, 0.23) (290, 0.11) (310, 0.11) (315, 0)
HF_Shet_dw = GRAPH (Time) (161, 0) (192, 0.2828) (224, 0.0921) (261, 0.0183) (290, 0.0143) (310, 0.0143) (315, 0)

HI_Shet_no = GRAPH (Time) (140, 0) (145, 1.57) (161, 1.57) (192, 2.51) (224, 2.74) (261, 0.57) (290, 0.57) (310, 0.57) (315, 0) (475, 0) (480, 0) (489, 0) (504, 2.29) (520, 2.67)
HI_Shet_dw = GRAPH (Time) (140, 0) (145, 0.0537) (161, 0.0537) (192, 0.1280) (224, 0.1566) (261, 0.0719) (290, 0.0639) (310, 0.0639) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0860) (520, 0.0079)

HV_Shet_no = GRAPH (Time) (504, 0) (520, 0.76)
HV_Shet_dw = GRAPH (Time) (504, 0) (520, 0.0036)

LD_Shet_no = GRAPH (Time) (140, 0) (145, 2.17) (161, 2.17) (192, 0.34) (224, 0)
LD_Shet_dw = GRAPH (Time) (140, 0) (145, 0.0162) (161, 0.0162) (192, 0.0328) (224, 0)

LS_Shet_no = GRAPH (Time) (140, 0) (145, 1.26) (161, 1.26) (192, 3.09) (224, 0.34) (261, 0) (290, 1.83) (310, 1.83) (315, 0)
LS_Shet_dw = GRAPH (Time) (140, 0) (145, 0.0149) (161, 0.0149) (192, 0.0668) (224, 0.0019) (261, 0) (290, 0.2944) (310, 0.2944) (315, 0)

LV_Shet_no = GRAPH (Time) (161, 0) (192, 0.76) (224, 2.71) (261, 0)
LV_Shet_dw = GRAPH (Time) (161, 0) (192, 0.0660) (224, 0.0146) (261, 0)

HE_Lhet_no = GRAPH (Time) (140, 0) (145, 0.38) (161, 0.38) (192, 0.34) (224, 1.14) (261, 0.34) (290, 0.23) (310, 0.23) (315, 0) (475, 0) (480, 0.57) (489, 0.57) (504, 0)
HE_Lhet_dw = GRAPH (Time) (140, 0) (145, 0.1922) (161, 0.1922) (192, 0.3406) (224, 2.1509) (261, 0.4483) (290, 0.1512) (310, 0.1512) (315, 0) (475, 0) (480, 0.2652) (489, 0.2652) (504, 0)

HF_Lhet_no = GRAPH (Time) (161, 0) (192, 0.57) (224, 1.49) (261, 1.14) (290, 0.80) (310, 0.80) (315, 0) (475, 0) (480, 0.57) (489, 0.57) (504, 0) (520, 0.19)
HF_Lhet_dw = GRAPH (Time) (161, 0) (192, 0.1538) (224, 0.6471) (261, 0.4567) (290, 0.3489) (310, 0.3489) (315, 0) (475, 0) (480, 0.2769) (489, 0.2769) (504, 0) (520, 0.1179)

HI_Lhet_no = GRAPH (Time) (140, 0) (145, 0.14) (161, 0.14) (192, 0) (224, 0.34) (261, 1.26) (290, 0.43) (310, 0.43) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.29) (520, 0)
HI_Lhet_dw = GRAPH (Time) (140, 0) (145, 0.1213) (161, 0.1213) (192, 0) (224, 0.2390) (261, 1.2386) (290, 0.2537) (310, 0.2537) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.1053) (520, 0)

LD_Lhet_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.46) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0.29) (489, 0.29) (504, 0)
LD_Lhet_dw = GRAPH (Time) (192, 0) (224, 0.0533) (261, 0.5028) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0.1703) (489, 0.1703) (504, 0)

LS_Lhet_no = GRAPH (Time) (224, 0) (261, 0.34) (290, 1.49) (310, 1.49) (315, 0)
LS_Lhet_dw = GRAPH (Time) (224, 0) (261, 0.1818) (290, 0.5346) (310, 0.5346) (315, 0)

LV_Lhet_no = GRAPH (Time) (161, 0) (192, 0.19) (224, 0.43) (261, 0) (290, 0.11) (310, 0.11) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.19)
LV_Lhet_dw = GRAPH (Time) (161, 0) (192, 0.0461) (224, 0.1745) (261, 0) (290, 0.0872) (310, 0.0872) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.1414)

HI_het_no = HI_Shet_no + HI_Lhet_no
HF_het_no = HF_Shet_no + HF_Lhet_no
HE_het_no = HE_Shet_no + HE_Lhet_no
HU_het_no = HU_Shet_no
HV_het_no = HV_Shet_no
LS_het_no = LS_Shet_no + LS_Lhet_no
LD_het_no = LD_Shet_no + LD_Lhet_no
LV_het_no = LV_Shet_no + LV_Lhet_no

HI_het_dw = HI_Shet_dw + HI_Lhet_dw
HF_het_dw = HF_Shet_dw + HF_Lhet_dw
HE_het_dw = HE_Shet_dw + HE_Lhet_dw
HU_het_dw = HU_Shet_dw
HV_het_dw = HV_Shet_dw
LS_het_dw = LS_Shet_dw + LS_Lhet_dw
LD_het_dw = LD_Shet_dw + LD_Lhet_dw
LV_het_dw = LV_Shet_dw + LV_Lhet_dw

{5 - Rainwater killifish (Lucania parva)}

HU_luc_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0)
HU_luc_dw = GRAPH (Time) (224, 0) (261, 0.0109) (290, 0)

HE_luc_no = GRAPH (Time) (192, 0) (224, 2.63) (261, 1.14) (290, 0.57) (310, 0.57) (315, 0) (475, 0) (480, 0.29) (489, 0.29) (504, 0)
HE_luc_dw = GRAPH (Time) (192, 0) (224, 0.3400) (261, 0.1721) (290, 0.0635) (310, 0.0635) (315, 0) (475, 0) (480, 0.0302) (489, 0.0302) (504, 0)

HF_luc_no = GRAPH (Time) (161, 0) (192, 0.11) (224, 0) (261, 0.34) (290, 0.34) (310, 0.34) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.19)
HF_luc_dw = GRAPH (Time) (161, 0) (192, 0.0979) (224, 0) (261, 0.0503) (290, 0.0485) (310, 0.0485) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.0033)

HI_luc_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.91) (290, 0.29) (310, 0.29) (315, 0)
HI_luc_dw = GRAPH (Time) (192, 0) (224, 0.0174) (261, 0.1067) (290, 0.0326) (310, 0.0326) (315, 0)

LD_luc_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0.14) (310, 0.14) (315, 0)
LD_luc_dw = GRAPH (Time) (224, 0) (261, 0.0135) (290, 0.0092) (310, 0.0092) (315, 0)

LS_luc_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0)
LS_luc_dw = GRAPH (Time) (192, 0) (224, 0.0016) (261, 0)

{6 - Striped Killifish (Fundulus heteroclitus) were second in total biomass of fishes to mummichogs. Striped killifishes did not use SAV habitats, even at low tide.}

HE_maj_no = GRAPH (Time) (192, 0) (224, 0.57) (261, 0) (290, 0.23) (310, 0.23) (315, 0) (475, 0) (480, 0) (489, 0) (504, 8.86) (520, 0)
HE_maj_dw = GRAPH (Time) (192, 0) (224, 0.2890) (261, 0) (290, 0.4141) (310, 0.4141) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0482) (520, 0)

HF_maj_no = GRAPH (Time) (224, 0) (261, 0.23) (290, 0.23) (310, 0.23) (315, 0)
HF_maj_dw = GRAPH (Time) (224, 0) (261, 0.1003) (290, 0.6944) (310, 0.6944) (315, 0)

HI_maj_no = GRAPH (Time) (140, 0) (145, 0.29) (161, 0.29) (192, 0) (224, 0.46) (261, 0.91) (290, 0.71) (310, 0.71) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.57) (520, 0)
HI_maj_dw = GRAPH (Time) (140, 0) (145, 0.2935) (161, 0.2935) (192, 0) (224, 0.1369) (261, 0.3954) (290, 0.2608) (310, 0.2608) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.6507) (520, 0)

LD_maj_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0.14) (310, 0.14) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.38)
LD_maj_dw = GRAPH (Time) (224, 0) (261, 0.0752) (290, 0.0597) (310, 0.0597) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.4544)

LS_maj_no = GRAPH (Time) (192, 0) (224, 0.57) (261, 1.14) (290, 1.83) (310, 1.83) (315, 0) (475, 0) (480, 4.86) (489, 4.86) (504, 0)
LS_maj_dw = GRAPH (Time) (192, 0) (224, 0.0618) (261, 0.2106) (290, 0.4188) (310, 0.4188) (315, 0) (475, 0) (480, 0.1945) (489, 0.1945) (504, 0)

{7- Atlantic silversides (Menidia menidia) were found foraging on the marsh surface and in open water. They were not often captured over SAV habitats in this study. Although silversides were found in the day-night study to be more abundant on the marsh surface during the night, they were also found not to be feeding on the marsh surface at night. Silverside abundances reported here represent the actively feeding daytime populations. Juvenile silversides were very abundant in the spring of 1996, run time to 520 and graph time = 430 - 520 to display these populations.}

HU_men_no = GRAPH (Time) (161, 0) (192, 0.11) (224, 0.69) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 24.86) (520, 0.19)
HU_men_dw = GRAPH (Time) (161, 0) (192, 0.0290) (224, 0.3074) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0385) (520, 0.0028)

HE_men_no = GRAPH (Time) (140, 0) (145, 0.19) (161, 0.19) (192, 0.46) (224, 1.49) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 7.14) (520, 6.67)
HE_men_dw = GRAPH (Time) (140, 0) (145, 0.0598) (161, 0.0598) (192, 0.0649) (224, 0.3615) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0285) (520, 0.0693)

HF_men_no = GRAPH (Time) (224, 0) (261, 0.80) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 16.57) (520, 3.05)
HF_men_dw = GRAPH (Time) (224, 0) (261, 0.2192) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0401) (520, 0.0258)

HI_men_no = GRAPH (Time) (140, 0) (145, 0.14) (161, 0.14) (192, 0) (224, 0.11) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.86) (520, 3.05)
HI_men_dw = GRAPH (Time) (140, 0) (145, 0.0136) (161, 0.0136) (192, 0) (224, 0.0202) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.0099) (520, 0.0973)

LD_men_no = GRAPH (Time) (489, 0) (504, 0.29) (520, 0)
LD_men_dw = GRAPH (Time) (489, 0) (504, 0.0013) (520, 0)

LS_men_no = GRAPH (Time) (489, 0) (504, 1.71) (520, 0)
LS_men_dw = GRAPH (Time) (489, 0) (504, 0.0091) (520, 0)

{8- Sciaenids, including silver perch (_bai_, Bairdiella chrysoura), speckled seatrout (_cyn_, Cynoscion nebulosus), spot (_lei_, Leiostomous xanthurus), and red drum (_soc_, Sciaenops ocellatus) used marsh and SAV habitats seasonally. They are grouped together here as SCI (numbers only).}

HE_bai_no = GRAPH (Time) (192, 0) (224, 0.23) (261, 0)
HE_bai_dw = GRAPH (Time) (192, 0) (224, 0.3385) (261, 0)

HI_bai_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0)
HI_bai_dw = GRAPH (Time) (192, 0) (224, 0.1205) (261, 0)

HE_cyn_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.11) (290, 0)
HE_cyn_dw = GRAPH (Time) (192, 0) (224, 0.1723) (261, 0.2902) (290, 0)

HU_lei_no = GRAPH (Time) (140, 0) (145, 0.38) (161, 0.38) (192, 0) (224, 0) (261, 0.57) (290, 0)
HU_lei_dw = GRAPH (Time) (140, 0) (145, 0.1620) (161, 0.1620) (192, 0) (224, 0) (261, 0.0118) (290, 0)

HE_lei_no = GRAPH (Time) (224, 0) (261, 0.23) (290, 0)
HE_lei_dw = GRAPH (Time) (224, 0) (261, 0.0158) (290, 0)

LD_soc_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0.14) (310, 0.14) (315, 0)
LD_soc_dw = GRAPH (Time) (224, 0) (261, 0.0002) (290, 0.0283) (310, 0.0283) (315, 0)

HU_SCI_no = GRAPH (Time) (140, 0) (145, 0.38) (161, 0.38) (192, 0) (224, 0) (261, 0.57) (290, 0)
HE_SCI_no = GRAPH (Time) (192, 0) (224, 0.34) (261, 0.34) (290, 0)
HI_SCI_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0)
LD_SCI_no = GRAPH (Time) (224, 0) (261, 0.11) (290, 0.14) (310, 0.14) (315, 0)

HU_SCI_dw = HU_lei_dw
HE_SCI_dw = HE_bai_dw + HE_cyn_dw + HE_lei_dw
HI_SCI_dw = HI_bai_dw
LD_SCI_dw = LD_soc_dw

{9- Small infrequent fishes (9 species) include bay anchovy (Anchoa mitchelli), sticklebacks (Apeltes quadracus), juvenile spadefish (Chaetodipterus faber), striped mullet (mugil cephalus), striped blenny (Chasmodes bosquianus), feather blenny (Hypsoblennius hentzi), and the green goby (Microgobius thalassinus). None of these species were sufficiently abundant to model separately.}

HU_SIF_no = GRAPH (Time) (161, 0) (192, 0.34) (224, 0) (261, 0.23) (290, 0)
HU_SIF_dw = GRAPH (Time) (161, 0) (192, 0.7566) (224, 0) (261, 0.0149) (290, 0)

HE_SIF_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.11) (290, 0.11) (310, 0.11) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.95)
HE_SIF_dw = GRAPH (Time) (192, 0) (224, 0.0506) (261, 0.1138) (290, 0.0319) (310, 0.0319) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.0038)

HF_SIF_no = GRAPH (Time) (161, 0) (192, 0.23) (224, 0) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.19)
HF_SIF_dw = GRAPH (Time) (161, 0) (192, 0.0386) (224, 0) (261, 0) (290, 0) (310, 0) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0.0034)

HI_SIF_no = GRAPH (Time) (145, 0) (161, 0.14) (192, 0) (224, 0) (261, 0.14) (290, 0.14) (310, 0.14) (315, 0)
HI_SIF_dw = GRAPH (Time) (145, 0) (161, 0.0269) (192, 0) (224, 0) (261, 0.0146) (290, 0.0146) (310, 0.0146) (315, 0)

LD_SIF_no = GRAPH (Time) (192, 0) (224, 0.23) (261, 0.23) (290, 0.14) (310, 0.14) (315, 0)
LD_SIF_dw = GRAPH (Time) (192, 0) (224, 0.0362) (261, 0.0665) (290, 0.0349) (310, 0.0349) (315, 0)

LS_SIF_no = GRAPH (Time) (161, 0) (192, 0.11) (224, 0.46) (261, 0.23) (290, 0)
LS_SIF_dw = GRAPH (Time) (161, 0) (192, 0.0036) (224, 0.0044) (261, 0.0380) (290, 0)

{10- Pipefishes (Syngnathus fuscus and Syngnathus floridae) were common SAV species.}

{See Goodwin Islands Descriptive Model for SAV habitat information.}

{Crustaceans:
B_CRUSTS_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}
{11 species of crustaceans are described in this model.}

{1- Blue crabs (Callinectes sapidus) were by far the biomass dominants in this study. They were found in every habitat and showed a recruitment of juveniles in late August, September and October. Crabs are further broken into size groups Lcal and Scal, see below.}

HU_cal_no = GRAPH (Time) (140, 0) (145, 0.76) (161, 0.76) (192, 0.11) (224, 0.34) (261, 6.51) (290, 3.20) (310, 3.20) (315, 0) (475, 0) (480, 1.43) (489, 1.43) (504, 0) (520, 0.38) (555, 0.38) (560, 0)
HU_cal_dw = GRAPH (Time) (140, 0) (145, 4.1110) (161, 4.1110) (192, 0.2197) (224, 2.2836) (261, 0.4280) (290, 1.1735) (310, 1.1735) (315, 0) (475, 0) (480, 0.5979) (489, 0.5979) (504, 0) (520, 1.0113) (555, 1.0113) (560, 0)

HE_cal_no = GRAPH (Time) (140, 0) (145, 0.38) (161, 0.38) (192, 0.23) (224, 0.69) (261, 11.43) (290, 5.37) (310, 5.37) (315, 0) (475, 0) (480, 0.57) (489, 0.57) (504, 1.43) (520, 1.14) (555, 1.14) (560, 0)
HE_cal_dw = GRAPH (Time) (140, 0) (145, 1.5407) (161, 1.5407) (192, 3.6751) (224, 1.9726) (261, 7.1926) (290, 4.9137) (310, 4.9137) (315, 0) (475, 0) (480, 1.0527) (489, 1.0527) (504, 3.6167) (520, 6.1398) (555, 6.1398) (560, 0)

HF_cal_no = GRAPH (Time) (161, 0) (192, 0.23) (224, 0.11) (261, 1.83) (290, 2.51) (310, 2.51) (315, 0) (475, 0) (480, 2.29) (489, 2.29) (504, 0.29) (520, 0.19) (555, 0.19) (560, 0)
HF_cal_dw = GRAPH (Time) (161, 0) (192, 0.4395) (224, 1.4217) (261, 1.3190) (290, 3.0749) (310, 3.0749) (315, 0) (475, 0) (480, 2.4811) (489, 2.4811) (504, 1.2472) (520, 1.4471) (555, 1.4471) (560, 0)

HI_cal_no = GRAPH (Time) (161, 0) (192, 0.11) (261, 1.03) (290, 1.43) (310, 1.43) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.29) (520, 0.19) (555, 0.19) (560, 0)
HI_cal_dw = GRAPH (Time) (161, 0) (192, 0.1416) (261, 3.2738) (290, 0.5367) (310, 0.5367) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.4821) (520, 0.9547) (555, 0.9547) (560, 0)

LD_cal_no = GRAPH (Time) (140, 0) (145, 1.03) (161, 1.03) (192, 0.11) (224, 0.46) (261, 9.71) (290, 7.29) (310, 7.29) (315, 0) (450, 0) (455, 1.71) (473, 1.71) (489, 2.00) (504, 0.57) (520, 0.76) (555, 0.76) (560, 0)
LD_cal_dw = GRAPH (Time) (140, 0) (145, 0.9790) (161, 0.9790) (192, 0.1802) (224, 1.5005) (261, 5.3161) (290, 1.4989) (310, 1.4989) (315, 0) (450, 0) (455, 0.1366) (473, 0.1366) (489, 0.3563) (504, 0.1749) (520, 0.3599) (555, 0.3599) (560, 0)

LS_cal_no = GRAPH (Time) (140, 0) (145, 0.34) (161, 0.34) (192, 0.23) (224, 0.69) (261, 5.71) (290, 4.91) (310, 4.91) (315, 0) (450, 0) (455, 0.57) (473, 0.57) (489, 0.86) (504, 0) (520, 0.38) (555, 0.38) (560, 0)
LS_cal_dw = GRAPH (Time) (140, 0) (145, 0.2680) (161, 0.2680) (192, 0.9855) (224, 0.0255) (261, 0.4244) (290, 0.3813) (310, 0.3813) (315, 0) (450, 0) (455, 0.0088) (473, 0.0088) (489, 0.0187) (504, 0) (520, 0.0725) (555, 0.0725) (560, 0)

{1a- Small blue crabs, carapace width ≤ 30 mm point-to-point.}

HU_Scal_no = GRAPH (Time) (140, 0) (145, 0.19) (161, 0.19) (192, 0) (224, 0) (261, 6.39) (290, 3.02) (310, 3.02) (315, 0) (475, 0) (480, 1.15) (489, 1.15) (504, 0) (520, 0.19) (555, 0.19) (560, 0)
HU_Scal_dw = GRAPH (Time) (140, 0) (145, 0.0741) (161, 0.0741) (192, 0) (224, 0) (261, 0.4280) (290, 0.2711) (310, 0.2711) (315, 0) (475, 0) (480, 0.2195) (489, 0.2195) (504, 0) (520, 0.0131) (555, 0.0131) (560, 0)

HE_Scal_no = GRAPH (Time) (140, 0) (145, 0.19) (161, 0.19) (192, 0) (224, 0.44) (261, 10.57) (290, 4.45) (310, 4.45) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.58) (520, 0) (555, 0) (560, 0)
HE_Scal_dw = GRAPH (Time) (140, 0) (145, 0.0370) (161, 0.0370) (192, 0) (224, 0.1107) (261, 0.8293) (290, 0.6978) (310, 0.6978) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.2056) (520, 0) (555, 0) (560, 0)

HF_Scal_no = GRAPH (Time) (161, 0) (192, 0) (224, 0) (261, 1.44) (290, 2.10) (310, 2.10) (315, 0) (475, 0) (480, 0.57) (489, 0.57) (504, 0) (520, 0) (555, 0) (560, 0)
HF_Scal_dw = GRAPH (Time) (161, 0) (192, 0) (224, 0) (261, 0.1579) (290, 0.3972) (310, 0.3972) (315, 0) (475, 0) (480, 0.1537) (489, 0.1537) (504, 0) (520, 0) (555, 0) (560, 0)

HI_Scal_no = GRAPH (Time) (161, 0) (192, 0) (261, 0.79) (290, 1.26) (310, 1.26) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0) (555, 0) (560, 0)
HI_Scal_dw = GRAPH (Time) (161, 0) (192, 0) (261, 0.0486) (290, 0.3113) (310, 0.3113) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0) (520, 0) (555, 0) (560, 0)

LD_Scal_no = GRAPH (Time) (140, 0) (145, 0.66) (161, 0.66) (192, 0) (224, 0.11) (261, 9.09) (290, 6.78) (310, 6.78) (315, 0) (450, 0) (455, 1.74) (473, 1.74) (489, 2.03) (504, 0.58) (520, 0.57) (555, 0.57) (560, 0)
LD_Scal_dw = GRAPH (Time) (140, 0) (145, 0.1696) (161, 0.1696) (192, 0) (224, 0.0097) (261, 1.3556) (290, 1.0941) (310, 1.0941) (315, 0) (450, 0) (455, 0.1365) (473, 0.1365) (489, 0.3563) (504, 0.1749) (520, 0.0595) (555, 0.0595) (560, 0)

LS_Scal_no = GRAPH (Time) (140, 0) (145, 0.22) (161, 0.22) (192, 0) (224, 0.68) (261, 5.51) (290, 4.71) (310, 4.71) (315, 0) (450, 0) (455, 0.58) (473, 0.58) (489, 0.87) (504, 0) (520, 0.38) (555, 0.38) (560, 0)
LS_Scal_dw = GRAPH (Time) (140, 0) (145, 0.0191) (161, 0.0191) (192, 0) (224, 0.0256) (261, 0.3317) (290, 0.3471) (310, 0.3471) (315, 0) (450, 0) (455, 0.0088) (473, 0.0088) (489, 0.0187) (504, 0) (520, 0.0725) (555, 0.0725) (560, 0)

{1b- Large blue crabs, carapace width > 30 mm point-to-point.}

HU_Lcal_no = GRAPH (Time) (140, 0) (145, 0.57) (161, 0.57) (192, 0.11) (224, 0.33) (261, 0) (290, 0.11) (310, 0.11) (315, 0) (475, 0) (480, 0.29) (489, 0.29) (504, 0) (520, 0.19) (555, 0.19) (560, 0)
HU_Lcal_dw = GRAPH (Time) (140, 0) (145, 4.0369) (161, 4.0369) (192, 0.2197) (224, 2.2835) (261, 0) (290, 0.9022) (310, 0.9022) (315, 0) (475, 0) (480, 0.3783) (489, 0.3783) (504, 0) (520, 0.9982) (555, 0.9982) (560, 0)

HE_Lcal_no = GRAPH (Time) (140, 0) (145, 0.19) (161, 0.19) (192, 0.22) (224, 0.22) (261, 0.77) (290, 0.77) (310, 0.77) (315, 0) (475, 0) (480, 0.58) (489, 0.58) (504, 0.87) (520, 1.14) (555, 1.14) (560, 0)
HE_Lcal_dw = GRAPH (Time) (140, 0) (145, 1.5036) (161, 1.5036) (192, 3.6751) (224, 1.8620) (261, 6.3635) (290, 4.2162) (310, 4.2162) (315, 0) (475, 0) (480, 1.0527) (489, 1.0527) (504, 3.4111) (520, 6.1399) (555, 6.1399) (560, 0)

HF_Lcal_no = GRAPH (Time) (161, 0) (192, 0.22) (224, 0) (261, 0.33) (290, 0.33) (310, 0.33) (315, 0) (475, 0) (480, 1.71) (489, 1.71) (504, 0.29) (520, 0.19) (555, 0.19) (560, 0)
HF_Lcal_dw = GRAPH (Time) (161, 0) (192, 0.4394) (224, 1.4217) (261, 1.1615) (290, 2.6779) (310, 2.6779) (315, 0) (475, 0) (480, 2.3273) (489, 2.3273) (504, 1.2472) (520, 1.4471) (555, 1.4471) (560, 0)

HI_Lcal_no = GRAPH (Time) (161, 0) (192, 0.11) (261, 0.22) (290, 0.14) (310, 0.14) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.29) (520, 0.19) (555, 0.19) (560, 0)
HI_Lcal_dw = GRAPH (Time) (161, 0) (192, 0.1416) (261, 3.2252) (290, 0.2253) (310, 0.2253) (315, 0) (475, 0) (480, 0) (489, 0) (504, 0.4821) (520, 0.9547) (555, 0.9547) (560, 0)

LD_Lcal_no = GRAPH (Time) (140, 0) (145, 0.33) (161, 0.33) (192, 0.11) (224, 0.33) (261, 0.44) (290, 0.42) (310, 0.42) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0) (504, 0) (520, 0.19) (555, 0.19) (560, 0)
LD_Lcal_dw = GRAPH (Time) (140, 0) (145, 0.8094) (161, 0.8094) (192, 0.1802) (224, 1.4909) (261, 3.9611) (290, 0.4047) (310, 0.4047) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0) (504, 0) (520, 0.3004) (555, 0.3004) (560, 0)

LS_Lcal_no = GRAPH (Time) (140, 0) (145, 0.11) (161, 0.11) (192, 0.22) (224, 0) (261, 0.11) (290, 0.11) (310, 0.11) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0) (504, 0) (520, 0) (555, 0) (560, 0)
LS_Lcal_dw = GRAPH (Time) (140, 0) (145, 0.2489) (161, 0.2489) (192, 0.9855) (224, 0) (261, 0.0926) (290, 0.0343) (310, 0.0343) (315, 0) (450, 0) (455, 0) (473, 0) (489, 0) (504, 0) (520, 0) (555, 0) (560, 0)

{2- Sand shrimp (Crangon septemspinosa) were found in SAV and unvegetated habitats.}

LD_cra_no = GRAPH (Time) (224, 0) (261, 0.23) (290, 3.43) (310, 3.43) (315, 0)
LD_cra_dw = GRAPH (Time) (224, 0) (261, 0.0026) (290, 0.0447) (310, 0.0447) (315, 0)

{3- Hippolyte shrimps were found predominantly in seagrass. This model does not truly attempt to quantify these creatures as the smallest size classes were not effectively sampled.}

LS_hyp_no = GRAPH (Time) (261, 0) (290, 0.91) (310, 0.91) (315, 0)
LS_hyp_dw = GRAPH (Time) (261, 0) (290, 0.0033) (310, 0.0033) (315, 0)

{4- Grass shrimp (Palaemonetes pugio, Palaemonetes vulgaris, and Palaemonetes intermedius) were the numerically dominant creature of the study. The separate model "Goodwin Islands Descriptive Model" includes all three species.}

HU_PAL_no = GRAPH (Time) (224, 0) (261, 1.49) (290, 1.14) (310, 1.14) (315, 0) (489, 0)
HU_PAL_dw = GRAPH (Time) (224, 0) (261, 0.0083) (290, 0.0114) (310, 0.0114) (315, 0) (489, 0)

HE_PAL_no = GRAPH (Time) (140, 0) (145, 0.76) (161, 0.76) (192, 13.37) (224, 5.71) (261, 42.17) (290, 9.83) (310, 9.83) (315, 0) (475, 0) (480, 7.14) (489, 7.14) (504, 0.57) (520, 1.14) (555, 1.14) (560, 0)
HE_PAL_dw = GRAPH (Time) (140, 0) (145, 0.0523) (161, 0.0523) (192, 1.0874) (224, 0.2903) (261, 1.021) (290, 0.2491) (310, 0.2491) (315, 0) (475, 0) (480, 0.4223) (489, 0.4223) (504, 0.0664) (520, 0.0545) (555, 0.0545) (560, 0)

HF_PAL_no = GRAPH (Time) (161, 0) (192, 18.97) (224, 8.11) (261, 1.26) (290, 6.74) (310, 6.74) (315, 0) (475, 0) (480, 1.14) (489, 1.14) (504, 0.86) (520, 0)
HF_PAL_dw = GRAPH (Time) (161, 0) (192, 0.9145) (224, 0.2663) (261, 0.0148) (290, 0.2370) (310, 0.2370) (315, 0) (475, 0) (480, 0.0149) (489, 0.0149) (504, 0.0807) (520, 0)

HI_PAL_no = GRAPH (Time) (140, 0) (145, 0.14) (161, 0.14) (192, 3.43) (224, 2.06) (261, 5.94) (290, 21.29) (310, 21.29) (315, 0) (475, 0) (480, 2.29) (489, 2.29) (504, 1.14) (520, 0)
HI_PAL_dw = GRAPH (Time) (140, 0) (145, 0.0160) (161, 0.0160) (192, 0.1096) (224, 0.0558) (261, 0.1516) (290, 0.4826) (310, 0.4826) (315, 0) (475, 0) (480, 0.0686) (489, 0.0686) (504, 0.0310) (520, 0)

LD_PAL_no = GRAPH (Time) (140, 0) (145, 1.14) (161, 1.14) (192, 0.11) (224, 0.46) (261, 5.03) (290, 32.86) (310, 32.86) (315, 0) (450, 0) (455, 1.43) (473, 1.43) (489, 0) (504, 0.86) (520, 0)
LD_PAL_dw = GRAPH (Time) (140, 0) (145, 0.1072) (161, 0.1072) (192, 0.0029) (224, 0.0142) (261, 0.0283) (290, 1.9029) (310, 1.9029) (315, 0) (450, 0) (455, 0.0679) (473, 0.0679) (489, 0) (504, 0.0675) (520, 0)

LS_PAL_no = GRAPH (Time) (140, 0) (145, 0.46) (161, 0.46) (192, 8.80) (224, 37.71) (261, 42.74) (290, 91.77) (310, 91.77) (315, 0) (450, 0) (455, 1.14) (473, 1.14) (489, 1.14) (504, 0)
LS_PAL_dw = GRAPH (Time) (140, 0) (145, 0.0058) (161, 0.0058) (192, 0.1413) (224, 0.4700) (261, 1.1723) (290, 2.7529) (310, 2.7529) (315, 0) (450, 0) (455, 0.0126) (473, 0.0126) (489, 0.0137) (504, 0)

{5- Miscellaneous crustaceans include hermit crabs (Pagurus longicarpus), unspeciated xanthid crabs, and alpheid shrimps (mostly Alpheus heterochaelus). They are included here as data but not in model calculations, as they are not considered nekton}

HU_MCR_no = GRAPH (Time) (224, 0) (261, 0.34) (290, 0.46) (310, 0.46) (315, 0)
HU_MCR_dw = GRAPH (Time) (224, 0) (261, 0.0146) (290, 0.0173) (310, 0.0173) (315, 0)

HE_MCR_no = GRAPH (Time) (161, 0) (192, 0.46) (224, 0.11) (261, 0.34) (290, 0) (504, 0) (520, 0.19) (555, 0.19) (560, 0)
HE_MCR_dw = GRAPH (Time) (161, 0) (192, 0.1954) (224, 0.0028) (261, 0.0612) (290, 0) (504, 0) (520, 0.0025) (555, 0.0025) (560, 0)

HF_MCR_no = GRAPH (Time) (489, 0) (504, 0.29) (520, 0.19) (555, 0.19) (560, 0)
HF_MCR_dw = GRAPH (Time) (489, 0) (504, 0.0011) (520, 0.0011) (555, 0.0011) (560, 0)

LD_MCR_no = GRAPH (Time) (140, 0) (145, 0.23) (161, 0.23) (192, 0) (224, 0.11) (261, 0.46) (290, 0.71) (310, 0.71) (315, 0) (489, 0) (504, 0.29) (520, 0.38) (555, 0.38) (560, 0)
LD_MCR_dw = GRAPH (Time) (140, 0) (145, 0.0097) (161, 0.0097) (192, 0) (224, 0.0028) (261, 0.0141) (290, 0.0296) (310, 0.0296) (315, 0) (489, 0) (504, 0.0065) (520, 0.0111) (555, 0.0111) (560, 0)

LS_MCR_no = GRAPH (Time) (140, 0) (145, 0.11) (161, 0.11) (192, 0.11) (224, 0.11) (261, 0.11) (290, 0.57) (310, 0.57) (315, 0)
LS_MCR_dw = GRAPH (Time) (140, 0) (145, 0.0018) (161, 0.0018) (192, 0.0062) (224, 0.0028) (261, 0.0039) (290, 0.0112) (310, 0.0112) (315, 0)

{6- Juvenile Penaid shrimps (Penaeus aztecus and Penaeus duorarum) were present in SAV and in deeper unvegetated habitats during the fall months.}

HU_PEN_no = GRAPH (Time) (224, 0) (261, 0.34) (290, 0)
HU_PEN_dw = GRAPH (Time) (224, 0) (261, 0.0692) (290, 0)

LD_PEN_no = GRAPH (Time) (192, 0) (224, 0.11) (261, 0.23) (290, 0)
LD_PEN_dw = GRAPH (Time) (192, 0) (224, 0.0050) (261, 0.0876) (290, 0)

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PART VI - NEKTON TOTALS, ARRANGED BY TAXA
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Totals are provided for fishes, crustaceans, and all natant macrofauna:}

HI_FISH_no = HI_het_no + HI_luc_no + HI_maj_no + HI_men_no + HI_SCI_no + HI_SIF_no
HF_FISH_no = HF_het_no + HF_luc_no + HF_maj_no + HF_men_no + HF_SIF_no
HE_FISH_no = HE_FLT_no + HE_het_no + HE_luc_no + HE_maj_no + HE_men_no + HE_SCI_no + HE_SIF_no + HE_gbo_no + HE_str_no
HU_FISH_no = HU_FLT_no + HU_het_no + HU_luc_no + HU_men_no + HU_SCI_no + HU_SIF_no + HU_gbo_no
LS_FISH_no = LS_gbo_no + LS_str_no + LS_het_no + LS_luc_no + LS_maj_no + LS_men_no + LS_SIF_no
LD_FISH_no = LD_FLT_no + LD_gbo_no + LD_str_no + LD_het_no + LD_luc_no + LD_maj_no + LD_men_no + LD_SCI_no + LD_SIF_no

HI_FISH_dw = HI_Shet_dw + HI_Lhet_dw + HI_luc_dw + HI_maj_dw + HI_men_dw + HI_bai_dw + HI_SIF_dw
HF_FISH_dw = HF_Shet_dw + HF_Lhet_dw + HF_luc_dw + HF_maj_dw + HF_men_dw + HF_SIF_dw
HE_FISH_dw = HE_FLT_dw + HE_Shet_dw + HE_Lhet_dw + HE_luc_dw + HE_maj_dw + HE_men_dw + HE_SCI_dw + HE_SIF_dw + HE_gbo_dw + HE_str_dw
HU_FISH_dw = HU_FLT_dw + HU_Shet_dw + HU_luc_dw + HU_men_dw + HU_SCI_dw + HU_SIF_dw + HU_gbo_dw
LS_FISH_dw = LS_gbo_dw + LS_str_dw + LS_Lhet_dw + LS_Shet_dw + LS_luc_dw + LS_maj_dw + LS_men_dw + LS_SIF_dw
LD_FISH_dw = LD_FLT_dw + LD_gbo_dw + LD_str_dw + LD_Shet_dw + LD_Lhet_dw + LD_luc_dw + LD_maj_dw + LD_men_dw + LD_SCI_dw + LD_SIF_dw

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ALL_FISH_no = (HI_FISH_no + HF_FISH_no + HE_FISH_no + HU_FISH_no + LS_FISH_no + LD_FISH_no)/6
ALL_FISH_dw = (HI_FISH_dw + HF_FISH_dw + HE_FISH_dw + HU_FISH_dw + LS_FISH_dw + LD_FISH_dw)/6

HI_CRST_no = HI_cal_no + HI_PAL_no
HF_CRST_no = HF_cal_no + HF_PAL_no + HF_MCR_no
HE_CRST_no = HE_cal_no + HE_PAL_no + HE_MCR_no
HU_CRST_no = HU_cal_no + HU_PAL_no + HU_MCR_no + HU_PEN_no
LS_CRST_no = LS_cal_no + LS_hyp_no + LS_PAL_no + LS_MCR_no
LD_CRST_no = LD_cal_no + LD_cra_no + LD_PAL_no + LD_MCR_no + LD_PEN_no

HI_CRST_dw = HI_cal_dw + HI_PAL_dw
HF_CRST_dw = HF_cal_dw + HF_PAL_dw + HF_MCR_dw
HE_CRST_dw = HE_cal_dw + HE_PAL_dw + HE_MCR_dw
HU_CRST_dw = HU_cal_dw + HU_PAL_dw + HU_MCR_dw + HU_PEN_dw
LS_CRST_dw = LS_cal_dw + LS_hyp_dw + LS_PAL_dw + LS_MCR_dw
LD_CRST_dw = LD_cal_dw + LD_cra_dw + LD_PAL_dw + LD_MCR_dw + LD_PEN_dw

ALL_CRST_no = (HI_CRST_no + HF_CRST_no + HE_CRST_no + HU_CRST_no  + LS_CRST_no +
    LD_CRST_no)/6
ALL_CRST_dw = (HI_CRST_dw + HF_CRST_dw + HE_CRST_dw + HU_CRST_dw + LS_CRST_dw +
    LD_CRST_dw)/6

HI_NEKT_no = HI_FISH_no + HI_CRST_no
HF_NEKT_no = HF_FISH_no + HF_CRST_no
HE_NEKT_no = HE_FISH_no + HE_CRST_no
HU_NEKT_no = HU_FISH_no + HU_CRST_no
LS_NEKT_no = LS_FISH_no + LS_CRST_no
LD_NEKT_no = LD_FISH_no + LD_CRST_no

HI_NEKT_dw = HI_FISH_dw + HI_CRST_dw
HF_NEKT_dw = HF_FISH_dw + HF_CRST_dw
HE_NEKT_dw = HE_FISH_dw + HE_CRST_dw
HU_NEKT_dw = HU_FISH_dw + HU_CRST_dw
LS_NEKT_dw = LS_FISH_dw + LS_CRST_dw
LD_NEKT_dw = LD_FISH_dw + LD_CRST_dw

ALL_NEKT_no = ALL_FISH_no + ALL_CRST_no
ALL_NEKT_dw = ALL_FISH_dw + ALL_CRST_dw

{Large blue crabs >30 mm have been removed from the following calculations, _SCRUST_
    and _SNEKT_.}

HI_SCRST_no = HI_Scal_no + HI_PAL_no
HF_SCRST_no = HF_Scal_no + HF_PAL_no + HF_MCR_no
HE_SCRST_no = HE_Scal_no + HE_PAL_no + HE_MCR_no
HU_SCRST_no = HU_Scal_no + HU_PAL_no + HU_MCR_no + HU_PEN_no
LS_SCRST_no = LS_Scal_no + LS_hyp_no + LS_PAL_no + LS_MCR_no
LD_SCRST_no = LD_Scal_no + LD_cra_no + LD_PAL_no + LD_MCR_no + LD_PEN_no

HI_SCRST_dw = HI_Scal_dw + HI_PAL_dw
HF_SCRST_dw = HF_Scal_dw + HF_PAL_dw + HF_MCR_dw
HE_SCRST_dw = HE_Scal_dw + HE_PAL_dw + HE_MCR_dw
HU_SCRST_dw = HU_Scal_dw + HU_PAL_dw + HU_MCR_dw + HU_PEN_dw
LS_SCRST_dw = LS_Scal_dw + LS_hyp_dw + LS_PAL_dw + LS_MCR_dw
LD_SCRST_dw = LD_Scal_dw + LD_cra_dw + LD_PAL_dw + LD_MCR_dw + LD_PEN_dw

ALL_SCRST_no = (HI_SCRST_no + HF_SCRST_no + HE_SCRST_no + HU_SCRST_no +  LS_SCRST_no +
    LD_SCRST_no)/6
ALL_SCRST_dw = (HI_SCRST_dw + HF_SCRST_dw + HE_SCRST_dw + HU_SCRST_dw + LS_SCRST_dw +
    LD_SCRST_dw)/6

HI_SNEKT_no = HI_FISH_no + HI_SCRST_no
HF_SNEKT_no = HF_FISH_no + HF_SCRST_no
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HE_SNEKT_no = HE_FISH_no + HE_SCRST_no
HU_SNEKT_no = HU_FISH_no + HU_SCRST_no
LS_SNEKT_no = LS_FISH_no + LS_SCRST_no
LD_SNEKT_no = LD_FISH_no + LD_SCRST_no

HI_SNEKT_dw = HI_FISH_dw + HI_SCRST_dw
HF_SNEKT_dw = HF_FISH_dw + HF_SCRST_dw
HE_SNEKT_dw = HE_FISH_dw + HE_SCRST_dw
HU_SNEKT_dw = HU_FISH_dw + HU_SCRST_dw
LS_SNEKT_dw = LS_FISH_dw + LS_SCRST_dw
LD_SNEKT_dw = LD_FISH_dw + LD_SCRST_dw

ALL_SNEKT_no = ALL_FISH_no + ALL_SCRST_no
ALL_SNEKT_dw = ALL_FISH_dw + ALL_SCRST_dw


{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
                              PART VII   TROPHIC CONNECTIONS
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This section calculates predation in each habitat due to the predators above.  These results
can be compared to prey data from above by simultaneously graphing predation and prey.
The model cannot mathematically handle all predator x prey combinations, so prey are entered
in groups four at a time into the last "parameters" section (fraction of predator gut content that
is each prey).  The model is run, then new prey can be entered and the model re-run.  A table of
fraction by weight of gut contents is included in the separate file "GUT Data".  The following
section is arranged in the order: totals, then calculations, then parameters.  The parameters
which need to be re-entered to display different prey categories are in the very last section.
Note that in order to compare nekton and invertebrates within a habitat, the following pairs
should be used:
     HI_  or H_ (nekton) and H_ (invertebrates) represent the same habitat - marsh interior
     HE_  or L_ (nekton) and L_ (invertebrates) represent the same habitat - marsh edge
     UF_  or U_ (nekton) and U_ (invertebrates) represent the same habitat - unvegetated area,
             which is a composite of habitats HU, LD and LS with time dry for nekton as tides move
             over the flat.

The model displays predation in two ways:  predation in grams dry weight removed per day (_Pr),
and as an integration of total grams dry weight removed over time. (_TPr).  If _TPr is used, the
model should be run for the desired length of time using the STARTTIME and STOPTIME parameters
in the window that appears on the first graph pad in the run menu.  After running for this length
of time, the end value of _TPr is read.  This calculates total predation over the specified length
of time for any predator/prey combination.}

VII__TROPHIC=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}

A_Totals_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}

{1 - Predation in grams dry weight removed per day.}

HU_PrA = HU_FLT_PrA + HU_gbo_PrA + HU_Shet_PrA + HU_luc_PrA + HU_men_PrA + HU_lei_PrA +
     HU_Scal_PrA + HU_Lcal_PrA + HU_PAL_PrA
HE_PrA = HE_FLT_PrA + HE_gbo_PrA + HE_str_PrA + HE_Shet_PrA + HE_Lhet_PrA + HE_luc_PrA +
     HE_maj_PrA + HE_men_PrA + HE_bai_PrA + HE_cyn_PrA + HE_lei_PrA + HE_Scal_PrA + HE_Lcal_PrA +
     HE_PAL_PrA
HF_PrA = HF_Shet_PrA + HF_Lhet_PrA + HF_luc_PrA + HF_maj_PrA + HF_men_PrA + HF_Scal_PrA +
     HF_Lcal_PrA + HF_PAL_PrA
HI_PrA = HI_Shet_PrA + HI_Lhet_PrA + HI_luc_PrA + HI_maj_PrA + HI_men_PrA + HI_bai_PrA +
     HI_Scal_PrA + HI_Lcal_PrA + HI_PAL_PrA
HV_PrA = HV_Shet_PrA
LD_PrA = LD_FLT_PrA + LD_gbo_PrA + LD_str_PrA + LD_Shet_PrA + LD_Lhet_PrA + LD_luc_PrA +
     LD_maj_PrA + LD_men_PrA + LD_soc_PrA + LD_Scal_PrA + LD_Lcal_PrA + LD_PAL_PrA
LS_PrA = LS_gbo_PrA + LS_str_PrA + LS_Shet_PrA + LS_Lhet_PrA + LS_luc_PrA + LS_maj_PrA +
     LS_men_PrA + LS_Scal_PrA + LS_Lcal_PrA + LS_PAL_PrA
LV_PrA = LV_Shet_PrA
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UF_PrA = HU_PrA + LD_PrA + LS_PrA

HU_PrB = HU_FLT_PrB + HU_gbo_PrB + HU_Shet_PrB + HU_luc_PrB + HU_men_PrB + HU_lei_PrB +
    HU_Scal_PrB + HU_Lcal_PrB + HU_PAL_PrB
HE_PrB = HE_FLT_PrB + HE_gbo_PrB + HE_str_PrB + HE_Shet_PrB + HE_Lhet_PrB + HE_luc_PrB +
    HE_maj_PrB + HE_men_PrB + HE_bai_PrB + HE_cyn_PrB + HE_lei_PrB + HE_Scal_PrB + HE_Lcal_PrB +
    HE_PAL_PrB
HF_PrB = HF_Shet_PrB + HF_Lhet_PrB + HF_luc_PrB + HF_maj_PrB + HF_men_PrB + HF_Scal_PrB +
    HF_Lcal_PrB + HF_PAL_PrB
HI_PrB = HI_Shet_PrB + HI_Lhet_PrB + HI_luc_PrB + HI_maj_PrB + HI_men_PrB + HI_bai_PrB + HI_Scal_PrB
    + HI_Lcal_PrB + HI_PAL_PrB
HV_PrB = HV_Shet_PrB
LD_PrB = LD_FLT_PrB + LD_gbo_PrB + LD_str_PrB + LD_Shet_PrB + LD_Lhet_PrB + LD_luc_PrB +
    LD_maj_PrB + LD_men_PrB + LD_soc_PrB + LD_Scal_PrB + LD_Lcal_PrB + LD_PAL_PrB
LS_PrB = LS_gbo_PrB + LS_str_PrB + LS_Shet_PrB + LS_Lhet_PrB + LS_luc_PrB + LS_maj_PrB +
    LS_men_PrB + LS_Scal_PrB + LS_Lcal_PrB + LS_PAL_PrB
LV_PrB = LV_Shet_PrB
UF_PrB = HU_PrB + LD_PrB + LS_PrB

{The following calculations graph monthly means for UF_PrB, HE_PrB, and HI_PrB  so that monthly
mean prey information can be better compared to predation information.}
UF_PrBmn = GRAPH (Time)  (168, 0.025) (198, 0.015) (228, 0.037) (258, 0.048) (288, 0.044)
HE_PrBmn = GRAPH (Time)  (168, 0.018) (198, 0.050) (228, 0.086) (258, 0.084) (288, 0.050)
HI_PrBmn = GRAPH (Time)  (168, 0.002) (198, 0.005) (228, 0.014) (258, 0.016) (288, 0.0085)

HU_PrC = HU_FLT_PrC + HU_gbo_PrC + HU_Shet_PrC + HU_luc_PrC + HU_men_PrC + HU_lei_PrC +
    HU_Scal_PrC + HU_Lcal_PrC + HU_PAL_PrC
HE_PrC = HE_FLT_PrC + HE_gbo_PrC + HE_str_PrC + HE_Shet_PrC + HE_Lhet_PrC + HE_luc_PrC +
    HE_maj_PrC + HE_men_PrC + HE_bai_PrC + HE_cyn_PrC + HE_lei_PrC + HE_Scal_PrC + HE_Lcal_PrC +
    HE_PAL_PrC
HF_PrC = HF_Shet_PrC + HF_Lhet_PrC + HF_luc_PrC + HF_maj_PrC + HF_men_PrC + HF_Scal_PrC +
    HF_Lcal_PrC + HF_PAL_PrC
HI_PrC = HI_Shet_PrC + HI_Lhet_PrC + HI_luc_PrC + HI_maj_PrC + HI_men_PrC + HI_bai_PrC + HI_Scal_PrC
    + HI_Lcal_PrC + HI_PAL_PrC
HV_PrC = HV_Shet_PrC
LD_PrC = LD_FLT_PrC + LD_gbo_PrC + LD_str_PrC + LD_Shet_PrC + LD_Lhet_PrC + LD_luc_PrC +
    LD_maj_PrC + LD_men_PrC + LD_soc_PrC + LD_Scal_PrC + LD_Lcal_PrC + LD_PAL_PrC
LS_PrC = LS_gbo_PrC + LS_str_PrC + LS_Shet_PrC + LS_Lhet_PrC + LS_luc_PrC + LS_maj_PrC +
    LS_men_PrC + LS_Scal_PrC + LS_Lcal_PrC + LS_PAL_PrC
LV_PrC = LV_Shet_PrC
UF_PrC = HU_PrC + LD_PrC + LS_PrC

HU_PrD = HU_FLT_PrD + HU_gbo_PrD + HU_Shet_PrD + HU_luc_PrD + HU_men_PrD + HU_lei_PrD +
    HU_Scal_PrD + HU_Lcal_PrD + HU_PAL_PrD
HE_PrD = HE_FLT_PrD + HE_gbo_PrD + HE_str_PrD + HE_Shet_PrD + HE_Lhet_PrD + HE_luc_PrD +
    HE_maj_PrD + HE_men_PrD + HE_bai_PrD + HE_cyn_PrD + HE_lei_PrD + HE_Scal_PrD + HE_Lcal_PrD +
    HE_PAL_PrD
HF_PrD = HF_Shet_PrD + HF_Lhet_PrD + HF_luc_PrD + HF_maj_PrD + HF_men_PrD + HF_Scal_PrD +
    HF_Lcal_PrD + HF_PAL_PrD
HI_PrD = HI_Shet_PrD + HI_Lhet_PrD + HI_luc_PrD + HI_maj_PrD + HI_men_PrD + HI_bai_PrD +
    HI_Scal_PrD + HI_Lcal_PrD + HI_PAL_PrD
HV_PrD = HV_Shet_PrD
LD_PrD = LD_FLT_PrD + LD_gbo_PrD + LD_str_PrD + LD_Shet_PrD + LD_Lhet_PrD + LD_luc_PrD +
    LD_maj_PrD + LD_men_PrD + LD_soc_PrD + LD_Scal_PrD + LD_Lcal_PrD + LD_PAL_PrD
LS_PrD = LS_gbo_PrD + LS_str_PrD + LS_Shet_PrD + LS_Lhet_PrD + LS_luc_PrD + LS_maj_PrD +
    LS_men_PrD + LS_Scal_PrD + LS_Lcal_PrD + LS_PAL_PrD
LV_PrD = LV_Shet_PrD
UF_PrD = HU_PrD + LD_PrD + LS_PrD

{2 - Predation in habitats, integration of total grams dry weight removed over time.}

HU_TPrA (t) =  HU_TPrA (t-dt) + (HU_PrA)*dt
INIT HU_TPrA = 0
HE_TPrA (t) =  HE_TPrA (t-dt) + (HE_PrA)*dt
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INIT HE_TPrA = 0
HF_TPrA (t) = HF_TPrA (t-dt) + (HF_PrA)*dt
INIT HF_TPrA = 0
HI_TPrA (t) = HI_TPrA (t-dt) + (HI_PrA)*dt
INIT HI_TPrA = 0
HV_TPrA (t) = HV_TPrA (t-dt) + (HV_PrA)*dt
INIT HV_TPrA = 0
LD_TPrA (t) = LD_TPrA (t-dt) + (LD_PrA)*dt
INIT LD_TPrA = 0
LS_TPrA (t) = LS_TPrA (t-dt) + (LS_PrA)*dt
INIT LS_TPrA = 0
LV_TPrA (t) = LV_TPrA (t-dt) + (LV_PrA)*dt
INIT LV_TPrA = 0

HU_TPrB (t) = HU_TPrB (t-dt) + (HU_PrB)*dt
INIT HU_TPrB = 0
HE_TPrB (t) = HE_TPrB (t-dt) + (HE_PrB)*dt
INIT HE_TPrB = 0
HF_TPrB (t) = HF_TPrB (t-dt) + (HF_PrB)*dt
INIT HF_TPrB = 0
HI_TPrB (t) = HI_TPrB (t-dt) + (HI_PrB)*dt
INIT HI_TPrB = 0
HV_TPrB (t) = HV_TPrB (t-dt) + (HV_PrB)*dt
INIT HV_TPrB = 0
LD_TPrB (t) = LD_TPrB (t-dt) + (LD_PrB)*dt
INIT LD_TPrB = 0
LS_TPrB (t) = LS_TPrB (t-dt) + (LS_PrB)*dt
INIT LS_TPrB = 0
LV_TPrB (t) = LV_TPrB (t-dt) + (LV_PrB)*dt
INIT LV_TPrB = 0

HU_TPrC (t) = HU_TPrC (t-dt) + (HU_PrC)*dt
INIT HU_TPrC = 0
HE_TPrC (t) = HE_TPrC (t-dt) + (HE_PrC)*dt
INIT HE_TPrC = 0
HF_TPrC (t) = HF_TPrC (t-dt) + (HF_PrC)*dt
INIT HF_TPrC = 0
HI_TPrC (t) = HI_TPrC (t-dt) + (HI_PrC)*dt
INIT HI_TPrC = 0
HV_TPrC (t) = HV_TPrC (t-dt) + (HV_PrC)*dt
INIT HV_TPrC = 0
LD_TPrC (t) = LD_TPrC (t-dt) + (LD_PrC)*dt
INIT LD_TPrC = 0
LS_TPrC (t) = LS_TPrC (t-dt) + (LS_PrC)*dt
INIT LS_TPrC = 0
LV_TPrC (t) = LV_TPrC (t-dt) + (LV_PrC)*dt
INIT LV_TPrC = 0

HU_TPrD (t) = HU_TPrD (t-dt) + (HU_PrD)*dt
INIT HU_TPrD = 0
HE_TPrD (t) = HE_TPrD (t-dt) + (HE_PrD)*dt
INIT HE_TPrD = 0
HF_TPrD (t) = HF_TPrD (t-dt) + (HF_PrD)*dt
INIT HF_TPrD = 0
HI_TPrD (t) = HI_TPrD (t-dt) + (HI_PrD)*dt
INIT HI_TPrD = 0
HV_TPrD (t) = HV_TPrD (t-dt) + (HV_PrD)*dt
INIT HV_TPrD = 0
LD_TPrD (t) = LD_TPrD (t-dt) + (LD_PrD)*dt
INIT LD_TPrD = 0
LS_TPrD (t) = LS_TPrD (t-dt) + (LS_PrD)*dt
INIT LS_TPrD = 0
LV_TPrD (t) = LV_TPrD (t-dt) + (LV_PrD)*dt
INIT LV_TPrD = 0
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{3 - Predation by species, integration of total grams dry weight removed
over time.}

HU_FLT_TPrA (t)  = HU_FLT_TPrA (t-dt) + (HU_FLT_PrA) * dt
HU_gbo_TPrA (t)  = HU_gbo_TPrA (t-dt) + (HU_gbo_PrA) * dt
HU_Shet_TPrA (t)  = HU_Shet_TPrA (t-dt) + (HU_Shet_PrA) * dt
HU_luc_TPrA (t)  = HU_luc_TPrA (t-dt) + (HU_luc_PrA) * dt
HU_men_TPrA (t)  = HU_men_TPrA (t-dt) + (HU_men_PrA) * dt
HU_lei_TPrA (t)  = HU_lei_TPrA (t-dt) + (HU_lei_PrA) * dt
HU_Scal_TPrA (t)  = HU_Scal_TPrA (t-dt) + (HU_Scal_PrA) * dt
HU_Lcal_TPrA (t)  = HU_Lcal_TPrA (t-dt) + (HU_Lcal_PrA) * dt
HU_PAL_TPrA (t)  = HU_PAL_TPrA (t-dt) + (HU_PAL_PrA) * dt
HU_cal_TPrA = HU_Lcal_TPrA + HU_Scal_TPrA
HU_fish_TPrA = HU_FLT_TPrA + HU_gbo_TPrA + HU_Shet_TPrA + HU_luc_TPrA + HU_men_TPrA +
    HU_lei_TPrA

HE_FLT_TPrA (t)  = HE_FLT_TPrA (t-dt) + (HE_FLT_PrA) * dt
HE_gbo_TPrA (t)  = HE_gbo_TPrA (t-dt) + (HE_gbo_PrA) * dt
HE_str_TPrA (t)  = HE_str_TPrA (t-dt) + (HE_str_PrA) * dt
HE_Shet_TPrA (t)  = HE_Shet_TPrA (t-dt) + (HE_Shet_PrA) * dt
HE_Lhet_TPrA (t)  = HE_Lhet_TPrA (t-dt) + (HE_Lhet_PrA) * dt
HE_het_TPrA = HE_Shet_TPrA + HE_Lhet_TPrA
HE_luc_TPrA (t)  = HE_luc_TPrA (t-dt) + (HE_luc_PrA) * dt
HE_maj_TPrA (t)  = HE_maj_TPrA (t-dt) + (HE_maj_PrA) * dt
HE_men_TPrA (t)  = HE_men_TPrA (t-dt) + (HE_men_PrA) * dt
HE_bai_TPrA (t)  = HE_bai_TPrA (t-dt) + (HE_bai_PrA) * dt
HE_cyn_TPrA (t)  = HE_cyn_TPrA (t-dt) + (HE_cyn_PrA) * dt
HE_lei_TPrA (t)  = HE_lei_TPrA (t-dt) + (HE_lei_PrA) * dt
HE_Scal_TPrA (t)  = HE_Scal_TPrA (t-dt) + (HE_Scal_PrA) * dt
HE_Lcal_TPrA (t)  = HE_Lcal_TPrA (t-dt) + (HE_Lcal_PrA) * dt
HE_PAL_TPrA (t)  = HE_PAL_TPrA (t-dt) + (HE_PAL_PrA) * dt
HE_cal_TPrA = HE_Lcal_TPrA + HE_Scal_TPrA
HE_SCI_TPrA = HE_cyn_TPrA + HE_bai_TPrA  + HE_lei_TPrA
HE_fish_TPrA = HE_FLT_TPrA + HE_gbo_TPrA + HE_Shet_TPrA + HE_luc_TPrA + HE_men_TPrA +
    HE_SCI_TPrA + HE_str_TPrA + HE_Lhet_TPrA + HE_maj_TPrA

HF_Shet_TPrA (t)  = HF_Shet_TPrA (t-dt) + (HF_Shet_PrA) * dt
HF_Lhet_TPrA (t)  = HF_Lhet_TPrA (t-dt) + (HF_Lhet_PrA) * dt
HF_het_TPrA = HF_Shet_TPrA + HF_Lhet_TPrA
HF_luc_TPrA (t)  = HF_luc_TPrA (t-dt) + (HF_luc_PrA) * dt
HF_maj_TPrA (t)  = HF_maj_TPrA (t-dt) + (HF_maj_PrA) * dt
HF_men_TPrA (t)  = HF_men_TPrA (t-dt) + (HF_men_PrA) * dt
HF_Scal_TPrA (t)  = HF_Scal_TPrA (t-dt) + (HF_Scal_PrA) * dt
HF_Lcal_TPrA (t)  = HF_Lcal_TPrA (t-dt) + (HF_Lcal_PrA) * dt
HF_PAL_TPrA (t)  = HF_PAL_TPrA (t-dt) + (HF_PAL_PrA) * dt
HF_cal_TPrA = HF_Lcal_TPrA + HF_Scal_TPrA
HF_fish_TPrA =  HF_Shet_TPrA + HF_luc_TPrA + HF_men_TPrA  + HF_Lhet_TPrA + HF_maj_TPrA

HI_Shet_TPrA (t)  = HI_Shet_TPrA (t-dt) + (HI_Shet_PrA) * dt
HI_Lhet_TPrA (t)  = HI_Lhet_TPrA (t-dt) + (HI_Lhet_PrA) * dt
HI_het_TPrA = HI_Shet_TPrA + HI_Lhet_TPrA
HI_luc_TPrA (t)  = HI_luc_TPrA (t-dt) + (HI_luc_PrA) * dt
HI_maj_TPrA (t)  = HI_maj_TPrA (t-dt) + (HI_maj_PrA) * dt
HI_men_TPrA (t)  = HI_men_TPrA (t-dt) + (HI_men_PrA) * dt
HI_bai_TPrA (t)  = HI_bai_TPrA (t-dt) + (HI_bai_PrA) * dt
HI_Scal_TPrA (t)  = HI_Scal_TPrA (t-dt) + (HI_Scal_PrA) * dt
HI_Lcal_TPrA (t)  = HI_Lcal_TPrA (t-dt) + (HI_Lcal_PrA) * dt
HI_PAL_TPrA (t)  = HI_PAL_TPrA (t-dt) + (HI_PAL_PrA) * dt
HI_cal_TPrA = HI_Lcal_TPrA + HI_Scal_TPrA
HI_fish_TPrA =  HI_Shet_TPrA + HI_luc_TPrA + HI_bai_TPrA + HI_men_TPrA + HI_Lhet_TPrA + HI_maj_TPrA

HV_Shet_TPrA (t)  = HV_Shet_TPrA (t-dt) + (HV_Shet_PrA) * dt
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LD_FLT_TPrA (t)  = LD_FLT_TPrA (t-dt) + (LD_FLT_PrA) * dt
LD_gbo_TPrA (t)  = LD_gbo_TPrA (t-dt) + (LD_gbo_PrA) * dt
LD_str_TPrA (t)  = LD_str_TPrA (t-dt) + (LD_str_PrA) * dt
LD_Shet_TPrA (t)  = LD_Shet_TPrA (t-dt) + (LD_Shet_PrA) * dt
LD_Lhet_TPrA (t)  = LD_Lhet_TPrA (t-dt) + (LD_Lhet_PrA) * dt
LD_het_TPrA = LD_Shet_TPrA + LD_Lhet_TPrA
LD_luc_TPrA (t)  = LD_luc_TPrA (t-dt) + (LD_luc_PrA) * dt
LD_maj_TPrA (t)  = LD_maj_TPrA (t-dt) + (LD_maj_PrA) * dt
LD_men_TPrA (t)  = LD_men_TPrA (t-dt) + (LD_men_PrA) * dt
LD_soc_TPrA (t)  = LD_soc_TPrA (t-dt) + (LD_soc_PrA) * dt
LD_Scal_TPrA (t)  = LD_Scal_TPrA (t-dt) + (LD_Scal_PrA) * dt
LD_Lcal_TPrA (t)  = LD_Lcal_TPrA (t-dt) + (LD_Lcal_PrA) * dt
LD_PAL_TPrA (t)  = LD_PAL_TPrA (t-dt) + (LD_PAL_PrA) * dt
LD_cal_TPrA = LD_Lcal_TPrA + LD_Scal_TPrA
LD_fish_TPrA = LD_FLT_TPrA + LD_gbo_TPrA + LD_Shet_TPrA + LD_luc_TPrA + LD_men_TPrA +
    LD_soc_TPrA + LD_str_TPrA + LD_Lhet_TPrA + LD_maj_TPrA

LS_gbo_TPrA (t)  = LS_gbo_TPrA (t-dt) + (LS_gbo_PrA) * dt
LS_str_TPrA (t)  = LS_str_TPrA (t-dt) + (LS_str_PrA) * dt
LS_Shet_TPrA (t)  = LS_Shet_TPrA (t-dt) + (LS_Shet_PrA) * dt
LS_Lhet_TPrA (t)  = LS_Lhet_TPrA (t-dt) + (LS_Lhet_PrA) * dt
LS_het_TPrA = LS_Shet_TPrA + LS_Lhet_TPrA
LS_luc_TPrA (t)  = LS_luc_TPrA (t-dt) + (LS_luc_PrA) * dt
LS_maj_TPrA (t)  = LS_maj_TPrA (t-dt) + (LS_maj_PrA) * dt
LS_men_TPrA (t)  = LS_men_TPrA (t-dt) + (LS_men_PrA) * dt
LS_Scal_TPrA (t)  = LS_Scal_TPrA (t-dt) + (LS_Scal_PrA) * dt
LS_Lcal_TPrA (t)  = LS_Lcal_TPrA (t-dt) + (LS_Lcal_PrA) * dt
LS_PAL_TPrA (t)  = LS_PAL_TPrA (t-dt) + (LS_PAL_PrA) * dt
LS_cal_TPrA = LS_Lcal_TPrA + LS_Scal_TPrA
LS_fish_TPrA = LS_gbo_TPrA + LS_Shet_TPrA + LS_luc_TPrA + LS_men_TPrA + LS_str_TPrA +
    LS_Lhet_TPrA + LS_maj_TPrA

LV_Shet_TPrA (t)  = LV_Shet_TPrA (t-dt) + (LV_Shet_PrA) * dt

UF_FLT_TPrA  = HU_FLT_TPrA + LD_FLT_TPrA
UF_gbo_TPrA  = HU_gbo_TPrA + LD_gbo_TPrA+ LS_gbo_TPrA
UF_maj_TPrA  = LD_maj_TPrA+ LS_maj_TPrA
UF_het_TPrA  = HU_Shet_TPrA + LD_het_TPrA+ LS_het_TPrA
UF_luc_TPrA  = HU_luc_TPrA+ LD_luc_TPrA+ LS_luc_TPrA
UF_men_TPrA  = HU_men_TPrA + LD_men_TPrA + LS_men_TPrA
UF_lei_TPrA  = HU_lei_TPrA
UF_Scal_TPrA  = HU_Scal_TPrA + LD_Scal_TPrA + LS_Scal_TPrA
UF_Lcal_TPrA  = HU_Scal_TPrA + LD_Scal_TPrA + LS_Scal_TPrA
UF_PAL_TPrA  = HU_PAL_TPrA + LD_PAL_TPrA + LS_PAL_TPrA
UF_cal_TPrA = HU_Lcal_TPrA + HU_Scal_TPrA+ LD_Scal_TPrA + LD_Lcal_TPrA + LS_Scal_TPrA +
    LS_Lcal_TPrA
UF_fish_TPrA = HU_fish_TPrA + LD_fish_TPrA + LS_fish_TPrA

INIT HU_FLT_TPrA = 0
INIT HU_gbo_TPrA = 0
INIT HU_Shet_TPrA = 0
INIT HU_luc_TPrA = 0
INIT HU_men_TPrA = 0
INIT HU_lei_TPrA = 0
INIT HU_Scal_TPrA = 0
INIT HU_Lcal_TPrA = 0
INIT HU_PAL_TPrA = 0
INIT HE_FLT_TPrA = 0
INIT HE_gbo_TPrA = 0
INIT HE_str_TPrA = 0
INIT HE_Shet_TPrA = 0
INIT HE_Lhet_TPrA = 0
INIT HE_luc_TPrA = 0
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INIT HE_maj_TPrA = 0
INIT HE_men_TPrA = 0
INIT HE_bai_TPrA = 0
INIT HE_cyn_TPrA = 0
INIT HE_lei_TPrA = 0
INIT HE_Scal_TPrA = 0
INIT HE_Lcal_TPrA = 0
INIT HE_PAL_TPrA = 0
INIT HF_Shet_TPrA = 0
INIT HF_Lhet_TPrA = 0
INIT HF_luc_TPrA = 0
INIT HF_maj_TPrA = 0
INIT HF_men_TPrA = 0
INIT HF_Scal_TPrA = 0
INIT HF_Lcal_TPrA = 0
INIT HF_PAL_TPrA = 0
INIT HI_Shet_TPrA = 0
INIT HI_Lhet_TPrA = 0
INIT HI_luc_TPrA = 0
INIT HI_maj_TPrA = 0
INIT HI_men_TPrA = 0
INIT HI_bai_TPrA = 0
INIT HI_Scal_TPrA = 0
INIT HI_Lcal_TPrA = 0
INIT HI_PAL_TPrA = 0
INIT HV_Shet_TPrA = 0
INIT LD_FLT_TPrA = 0
INIT LD_gbo_TPrA = 0
INIT LD_str_TPrA = 0
INIT LD_Shet_TPrA = 0
INIT LD_Lhet_TPrA = 0
INIT LD_luc_TPrA = 0
INIT LD_maj_TPrA = 0
INIT LD_men_TPrA = 0
INIT LD_soc_TPrA = 0
INIT LD_Scal_TPrA = 0
INIT LD_Lcal_TPrA = 0
INIT LD_PAL_TPrA = 0
INIT LS_gbo_TPrA = 0
INIT LS_str_TPrA = 0
INIT LS_Shet_TPrA = 0
INIT LS_Lhet_TPrA = 0
INIT LS_luc_TPrA = 0
INIT LS_maj_TPrA = 0
INIT LS_men_TPrA = 0
INIT LS_Scal_TPrA = 0
INIT LS_Lcal_TPrA = 0
INIT LS_PAL_TPrA = 0
INIT LV_Shet_TPrA = 0

HU_FLT_TPrB (t) = HU_FLT_TPrB (t-dt) + (HU_FLT_PrB) * dt
HU_gbo_TPrB (t) = HU_gbo_TPrB (t-dt) + (HU_gbo_PrB) * dt
HU_Shet_TPrB (t) = HU_Shet_TPrB (t-dt) + (HU_Shet_PrB) * dt
HU_luc_TPrB (t) = HU_luc_TPrB (t-dt) + (HU_luc_PrB) * dt
HU_men_TPrB (t) = HU_men_TPrB (t-dt) + (HU_men_PrB) * dt
HU_lei_TPrB (t) = HU_lei_TPrB (t-dt) + (HU_lei_PrB) * dt
HU_Scal_TPrB (t) = HU_Scal_TPrB (t-dt) + (HU_Scal_PrB) * dt
HU_Lcal_TPrB (t) = HU_Lcal_TPrB (t-dt) + (HU_Lcal_PrB) * dt
HU_PAL_TPrB (t) = HU_PAL_TPrB (t-dt) + (HU_PAL_PrB) * dt
HU_cal_TPrB = HU_Lcal_TPrB + HU_Scal_TPrB
HU_fish_TPrB = HU_FLT_TPrB + HU_gbo_TPrB + HU_Shet_TPrB + HU_luc_TPrB + HU_men_TPrB +
    HU_lei_TPrB

UF_FLT_TPrB = HU_FLT_TPrB + LD_FLT_TPrB
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UF_gbo_TPrB  = HU_gbo_TPrB + LD_gbo_TPrB+ LS_gbo_TPrB
UF_maj_TPrB  = LD_maj_TPrB+ LS_maj_TPrB
UF_het_TPrB  = HU_Shet_TPrB + LD_het_TPrB+ LS_het_TPrB
UF_luc_TPrB  = HU_luc_TPrB+ LD_luc_TPrB+ LS_luc_TPrB
UF_men_TPrB  = HU_men_TPrB + LD_men_TPrB + LS_men_TPrB
UF_lei_TPrB  = HU_lei_TPrB
UF_Scal_TPrB  = HU_Scal_TPrB + LD_Scal_TPrB + LS_Scal_TPrB
UF_Lcal_TPrB  = HU_Scal_TPrB + LD_Scal_TPrB + LS_Scal_TPrB
UF_PAL_TPrB  = HU_PAL_TPrB + LD_PAL_TPrB + LS_PAL_TPrB
UF_cal_TPrB = HU_Lcal_TPrB + HU_Scal_TPrB+ LD_Scal_TPrB + LD_Lcal_TPrB + LS_Scal_TPrB + LS_Lcal_TPrB
UF_fish_TPrB = HU_fish_TPrB + LD_fish_TPrB + LS_fish_TPrB


HE_FLT_TPrB (t)  = HE_FLT_TPrB (t-dt) + (HE_FLT_PrB) * dt
HE_gbo_TPrB (t)  = HE_gbo_TPrB (t-dt) + (HE_gbo_PrB) * dt
HE_str_TPrB (t)  = HE_str_TPrB (t-dt) + (HE_str_PrB) * dt
HE_Shet_TPrB (t)  = HE_Shet_TPrB (t-dt) + (HE_Shet_PrB) * dt
HE_Lhet_TPrB (t)  = HE_Lhet_TPrB (t-dt) + (HE_Lhet_PrB) * dt
HE_het_TPrB = HE_Shet_TPrB + HE_Lhet_TPrB
HE_luc_TPrB (t)  = HE_luc_TPrB (t-dt) + (HE_luc_PrB) * dt
HE_maj_TPrB (t)  = HE_maj_TPrB (t-dt) + (HE_maj_PrB) * dt
HE_men_TPrB (t)  = HE_men_TPrB (t-dt) + (HE_men_PrB) * dt
HE_bai_TPrB (t)  = HE_bai_TPrB (t-dt) + (HE_bai_PrB) * dt
HE_cyn_TPrB (t)  = HE_cyn_TPrB (t-dt) + (HE_cyn_PrB) * dt
HE_lei_TPrB (t)  = HE_lei_TPrB (t-dt) + (HE_lei_PrB) * dt
HE_Scal_TPrB (t)  = HE_Scal_TPrB (t-dt) + (HE_Scal_PrB) * dt
HE_Lcal_TPrB (t)  = HE_Lcal_TPrB (t-dt) + (HE_Lcal_PrB) * dt
HE_PAL_TPrB (t)  = HE_PAL_TPrB (t-dt) + (HE_PAL_PrB) * dt
HE_cal_TPrB = HE_Lcal_TPrB + HE_Scal_TPrB
HE_SCI_TPrB = HE_cyn_TPrB + HE_bai_TPrB  + HE_lei_TPrB
HE_fish_TPrB = HE_FLT_TPrB + HE_gbo_TPrB + HE_Shet_TPrB + HE_luc_TPrB + HE_men_TPrB +
    HE_SCI_TPrB + HE_str_TPrB + HE_Lhet_TPrB + HE_maj_TPrB

HF_Shet_TPrB (t)  = HF_Shet_TPrB (t-dt) + (HF_Shet_PrB) * dt
HF_Lhet_TPrB (t)  = HF_Lhet_TPrB (t-dt) + (HF_Lhet_PrB) * dt
HF_het_TPrB = HF_Shet_TPrB + HF_Lhet_TPrB
HF_luc_TPrB (t)  = HF_luc_TPrB (t-dt) + (HF_luc_PrB) * dt
HF_maj_TPrB (t)  = HF_maj_TPrB (t-dt) + (HF_maj_PrB) * dt
HF_men_TPrB (t)  = HF_men_TPrB (t-dt) + (HF_men_PrB) * dt
HF_Scal_TPrB (t)  = HF_Scal_TPrB (t-dt) + (HF_Scal_PrB) * dt
HF_Lcal_TPrB (t)  = HF_Lcal_TPrB (t-dt) + (HF_Lcal_PrB) * dt
HF_PAL_TPrB (t)  = HF_PAL_TPrB (t-dt) + (HF_PAL_PrB) * dt
HF_cal_TPrB = HF_Lcal_TPrB + HF_Scal_TPrB
HF_fish_TPrB =  HF_Shet_TPrB + HF_luc_TPrB + HF_men_TPrB  + HF_Lhet_TPrB + HF_maj_TPrB

HI_Shet_TPrB (t)  = HI_Shet_TPrB (t-dt) + (HI_Shet_PrB) * dt
HI_Lhet_TPrB (t)  = HI_Lhet_TPrB (t-dt) + (HI_Lhet_PrB) * dt
HI_het_TPrB = HI_Shet_TPrB + HI_Lhet_TPrB
HI_luc_TPrB (t)  = HI_luc_TPrB (t-dt) + (HI_luc_PrB) * dt
HI_maj_TPrB (t)  = HI_maj_TPrB (t-dt) + (HI_maj_PrB) * dt
HI_men_TPrB (t)  = HI_men_TPrB (t-dt) + (HI_men_PrB) * dt
HI_bai_TPrB (t)  = HI_bai_TPrB (t-dt) + (HI_bai_PrB) * dt
HI_Scal_TPrB (t)  = HI_Scal_TPrB (t-dt) + (HI_Scal_PrB) * dt
HI_Lcal_TPrB (t)  = HI_Lcal_TPrB (t-dt) + (HI_Lcal_PrB) * dt
HI_PAL_TPrB (t)  = HI_PAL_TPrB (t-dt) + (HI_PAL_PrB) * dt
HI_cal_TPrB = HI_Lcal_TPrB + HI_Scal_TPrB
HI_fish_TPrB =  HI_Shet_TPrB + HI_luc_TPrB + HI_bai_TPrB + HI_men_TPrB + HI_Lhet_TPrB + HI_maj_TPrB

HV_Shet_TPrB (t)  = HV_Shet_TPrB (t-dt) + (HV_Shet_PrB) * dt

LD_FLT_TPrB (t)  = LD_FLT_TPrB (t-dt) + (LD_FLT_PrB) * dt
LD_gbo_TPrB (t)  = LD_gbo_TPrB (t-dt) + (LD_gbo_PrB) * dt
LD_str_TPrB (t)  = LD_str_TPrB (t-dt) + (LD_str_PrB) * dt
LD_Shet_TPrB (t)  = LD_Shet_TPrB (t-dt) + (LD_Shet_PrB) * dt
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LD_Lhet_TPrB (t)  = LD_Lhet_TPrB (t-dt) + (LD_Lhet_PrB) * dt
LD_het_TPrB = LD_Shet_TPrB + LD_Lhet_TPrB
LD_luc_TPrB (t)  = LD_luc_TPrB (t-dt) + (LD_luc_PrB) * dt
LD_maj_TPrB (t)  = LD_maj_TPrB (t-dt) + (LD_maj_PrB) * dt
LD_men_TPrB (t)  = LD_men_TPrB (t-dt) + (LD_men_PrB) * dt
LD_soc_TPrB (t)  = LD_soc_TPrB (t-dt) + (LD_soc_PrB) * dt
LD_Scal_TPrB (t)  = LD_Scal_TPrB (t-dt) + (LD_Scal_PrB) * dt
LD_Lcal_TPrB (t)  = LD_Lcal_TPrB (t-dt) + (LD_Lcal_PrB) * dt
LD_PAL_TPrB (t)  = LD_PAL_TPrB (t-dt) + (LD_PAL_PrB) * dt
LD_cal_TPrB = LD_Lcal_TPrB + LD_Scal_TPrB
LD_fish_TPrB = LD_FLT_TPrB + LD_gbo_TPrB + LD_Shet_TPrB + LD_luc_TPrB + LD_men_TPrB +
    LD_soc_TPrB + LD_str_TPrB + LD_Lhet_TPrB + LD_maj_TPrB

LS_gbo_TPrB (t)  = LS_gbo_TPrB (t-dt) + (LS_gbo_PrB) * dt
LS_str_TPrB (t)  = LS_str_TPrB (t-dt) + (LS_str_PrB) * dt
LS_Shet_TPrB (t)  = LS_Shet_TPrB (t-dt) + (LS_Shet_PrB) * dt
LS_Lhet_TPrB (t)  = LS_Lhet_TPrB (t-dt) + (LS_Lhet_PrB) * dt
LS_het_TPrB = LS_Shet_TPrB + LS_Lhet_TPrB
LS_luc_TPrB (t)  = LS_luc_TPrB (t-dt) + (LS_luc_PrB) * dt
LS_maj_TPrB (t)  = LS_maj_TPrB (t-dt) + (LS_maj_PrB) * dt
LS_men_TPrB (t)  = LS_men_TPrB (t-dt) + (LS_men_PrB) * dt
LS_Scal_TPrB (t)  = LS_Scal_TPrB (t-dt) + (LS_Scal_PrB) * dt
LS_Lcal_TPrB (t)  = LS_Lcal_TPrB (t-dt) + (LS_Lcal_PrB) * dt
LS_PAL_TPrB (t)  = LS_PAL_TPrB (t-dt) + (LS_PAL_PrB) * dt
LS_cal_TPrB = LS_Lcal_TPrB + LS_Scal_TPrB
LS_fish_TPrB = LS_gbo_TPrB + LS_Shet_TPrB + LS_luc_TPrB + LS_men_TPrB + LS_str_TPrB +
    LS_Lhet_TPrB + LS_maj_TPrB

LV_Shet_TPrB (t)  = LV_Shet_TPrB (t-dt) + (LV_Shet_PrB) * dt

INIT HU_FLT_TPrB = 0
INIT HU_gbo_TPrB = 0
INIT HU_Shet_TPrB = 0
INIT HU_luc_TPrB = 0
INIT HU_men_TPrB = 0
INIT HU_lei_TPrB = 0
INIT HU_Scal_TPrB = 0
INIT HU_Lcal_TPrB = 0
INIT HU_PAL_TPrB = 0
INIT HE_FLT_TPrB = 0
INIT HE_gbo_TPrB = 0
INIT HE_str_TPrB = 0
INIT HE_Shet_TPrB = 0
INIT HE_Lhet_TPrB = 0
INIT HE_luc_TPrB = 0
INIT HE_maj_TPrB = 0
INIT HE_men_TPrB = 0
INIT HE_bai_TPrB = 0
INIT HE_cyn_TPrB = 0
INIT HE_lei_TPrB = 0
INIT HE_Scal_TPrB = 0
INIT HE_Lcal_TPrB = 0
INIT HE_PAL_TPrB = 0
INIT HF_Shet_TPrB = 0
INIT HF_Lhet_TPrB = 0
INIT HF_luc_TPrB = 0
INIT HF_maj_TPrB = 0
INIT HF_men_TPrB = 0
INIT HF_Scal_TPrB = 0
INIT HF_Lcal_TPrB = 0
INIT HF_PAL_TPrB = 0
INIT HI_Shet_TPrB = 0
INIT HI_Lhet_TPrB = 0
INIT HI_luc_TPrB = 0
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INIT HI_maj_TPrB = 0
INIT HI_men_TPrB = 0
INIT HI_bai_TPrB = 0
INIT HI_Scal_TPrB = 0
INIT HI_Lcal_TPrB = 0
INIT HI_PAL_TPrB = 0
INIT HV_Shet_TPrB = 0
INIT LD_FLT_TPrB = 0
INIT LD_gbo_TPrB = 0
INIT LD_str_TPrB = 0
INIT LD_Shet_TPrB = 0
INIT LD_Lhet_TPrB = 0
INIT LD_luc_TPrB = 0
INIT LD_maj_TPrB = 0
INIT LD_men_TPrB = 0
INIT LD_soc_TPrB = 0
INIT LD_Scal_TPrB = 0
INIT LD_Lcal_TPrB = 0
INIT LD_PAL_TPrB = 0
INIT LS_gbo_TPrB = 0
INIT LS_str_TPrB = 0
INIT LS_Shet_TPrB = 0
INIT LS_Lhet_TPrB = 0
INIT LS_luc_TPrB = 0
INIT LS_maj_TPrB = 0
INIT LS_men_TPrB = 0
INIT LS_Scal_TPrB = 0
INIT LS_Lcal_TPrB = 0
INIT LS_PAL_TPrB = 0
INIT LV_Shet_TPrB = 0

HU_FLT_TPrC (t) = HU_FLT_TPrC (t-dt) + (HU_FLT_PrC) * dt
HU_gbo_TPrC (t) = HU_gbo_TPrC (t-dt) + (HU_gbo_PrC) * dt
HU_Shet_TPrC (t) = HU_Shet_TPrC (t-dt) + (HU_Shet_PrC) * dt
HU_luc_TPrC (t) = HU_luc_TPrC (t-dt) + (HU_luc_PrC) * dt
HU_men_TPrC (t) = HU_men_TPrC (t-dt) + (HU_men_PrC) * dt
HU_lei_TPrC (t) = HU_lei_TPrC (t-dt) + (HU_lei_PrC) * dt
HU_Scal_TPrC (t) = HU_Scal_TPrC (t-dt) + (HU_Scal_PrC) * dt
HU_Lcal_TPrC (t) = HU_Lcal_TPrC (t-dt) + (HU_Lcal_PrC) * dt
HU_PAL_TPrC (t) = HU_PAL_TPrC (t-dt) + (HU_PAL_PrC) * dt
HU_cal_TPrC = HU_Lcal_TPrC + HU_Scal_TPrC
HU_fish_TPrC = HU_FLT_TPrC + HU_gbo_TPrC + HU_Shet_TPrC + HU_luc_TPrC + HU_men_TPrC +
    HU_lei_TPrC

HE_FLT_TPrC (t) = HE_FLT_TPrC (t-dt) + (HE_FLT_PrC) * dt
HE_gbo_TPrC (t) = HE_gbo_TPrC (t-dt) + (HE_gbo_PrC) * dt
HE_str_TPrC (t) = HE_str_TPrC (t-dt) + (HE_str_PrC) * dt
HE_Shet_TPrC (t) = HE_Shet_TPrC (t-dt) + (HE_Shet_PrC) * dt
HE_Lhet_TPrC (t) = HE_Lhet_TPrC (t-dt) + (HE_Lhet_PrC) * dt
HE_het_TPrC = HE_Shet_TPrC + HE_Lhet_TPrC
HE_luc_TPrC (t) = HE_luc_TPrC (t-dt) + (HE_luc_PrC) * dt
HE_maj_TPrC (t) = HE_maj_TPrC (t-dt) + (HE_maj_PrC) * dt
HE_men_TPrC (t) = HE_men_TPrC (t-dt) + (HE_men_PrC) * dt
HE_bai_TPrC (t) = HE_bai_TPrC (t-dt) + (HE_bai_PrC) * dt
HE_cyn_TPrC (t) = HE_cyn_TPrC (t-dt) + (HE_cyn_PrC) * dt
HE_lei_TPrC (t) = HE_lei_TPrC (t-dt) + (HE_lei_PrC) * dt
HE_Scal_TPrC (t) = HE_Scal_TPrC (t-dt) + (HE_Scal_PrC) * dt
HE_Lcal_TPrC (t) = HE_Lcal_TPrC (t-dt) + (HE_Lcal_PrC) * dt
HE_PAL_TPrC (t) = HE_PAL_TPrC (t-dt) + (HE_PAL_PrC) * dt
HE_cal_TPrC = HE_Lcal_TPrC + HE_Scal_TPrC
HE_SCI_TPrC = HE_cyn_TPrC + HE_bai_TPrC + HE_lei_TPrC
HE_fish_TPrC = HE_FLT_TPrC + HE_gbo_TPrC + HE_Shet_TPrC + HE_luc_TPrC + HE_men_TPrC +
    HE_SCI_TPrC + HE_str_TPrC + HE_Lhet_TPrC + HE_maj_TPrC
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HF_Shet_TPrC (t)  = HF_Shet_TPrC (t-dt) + (HF_Shet_PrC) * dt
HF_Lhet_TPrC (t)  = HF_Lhet_TPrC (t-dt) + (HF_Lhet_PrC) * dt
HF_het_TPrC = HF_Shet_TPrC + HF_Lhet_TPrC
HF_luc_TPrC (t)  = HF_luc_TPrC (t-dt) + (HF_luc_PrC) * dt
HF_maj_TPrC (t)  = HF_maj_TPrC (t-dt) + (HF_maj_PrC) * dt
HF_men_TPrC (t)  = HF_men_TPrC (t-dt) + (HF_men_PrC) * dt
HF_Scal_TPrC (t)  = HF_Scal_TPrC (t-dt) + (HF_Scal_PrC) * dt
HF_Lcal_TPrC (t)  = HF_Lcal_TPrC (t-dt) + (HF_Lcal_PrC) * dt
HF_PAL_TPrC (t)  = HF_PAL_TPrC (t-dt) + (HF_PAL_PrC) * dt
HF_cal_TPrC = HF_Lcal_TPrC + HF_Scal_TPrC
HF_fish_TPrC =  HF_Shet_TPrC + HF_luc_TPrC + HF_men_TPrC  + HF_Lhet_TPrC + HF_maj_TPrC

HI_Shet_TPrC (t)  = HI_Shet_TPrC (t-dt) + (HI_Shet_PrC) * dt
HI_Lhet_TPrC (t)  = HI_Lhet_TPrC (t-dt) + (HI_Lhet_PrC) * dt
HI_het_TPrC = HI_Shet_TPrC + HI_Lhet_TPrC
HI_luc_TPrC (t)  = HI_luc_TPrC (t-dt) + (HI_luc_PrC) * dt
HI_maj_TPrC (t)  = HI_maj_TPrC (t-dt) + (HI_maj_PrC) * dt
HI_men_TPrC (t)  = HI_men_TPrC (t-dt) + (HI_men_PrC) * dt
HI_bai_TPrC (t)  = HI_bai_TPrC (t-dt) + (HI_bai_PrC) * dt
HI_Scal_TPrC (t)  = HI_Scal_TPrC (t-dt) + (HI_Scal_PrC) * dt
HI_Lcal_TPrC (t)  = HI_Lcal_TPrC (t-dt) + (HI_Lcal_PrC) * dt
HI_PAL_TPrC (t)  = HI_PAL_TPrC (t-dt) + (HI_PAL_PrC) * dt
HI_cal_TPrC = HI_Lcal_TPrC + HI_Scal_TPrC
HI_fish_TPrC =  HI_Shet_TPrC + HI_luc_TPrC + HI_bai_TPrC + HI_men_TPrC + HI_Lhet_TPrC + HI_maj_TPrC

HV_Shet_TPrC (t)  = HV_Shet_TPrC (t-dt) + (HV_Shet_PrC) * dt

LD_FLT_TPrC (t)  = LD_FLT_TPrC (t-dt) + (LD_FLT_PrC) * dt
LD_gbo_TPrC (t)  = LD_gbo_TPrC (t-dt) + (LD_gbo_PrC) * dt
LD_str_TPrC (t)  = LD_str_TPrC (t-dt) + (LD_str_PrC) * dt
LD_Shet_TPrC (t)  = LD_Shet_TPrC (t-dt) + (LD_Shet_PrC) * dt
LD_Lhet_TPrC (t)  = LD_Lhet_TPrC (t-dt) + (LD_Lhet_PrC) * dt
LD_het_TPrC = LD_Shet_TPrC + LD_Lhet_TPrC
LD_luc_TPrC (t)  = LD_luc_TPrC (t-dt) + (LD_luc_PrC) * dt
LD_maj_TPrC (t)  = LD_maj_TPrC (t-dt) + (LD_maj_PrC) * dt
LD_men_TPrC (t)  = LD_men_TPrC (t-dt) + (LD_men_PrC) * dt
LD_soc_TPrC (t)  = LD_soc_TPrC (t-dt) + (LD_soc_PrC) * dt
LD_Scal_TPrC (t)  = LD_Scal_TPrC (t-dt) + (LD_Scal_PrC) * dt
LD_Lcal_TPrC (t)  = LD_Lcal_TPrC (t-dt) + (LD_Lcal_PrC) * dt
LD_PAL_TPrC (t)  = LD_PAL_TPrC (t-dt) + (LD_PAL_PrC) * dt
LD_cal_TPrC = LD_Lcal_TPrC + LD_Scal_TPrC
LD_fish_TPrC = LD_FLT_TPrC + LD_gbo_TPrC + LD_Shet_TPrC + LD_luc_TPrC + LD_men_TPrC +
    LD_soc_TPrC + LD_str_TPrC + LD_Lhet_TPrC + LD_maj_TPrC

LS_gbo_TPrC (t)  = LS_gbo_TPrC (t-dt) + (LS_gbo_PrC) * dt
LS_str_TPrC (t)  = LS_str_TPrC (t-dt) + (LS_str_PrC) * dt
LS_Shet_TPrC (t)  = LS_Shet_TPrC (t-dt) + (LS_Shet_PrC) * dt
LS_Lhet_TPrC (t)  = LS_Lhet_TPrC (t-dt) + (LS_Lhet_PrC) * dt
LS_het_TPrC = LS_Shet_TPrC + LS_Lhet_TPrC
LS_luc_TPrC (t)  = LS_luc_TPrC (t-dt) + (LS_luc_PrC) * dt
LS_maj_TPrC (t)  = LS_maj_TPrC (t-dt) + (LS_maj_PrC) * dt
LS_men_TPrC (t)  = LS_men_TPrC (t-dt) + (LS_men_PrC) * dt
LS_Scal_TPrC (t)  = LS_Scal_TPrC (t-dt) + (LS_Scal_PrC) * dt
LS_Lcal_TPrC (t)  = LS_Lcal_TPrC (t-dt) + (LS_Lcal_PrC) * dt
LS_PAL_TPrC (t)  = LS_PAL_TPrC (t-dt) + (LS_PAL_PrC) * dt
LS_cal_TPrC = LS_Lcal_TPrC + LS_Scal_TPrC
LS_fish_TPrC = LS_gbo_TPrC + LS_Shet_TPrC + LS_luc_TPrC + LS_men_TPrC + LS_str_TPrC +
    LS_Lhet_TPrC + LS_maj_TPrC

LV_Shet_TPrC (t)  = LV_Shet_TPrC (t-dt) + (LV_Shet_PrC) * dt

INIT HU_FLT_TPrC = 0
INIT HU_gbo_TPrC = 0
INIT HU_Shet_TPrC = 0
```

```
INIT HU_luc_TPrC = 0
INIT HU_men_TPrC = 0
INIT HU_lei_TPrC = 0
INIT HU_Scal_TPrC = 0
INIT HU_Lcal_TPrC = 0
INIT HU_PAL_TPrC = 0
INIT HE_FLT_TPrC = 0
INIT HE_gbo_TPrC = 0
INIT HE_str_TPrC = 0
INIT HE_Shet_TPrC = 0
INIT HE_Lhet_TPrC = 0
INIT HE_luc_TPrC = 0
INIT HE_maj_TPrC = 0
INIT HE_men_TPrC = 0
INIT HE_bai_TPrC = 0
INIT HE_cyn_TPrC = 0
INIT HE_lei_TPrC = 0
INIT HE_Scal_TPrC = 0
INIT HE_Lcal_TPrC = 0
INIT HE_PAL_TPrC = 0
INIT HF_Shet_TPrC = 0
INIT HF_Lhet_TPrC = 0
INIT HF_luc_TPrC = 0
INIT HF_maj_TPrC = 0
INIT HF_men_TPrC = 0
INIT HF_Scal_TPrC = 0
INIT HF_Lcal_TPrC = 0
INIT HF_PAL_TPrC = 0
INIT HI_Shet_TPrC = 0
INIT HI_Lhet_TPrC = 0
INIT HI_luc_TPrC = 0
INIT HI_maj_TPrC = 0
INIT HI_men_TPrC = 0
INIT HI_bai_TPrC = 0
INIT HI_Scal_TPrC = 0
INIT HI_Lcal_TPrC = 0
INIT HI_PAL_TPrC = 0
INIT HV_Shet_TPrC = 0
INIT LD_FLT_TPrC = 0
INIT LD_gbo_TPrC = 0
INIT LD_str_TPrC = 0
INIT LD_Shet_TPrC = 0
INIT LD_Lhet_TPrC = 0
INIT LD_luc_TPrC = 0
INIT LD_maj_TPrC = 0
INIT LD_men_TPrC = 0
INIT LD_soc_TPrC = 0
INIT LD_Scal_TPrC = 0
INIT LD_Lcal_TPrC = 0
INIT LD_PAL_TPrC = 0
INIT LS_gbo_TPrC = 0
INIT LS_str_TPrC = 0
INIT LS_Shet_TPrC = 0
INIT LS_Lhet_TPrC = 0
INIT LS_luc_TPrC = 0
INIT LS_maj_TPrC = 0
INIT LS_men_TPrC = 0
INIT LS_Scal_TPrC = 0
INIT LS_Lcal_TPrC = 0
INIT LS_PAL_TPrC = 0
INIT LV_Shet_TPrC = 0

HU_FLT_TPrD (t) = HU_FLT_TPrD (t-dt) + (HU_FLT_PrD) * dt
HU_gbo_TPrD (t) = HU_gbo_TPrD (t-dt) + (HU_gbo_PrD) * dt
```

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HU_Shet_TPrD (t)  = HU_Shet_TPrD (t-dt) + (HU_Shet_PrD) * dt
HU_luc_TPrD (t)  = HU_luc_TPrD (t-dt) + (HU_luc_PrD) * dt
HU_men_TPrD (t)  = HU_men_TPrD (t-dt) + (HU_men_PrD) * dt
HU_lei_TPrD (t)  = HU_lei_TPrD (t-dt) + (HU_lei_PrD) * dt
HU_Scal_TPrD (t)  = HU_Scal_TPrD (t-dt) + (HU_Scal_PrD) * dt
HU_Lcal_TPrD (t)  = HU_Lcal_TPrD (t-dt) + (HU_Lcal_PrD) * dt
HU_PAL_TPrD (t)  = HU_PAL_TPrD (t-dt) + (HU_PAL_PrD) * dt
HU_cal_TPrD = HU_Lcal_TPrD + HU_Scal_TPrD
HU_fish_TPrD = HU_FLT_TPrD + HU_gbo_TPrD + HU_Shet_TPrD + HU_luc_TPrD + HU_men_TPrD +
    HU_lei_TPrD

HE_FLT_TPrD (t)  = HE_FLT_TPrD (t-dt) + (HE_FLT_PrD) * dt
HE_gbo_TPrD (t)  = HE_gbo_TPrD (t-dt) + (HE_gbo_PrD) * dt
HE_str_TPrD (t)  = HE_str_TPrD (t-dt) + (HE_str_PrD) * dt
HE_Shet_TPrD (t)  = HE_Shet_TPrD (t-dt) + (HE_Shet_PrD) * dt
HE_Lhet_TPrD (t)  = HE_Lhet_TPrD (t-dt) + (HE_Lhet_PrD) * dt
HE_het_TPrD = HE_Shet_TPrD + HE_Lhet_TPrD
HE_luc_TPrD (t)  = HE_luc_TPrD (t-dt) + (HE_luc_PrD) * dt
HE_maj_TPrD (t)  = HE_maj_TPrD (t-dt) + (HE_maj_PrD) * dt
HE_men_TPrD (t)  = HE_men_TPrD (t-dt) + (HE_men_PrD) * dt
HE_bai_TPrD (t)  = HE_bai_TPrD (t-dt) + (HE_bai_PrD) * dt
HE_cyn_TPrD (t)  = HE_cyn_TPrD (t-dt) + (HE_cyn_PrD) * dt
HE_lei_TPrD (t)  = HE_lei_TPrD (t-dt) + (HE_lei_PrD) * dt
HE_Scal_TPrD (t)  = HE_Scal_TPrD (t-dt) + (HE_Scal_PrD) * dt
HE_Lcal_TPrD (t)  = HE_Lcal_TPrD (t-dt) + (HE_Lcal_PrD) * dt
HE_PAL_TPrD (t)  = HE_PAL_TPrD (t-dt) + (HE_PAL_PrD) * dt
HE_cal_TPrD = HE_Lcal_TPrD + HE_Scal_TPrD
HE_SCI_TPrD = HE_cyn_TPrD + HE_bai_TPrD  + HE_lei_TPrD
HE_fish_TPrD = HE_FLT_TPrD + HE_gbo_TPrD + HE_Shet_TPrD + HE_luc_TPrD + HE_men_TPrD +
    HE_SCI_TPrD + HE_str_TPrD + HE_Lhet_TPrD + HE_maj_TPrD

HF_Shet_TPrD (t)  = HF_Shet_TPrD (t-dt) + (HF_Shet_PrD) * dt
HF_Lhet_TPrD (t)  = HF_Lhet_TPrD (t-dt) + (HF_Lhet_PrD) * dt
HF_het_TPrD = HF_Shet_TPrD + HF_Lhet_TPrD
HF_luc_TPrD (t)  = HF_luc_TPrD (t-dt) + (HF_luc_PrD) * dt
HF_maj_TPrD (t)  = HF_maj_TPrD (t-dt) + (HF_maj_PrD) * dt
HF_men_TPrD (t)  = HF_men_TPrD (t-dt) + (HF_men_PrD) * dt
HF_Scal_TPrD (t)  = HF_Scal_TPrD (t-dt) + (HF_Scal_PrD) * dt
HF_Lcal_TPrD (t)  = HF_Lcal_TPrD (t-dt) + (HF_Lcal_PrD) * dt
HF_PAL_TPrD (t)  = HF_PAL_TPrD (t-dt) + (HF_PAL_PrD) * dt
HF_cal_TPrD = HF_Lcal_TPrD + HF_Scal_TPrD
HF_fish_TPrD =  HF_Shet_TPrD + HF_luc_TPrD + HF_men_TPrD  + HF_Lhet_TPrD + HF_maj_TPrD

HI_Shet_TPrD (t)  = HI_Shet_TPrD (t-dt) + (HI_Shet_PrD) * dt
HI_Lhet_TPrD (t)  = HI_Lhet_TPrD (t-dt) + (HI_Lhet_PrD) * dt
HI_het_TPrD = HI_Shet_TPrD + HI_Lhet_TPrD
HI_luc_TPrD (t)  = HI_luc_TPrD (t-dt) + (HI_luc_PrD) * dt
HI_maj_TPrD (t)  = HI_maj_TPrD (t-dt) + (HI_maj_PrD) * dt
HI_men_TPrD (t)  = HI_men_TPrD (t-dt) + (HI_men_PrD) * dt
HI_bai_TPrD (t)  = HI_bai_TPrD (t-dt) + (HI_bai_PrD) * dt
HI_Scal_TPrD (t)  = HI_Scal_TPrD (t-dt) + (HI_Scal_PrD) * dt
HI_Lcal_TPrD (t)  = HI_Lcal_TPrD (t-dt) + (HI_Lcal_PrD) * dt
HI_PAL_TPrD (t)  = HI_PAL_TPrD (t-dt) + (HI_PAL_PrD) * dt
HI_cal_TPrD = HI_Lcal_TPrD + HI_Scal_TPrD
HI_fish_TPrD =  HI_Shet_TPrD + HI_luc_TPrD + HI_bai_TPrD + HI_men_TPrD + HI_Lhet_TPrD + HI_maj_TPrD

HV_Shet_TPrD (t)  = HV_Shet_TPrD (t-dt) + (HV_Shet_PrD) * dt

LD_FLT_TPrD (t)  = LD_FLT_TPrD (t-dt) + (LD_FLT_PrD) * dt
LD_gbo_TPrD (t)  = LD_gbo_TPrD (t-dt) + (LD_gbo_PrD) * dt
LD_str_TPrD (t)  = LD_str_TPrD (t-dt) + (LD_str_PrD) * dt
LD_Shet_TPrD (t)  = LD_Shet_TPrD (t-dt) + (LD_Shet_PrD) * dt
LD_Lhet_TPrD (t)  = LD_Lhet_TPrD (t-dt) + (LD_Lhet_PrD) * dt
LD_het_TPrD = LD_Shet_TPrD + LD_Lhet_TPrD
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LD_luc_TPrD (t)  = LD_luc_TPrD (t-dt) + (LD_luc_PrD) * dt
LD_maj_TPrD (t)  = LD_maj_TPrD (t-dt) + (LD_maj_PrD) * dt
LD_men_TPrD (t)  = LD_men_TPrD (t-dt) + (LD_men_PrD) * dt
LD_soc_TPrD (t)  = LD_soc_TPrD (t-dt) + (LD_soc_PrD) * dt
LD_Scal_TPrD (t)  = LD_Scal_TPrD (t-dt) + (LD_Scal_PrD) * dt
LD_Lcal_TPrD (t)  = LD_Lcal_TPrD (t-dt) + (LD_Lcal_PrD) * dt
LD_PAL_TPrD (t)  = LD_PAL_TPrD (t-dt) + (LD_PAL_PrD) * dt
LD_cal_TPrD = LD_Lcal_TPrD + LD_Scal_TPrD
LD_fish_TPrD = LD_FLT_TPrD + LD_gbo_TPrD + LD_Shet_TPrD + LD_luc_TPrD + LD_men_TPrD +
    LD_soc_TPrD + LD_str_TPrD + LD_Lhet_TPrD + LD_maj_TPrD

LS_gbo_TPrD (t)  = LS_gbo_TPrD (t-dt) + (LS_gbo_PrD) * dt
LS_str_TPrD (t)  = LS_str_TPrD (t-dt) + (LS_str_PrD) * dt
LS_Shet_TPrD (t)  = LS_Shet_TPrD (t-dt) + (LS_Shet_PrD) * dt
LS_Lhet_TPrD (t)  = LS_Lhet_TPrD (t-dt) + (LS_Lhet_PrD) * dt
LS_het_TPrD = LS_Shet_TPrD + LS_Lhet_TPrD
LS_luc_TPrD (t)  = LS_luc_TPrD (t-dt) + (LS_luc_PrD) * dt
LS_maj_TPrD (t)  = LS_maj_TPrD (t-dt) + (LS_maj_PrD) * dt
LS_men_TPrD (t)  = LS_men_TPrD (t-dt) + (LS_men_PrD) * dt
LS_Scal_TPrD (t)  = LS_Scal_TPrD (t-dt) + (LS_Scal_PrD) * dt
LS_Lcal_TPrD (t)  = LS_Lcal_TPrD (t-dt) + (LS_Lcal_PrD) * dt
LS_PAL_TPrD (t)  = LS_PAL_TPrD (t-dt) + (LS_PAL_PrD) * dt
LS_cal_TPrD = LS_Lcal_TPrD + LS_Scal_TPrD
LS_fish_TPrD = LS_gbo_TPrD + LS_Shet_TPrD + LS_luc_TPrD + LS_men_TPrD + LS_str_TPrD +
    LS_Lhet_TPrD + LS_maj_TPrD

LV_Shet_TPrD (t)  = LV_Shet_TPrD (t-dt) + (LV_Shet_PrD) * dt

INIT HU_FLT_TPrD = 0
INIT HU_gbo_TPrD = 0
INIT HU_Shet_TPrD = 0
INIT HU_luc_TPrD = 0
INIT HU_men_TPrD = 0
INIT HU_lei_TPrD = 0
INIT HU_Scal_TPrD = 0
INIT HU_Lcal_TPrD = 0
INIT HU_PAL_TPrD = 0
INIT HE_FLT_TPrD = 0
INIT HE_gbo_TPrD = 0
INIT HE_str_TPrD = 0
INIT HE_Shet_TPrD = 0
INIT HE_Lhet_TPrD = 0
INIT HE_luc_TPrD = 0
INIT HE_maj_TPrD = 0
INIT HE_men_TPrD = 0
INIT HE_bai_TPrD = 0
INIT HE_cyn_TPrD = 0
INIT HE_lei_TPrD = 0
INIT HE_Scal_TPrD = 0
INIT HE_Lcal_TPrD = 0
INIT HE_PAL_TPrD = 0
INIT HF_Shet_TPrD = 0
INIT HF_Lhet_TPrD = 0
INIT HF_luc_TPrD = 0
INIT HF_maj_TPrD = 0
INIT HF_men_TPrD = 0
INIT HF_Scal_TPrD = 0
INIT HF_Lcal_TPrD = 0
INIT HF_PAL_TPrD = 0
INIT HI_Shet_TPrD = 0
INIT HI_Lhet_TPrD = 0
INIT HI_luc_TPrD = 0
INIT HI_maj_TPrD = 0
INIT HI_men_TPrD = 0
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INIT HI_bai_TPrD = 0
INIT HI_Scal_TPrD = 0
INIT HI_Lcal_TPrD = 0
INIT HI_PAL_TPrD = 0
INIT HV_Shet_TPrD = 0
INIT LD_FLT_TPrD = 0
INIT LD_gbo_TPrD = 0
INIT LD_str_TPrD = 0
INIT LD_Shet_TPrD = 0
INIT LD_Lhet_TPrD = 0
INIT LD_luc_TPrD = 0
INIT LD_maj_TPrD = 0
INIT LD_men_TPrD = 0
INIT LD_soc_TPrD = 0
INIT LD_Scal_TPrD = 0
INIT LD_Lcal_TPrD = 0
INIT LD_PAL_TPrD = 0
INIT LS_gbo_TPrD = 0
INIT LS_str_TPrD = 0
INIT LS_Shet_TPrD = 0
INIT LS_Lhet_TPrD = 0
INIT LS_luc_TPrD = 0
INIT LS_maj_TPrD = 0
INIT LS_men_TPrD = 0
INIT LS_Scal_TPrD = 0
INIT LS_Lcal_TPrD = 0
INIT LS_PAL_TPrD = 0
INIT LV_Shet_TPrD = 0

B_Calculations_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}

{B1 - FISH PREDATION}

HU_FLT_PrA = genDRtwCIg * HU_FLT_dw * FLT_HTd_pA * genQIO * (((5.00 * HU_FLT_dw + .000001) /
    (HU_FLT_no + .000001))^-0.2) * HU_SubTime * FLT_HDiel * FLT_H_ForEff
HU_FLT_PrB = genDRtwCIg * HU_FLT_dw * FLT_HTd_pB * genQIO * (((5.00 * HU_FLT_dw + .000001) /
    (HU_FLT_no + .000001))^-0.2) * HU_SubTime * FLT_HDiel * FLT_H_ForEff
HU_FLT_PrC = genDRtwCIg * HU_FLT_dw * FLT_HTd_pC * genQIO * (((5.00 * HU_FLT_dw + .000001) /
    (HU_FLT_no + .000001))^-0.2) * HU_SubTime * FLT_HDiel * FLT_H_ForEff
HU_FLT_PrD = genDRtwCIg * HU_FLT_dw * FLT_HTd_pD * genQIO * (((5.00 * HU_FLT_dw + .000001) /
    (HU_FLT_no + .000001))^-0.2) * HU_SubTime * FLT_HDiel * FLT_H_ForEff
HE_FLT_PrA = genDRtwCIg * HE_FLT_dw * FLT_HTd_pA * genQIO * (((5.00 * HE_FLT_dw + .000001) /
    (HE_FLT_no + .000001))^-0.2) * HE_SubTime * FLT_HDiel * FLT_H_ForEff
HE_FLT_PrB = genDRtwCIg * HE_FLT_dw * FLT_HTd_pB * genQIO * (((5.00 * HE_FLT_dw + .000001) /
    (HE_FLT_no + .000001))^-0.2) * HE_SubTime * FLT_HDiel * FLT_H_ForEff
HE_FLT_PrC = genDRtwCIg * HE_FLT_dw * FLT_HTd_pC * genQIO * (((5.00 * HE_FLT_dw + .000001) /
    (HE_FLT_no + .000001))^-0.2) * HE_SubTime * FLT_HDiel * FLT_H_ForEff
HE_FLT_PrD = genDRtwCIg * HE_FLT_dw * FLT_HTd_pD * genQIO * (((5.00 * HE_FLT_dw + .000001) /
    (HE_FLT_no + .000001))^-0.2) * HE_SubTime * FLT_HDiel * FLT_H_ForEff
LD_FLT_PrA = genDRtwCIg * LD_FLT_dw * FLT_LTd_pA * genQIO * (((5.00 * LD_FLT_dw + .000001) /
    (LD_FLT_no + .000001))^-0.2) * LD_SubTime * FLT_LDiel * FLT_L_ForEff
LD_FLT_PrB = genDRtwCIg * LD_FLT_dw * FLT_LTd_pB * genQIO * (((5.00 * LD_FLT_dw + .000001) /
    (LD_FLT_no + .000001))^-0.2) * LD_SubTime * FLT_LDiel * FLT_L_ForEff
LD_FLT_PrC = genDRtwCIg * LD_FLT_dw * FLT_LTd_pC * genQIO * (((5.00 * LD_FLT_dw + .000001) /
    (LD_FLT_no + .000001))^-0.2) * LD_SubTime * FLT_LDiel * FLT_L_ForEff
LD_FLT_PrD = genDRtwCIg * LD_FLT_dw * FLT_LTd_pD * genQIO * (((5.00 * LD_FLT_dw + .000001) /
    (LD_FLT_no + .000001))^-0.2) * LD_SubTime * FLT_LDiel * FLT_L_ForEff

HU_gbo_PrA = genDRtwCIg * HU_gbo_dw * gbo_All_pA * genQIO * (((4.00 * HU_gbo_dw + .000001) /
    (HU_gbo_no + .000001))^-0.2) * HU_SubTime * gbo_HDiel * gbo_H_ForEff
HU_gbo_PrB = genDRtwCIg * HU_gbo_dw * gbo_All_pB * genQIO * (((4.00 * HU_gbo_dw + .000001) /
    (HU_gbo_no + .000001))^-0.2) * HU_SubTime * gbo_HDiel * gbo_H_ForEff
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HU_gbo_PrC = genDRtwClg * HU_gbo_dw * gbo_All_pC * genQIO * (((4.00 * HU_gbo_dw + .000001) /
    (HU_gbo_no + .000001))^-0.2) * HU_SubTime * gbo_HDiel * gbo_H_ForEff
HU_gbo_PrD = genDRtwClg * HU_gbo_dw * gbo_All_pD * genQIO * (((4.00 * HU_gbo_dw + .000001) /
    (HU_gbo_no + .000001))^-0.2) * HU_SubTime * gbo_HDiel * gbo_H_ForEff
HE_gbo_PrA = genDRtwClg * HE_gbo_dw * gbo_All_pA * genQIO * (((4.00 * HE_gbo_dw + .000001) /
    (HE_gbo_no + .000001))^-0.2) * HE_SubTime * gbo_HDiel * gbo_H_ForEff
HE_gbo_PrB = genDRtwClg * HE_gbo_dw * gbo_All_pB * genQIO * (((4.00 * HE_gbo_dw + .000001) /
    (HE_gbo_no + .000001))^-0.2) * HE_SubTime * gbo_HDiel * gbo_H_ForEff
HE_gbo_PrC = genDRtwClg * HE_gbo_dw * gbo_All_pC * genQIO * (((4.00 * HE_gbo_dw + .000001) /
    (HE_gbo_no + .000001))^-0.2) * HE_SubTime * gbo_HDiel * gbo_H_ForEff
HE_gbo_PrD = genDRtwClg * HE_gbo_dw * gbo_All_pD * genQIO * (((4.00 * HE_gbo_dw + .000001) /
    (HE_gbo_no + .000001))^-0.2) * HE_SubTime * gbo_HDiel * gbo_H_ForEff
LD_gbo_PrA = genDRtwClg * LD_gbo_dw * gbo_All_pA * genQIO * (((4.00 * LD_gbo_dw + .000001) /
    (LD_gbo_no + .000001))^-0.2) * LD_SubTime * gbo_LDiel * gbo_L_ForEff
LD_gbo_PrB = genDRtwClg * LD_gbo_dw * gbo_All_pB * genQIO * (((4.00 * LD_gbo_dw + .000001) /
    (LD_gbo_no + .000001))^-0.2) * LD_SubTime * gbo_LDiel * gbo_L_ForEff
LD_gbo_PrC = genDRtwClg * LD_gbo_dw * gbo_All_pC * genQIO * (((4.00 * LD_gbo_dw + .000001) /
    (LD_gbo_no + .000001))^-0.2) * LD_SubTime * gbo_LDiel * gbo_L_ForEff
LD_gbo_PrD = genDRtwClg * LD_gbo_dw * gbo_All_pD * genQIO * (((4.00 * LD_gbo_dw + .000001) /
    (LD_gbo_no + .000001))^-0.2) * LD_SubTime * gbo_LDiel * gbo_L_ForEff
LS_gbo_PrA = genDRtwClg * LS_gbo_dw * gbo_All_pA * genQIO * (((4.00 * LS_gbo_dw + .000001) /
    (LS_gbo_no + .000001))^-0.2) * LS_SubTime * gbo_LDiel * gbo_L_ForEff
LS_gbo_PrB = genDRtwClg * LS_gbo_dw * gbo_All_pB * genQIO * (((4.00 * LS_gbo_dw + .000001) /
    (LS_gbo_no + .000001))^-0.2) * LS_SubTime * gbo_LDiel * gbo_L_ForEff
LS_gbo_PrC = genDRtwClg * LS_gbo_dw * gbo_All_pC * genQIO * (((4.00 * LS_gbo_dw + .000001) /
    (LS_gbo_no + .000001))^-0.2) * LS_SubTime * gbo_LDiel * gbo_L_ForEff
LS_gbo_PrD = genDRtwClg * LS_gbo_dw * gbo_All_pD * genQIO * (((4.00 * LS_gbo_dw + .000001) /
    (LS_gbo_no + .000001))^-0.2) * LS_SubTime * gbo_LDiel * gbo_L_ForEff

HE_str_PrA = genDRtwClg * HE_str_dw * str_All_pA * genQIO * (((4.00 * HE_str_dw + .000001) /
    (HE_str_no + .000001))^-0.2) * HE_SubTime * str_HDiel * str_H_ForEff
HE_str_PrB = genDRtwClg * HE_str_dw * str_All_pB * genQIO * (((4.00 * HE_str_dw + .000001) /
    (HE_str_no + .000001))^-0.2) * HE_SubTime * str_HDiel * str_H_ForEff
HE_str_PrC = genDRtwClg * HE_str_dw * str_All_pC * genQIO * (((4.00 * HE_str_dw + .000001) /
    (HE_str_no + .000001))^-0.2) * HE_SubTime * str_HDiel * str_H_ForEff
HE_str_PrD = genDRtwClg * HE_str_dw * str_All_pD * genQIO * (((4.00 * HE_str_dw + .000001) /
    (HE_str_no + .000001))^-0.2) * HE_SubTime * str_HDiel * str_H_ForEff
LD_str_PrA = genDRtwClg * LD_str_dw * str_All_pA * genQIO * (((4.00 * LD_str_dw + .000001) /
    (LD_str_no + .000001))^-0.2) * LD_SubTime * str_LDiel * str_L_ForEff
LD_str_PrB = genDRtwClg * LD_str_dw * str_All_pB * genQIO * (((4.00 * LD_str_dw + .000001) /
    (LD_str_no + .000001))^-0.2) * LD_SubTime * str_LDiel * str_L_ForEff
LD_str_PrC = genDRtwClg * LD_str_dw * str_All_pC * genQIO * (((4.00 * LD_str_dw + .000001) /
    (LD_str_no + .000001))^-0.2) * LD_SubTime * str_LDiel * str_L_ForEff
LD_str_PrD = genDRtwClg * LD_str_dw * str_All_pD * genQIO * (((4.00 * LD_str_dw + .000001) /
    (LD_str_no + .000001))^-0.2) * LD_SubTime * str_LDiel * str_L_ForEff
LS_str_PrA = genDRtwClg * LS_str_dw * str_All_pA * genQIO * (((4.00 * LS_str_dw + .000001) /
    (LS_str_no + .000001))^-0.2) * LS_SubTime * str_LDiel * str_L_ForEff
LS_str_PrB = genDRtwClg * LS_str_dw * str_All_pB * genQIO * (((4.00 * LS_str_dw + .000001) /
    (LS_str_no + .000001))^-0.2) * LS_SubTime * str_LDiel * str_L_ForEff
LS_str_PrC = genDRtwClg * LS_str_dw * str_All_pC * genQIO * (((4.00 * LS_str_dw + .000001) /
    (LS_str_no + .000001))^-0.2) * LS_SubTime * str_LDiel * str_L_ForEff
LS_str_PrD = genDRtwClg * LS_str_dw * str_All_pD * genQIO * (((4.00 * LS_str_dw + .000001) /
    (LS_str_no + .000001))^-0.2) * LS_SubTime * str_LDiel * str_L_ForEff

HE_Lhet_PrA = hetDRtwClg * HE_Lhet_dw * Lhet_HE_pA * hetQIO * (((4.26* HE_Lhet_dw + .000001) /
    (HE_Lhet_no + .000001))^-0.2) * HE_SubTime * Lhet_HDiel * Lhet_H_ForEff
HE_Lhet_PrB = hetDRtwClg * HE_Lhet_dw * Lhet_HE_pB * hetQIO * (((4.26* HE_Lhet_dw + .000001) /
    (HE_Lhet_no + .000001))^-0.2) * HE_SubTime * Lhet_HDiel * Lhet_H_ForEff
HE_Lhet_PrC = hetDRtwClg * HE_Lhet_dw * Lhet_HE_pC * hetQIO * (((4.26* HE_Lhet_dw + .000001) /
    (HE_Lhet_no + .000001))^-0.2) * HE_SubTime * Lhet_HDiel * Lhet_H_ForEff
HE_Lhet_PrD = hetDRtwClg * HE_Lhet_dw * Lhet_HE_pD * hetQIO * (((4.26 * HE_Lhet_dw + .000001)
    / (HE_Lhet_no + .000001))^-0.2) * HE_SubTime * Lhet_HDiel * Lhet_H_ForEff
HF_Lhet_PrA = hetDRtwClg * HF_Lhet_dw * Lhet_HF_pA * hetQIO * (((4.26 * HF_Lhet_dw + .000001) /
    (HF_Lhet_no + .000001))^-0.2) * HF_SubTime * Lhet_HDiel * Lhet_H_ForEff
```

```
HF_Lhet_PrB  =  hetDRtwCIg * HF_Lhet_dw * Lhet_HF_pB * hetQIO * (((4.26 *  HF_Lhet_dw + .000001) /
    (HF_Lhet_no + .000001))^-0.2) * HF_SubTime * Lhet_HDiel * Lhet_H_ForEff
HF_Lhet_PrC  =  hetDRtwCIg * HF_Lhet_dw * Lhet_HF_pC * hetQIO * (((4.26 *  HF_Lhet_dw + .000001) /
    (HF_Lhet_no + .000001))^-0.2) * HF_SubTime * Lhet_HDiel * Lhet_H_ForEff
HF_Lhet_PrD  =  hetDRtwCIg * HF_Lhet_dw * Lhet_HF_pD * hetQIO * (((4.26 *  HF_Lhet_dw + .000001) /
    (HF_Lhet_no + .000001))^-0.2) * HF_SubTime * Lhet_HDiel * Lhet_H_ForEff
HI_Lhet_PrA  =  hetDRtwCIg * HI_Lhet_dw * Lhet_HI_pA * hetQIO * (((4.26 *  HI_Lhet_dw + .000001) /
    (HI_Lhet_no + .000001))^-0.2) * HI_SubTime * Lhet_HDiel * Lhet_H_ForEff
HI_Lhet_PrB  =  hetDRtwCIg * HI_Lhet_dw * Lhet_HI_pB * hetQIO * (((4.26 *  HI_Lhet_dw + .000001) /
    (HI_Lhet_no + .000001))^-0.2) * HI_SubTime * Lhet_HDiel * Lhet_H_ForEff
HI_Lhet_PrC  =  hetDRtwCIg * HI_Lhet_dw * Lhet_HI_pC * hetQIO * (((4.26 *  HI_Lhet_dw + .000001) /
    (HI_Lhet_no + .000001))^-0.2) * HI_SubTime * Lhet_HDiel * Lhet_H_ForEff
HI_Lhet_PrD  =  hetDRtwCIg * HI_Lhet_dw * Lhet_HI_pD * hetQIO * (((4.26 *  HI_Lhet_dw + .000001) /
    (HI_Lhet_no + .000001))^-0.2) * HI_SubTime * Lhet_HDiel * Lhet_H_ForEff
LD_Lhet_PrA  =  hetDRtwCIg * LD_Lhet_dw * Lhet_LTd_pA * hetQIO * (((4.26 *  LD_Lhet_dw + .000001)
    / (LD_Lhet_no + .000001))^-0.2) * LD_SubTime * Lhet_LDiel * Lhet_L_ForEff
LD_Lhet_PrB  =  hetDRtwCIg * LD_Lhet_dw * Lhet_LTd_pB * hetQIO * (((4.26 *  LD_Lhet_dw + .000001)
    / (LD_Lhet_no + .000001))^-0.2) * LD_SubTime * Lhet_LDiel * Lhet_L_ForEff
LD_Lhet_PrC  =  hetDRtwCIg * LD_Lhet_dw * Lhet_LTd_pC * hetQIO * (((4.26 *  LD_Lhet_dw + .000001)
    / (LD_Lhet_no + .000001))^-0.2) * LD_SubTime * Lhet_LDiel * Lhet_L_ForEff
LD_Lhet_PrD  =  hetDRtwCIg * LD_Lhet_dw * Lhet_LTd_pD * hetQIO * (((4.26 *  LD_Lhet_dw + .000001)
    / (LD_Lhet_no + .000001))^-0.2) * LD_SubTime * Lhet_LDiel * Lhet_L_ForEff
LS_Lhet_PrA  =  hetDRtwCIg * LS_Lhet_dw * Lhet_LTd_pA * hetQIO * (((4.26 *  LS_Lhet_dw + .000001)
    / (LS_Lhet_no + .000001))^-0.2) * LS_SubTime * Lhet_LDiel * Lhet_L_ForEff
LS_Lhet_PrB  =  hetDRtwCIg * LS_Lhet_dw * Lhet_LTd_pB * hetQIO * (((4.26 *  LS_Lhet_dw + .000001)
    / (LS_Lhet_no + .000001))^-0.2) * LS_SubTime * Lhet_LDiel * Lhet_L_ForEff
LS_Lhet_PrC  =  hetDRtwCIg * LS_Lhet_dw * Lhet_LTd_pC * hetQIO * (((4.26 *  LS_Lhet_dw + .000001)
    / (LS_Lhet_no + .000001))^-0.2) * LS_SubTime * Lhet_LDiel * Lhet_L_ForEff
LS_Lhet_PrD  =  hetDRtwCIg * LS_Lhet_dw * Lhet_LTd_pD * hetQIO * (((4.26 *  LS_Lhet_dw + .000001)
    / (LS_Lhet_no + .000001))^-0.2) * LS_SubTime * Lhet_LDiel * Lhet_L_ForEff

HU_luc_PrA  =  hetDRtwCIg * HU_luc_dw * luc_HU_pA * hetQIO *  (((3.51 *  HU_luc_dw + .000001) /
    (HU_luc_no + .000001))^-0.2) * HU_SubTime * luc_HDiel * luc_H_ForEff
HU_luc_PrB  =  hetDRtwCIg * HU_luc_dw * luc_HU_pB * hetQIO *  (((3.51 *  HU_luc_dw + .000001) /
    (HU_luc_no + .000001))^-0.2) * HU_SubTime * luc_HDiel * luc_H_ForEff
HU_luc_PrC  =  hetDRtwCIg * HU_luc_dw * luc_HU_pC * hetQIO *  (((3.51 *  HU_luc_dw + .000001) /
    (HU_luc_no + .000001))^-0.2) * HU_SubTime * luc_HDiel * luc_H_ForEff
HU_luc_PrD  =  hetDRtwCIg * HU_luc_dw * luc_HU_pD * hetQIO *  (((3.51 *  HU_luc_dw + .000001) /
    (HU_luc_no + .000001))^-0.2) * HU_SubTime * luc_HDiel * luc_H_ForEff
HE_luc_PrA  =  hetDRtwCIg * HE_luc_dw * luc_HE_pA * hetQIO *  (((3.51 *  HE_luc_dw + .000001) /
    (HE_luc_no + .000001))^-0.2) * HE_SubTime * luc_HDiel * luc_H_ForEff
HE_luc_PrB  =  hetDRtwCIg * HE_luc_dw * luc_HE_pB * hetQIO *  (((3.51 *  HE_luc_dw + .000001) /
    (HE_luc_no + .000001))^-0.2) * HE_SubTime * luc_HDiel * luc_H_ForEff
HE_luc_PrC  =  hetDRtwCIg * HE_luc_dw * luc_HE_pC * hetQIO *  (((3.51 *  HE_luc_dw + .000001) /
    (HE_luc_no + .000001))^-0.2) * HE_SubTime * luc_HDiel * luc_H_ForEff
HE_luc_PrD  =  hetDRtwCIg * HE_luc_dw * luc_HE_pD * hetQIO *  (((3.51 *  HE_luc_dw + .000001) /
    (HE_luc_no + .000001))^-0.2) * HE_SubTime * luc_HDiel * luc_H_ForEff
HF_luc_PrA  =  hetDRtwCIg * HF_luc_dw * luc_HIF_pA * hetQIO *  (((3.51 *  HF_luc_dw + .000001) /
    (HF_luc_no + .000001))^-0.2) * HF_SubTime * luc_HDiel * luc_H_ForEff
HF_luc_PrB  =  hetDRtwCIg * HF_luc_dw * luc_HIF_pB * hetQIO *  (((3.51 *  HF_luc_dw + .000001) /
    (HF_luc_no + .000001))^-0.2) * HF_SubTime * luc_HDiel * luc_H_ForEff
HF_luc_PrC  =  hetDRtwCIg * HF_luc_dw * luc_HIF_pC * hetQIO *  (((3.51 *  HF_luc_dw + .000001) /
    (HF_luc_no + .000001))^-0.2) * HF_SubTime * luc_HDiel * luc_H_ForEff
HF_luc_PrD  =  hetDRtwCIg * HF_luc_dw * luc_HIF_pD * hetQIO *  (((3.51 *  HF_luc_dw + .000001) /
    (HF_luc_no + .000001))^-0.2) * HF_SubTime * luc_HDiel * luc_H_ForEff
HI_luc_PrA  =  hetDRtwCIg * HI_luc_dw * luc_HIF_pA * hetQIO *  (((3.51 *  HI_luc_dw + .000001) /
    (HI_luc_no + .000001))^-0.2) * HI_SubTime * luc_HDiel * luc_H_ForEff
HI_luc_PrB  =  hetDRtwCIg * HI_luc_dw * luc_HIF_pB * hetQIO *  (((3.51 *  HI_luc_dw + .000001) /
    (HI_luc_no + .000001))^-0.2) * HI_SubTime * luc_HDiel * luc_H_ForEff
HI_luc_PrC  =  hetDRtwCIg * HI_luc_dw * luc_HIF_pC * hetQIO *  (((3.51 *  HI_luc_dw + .000001) /
    (HI_luc_no + .000001))^-0.2) * HI_SubTime * luc_HDiel * luc_H_ForEff
HI_luc_PrD  =  hetDRtwCIg * HI_luc_dw * luc_HIF_pD * hetQIO *  (((3.51 *  HI_luc_dw + .000001) /
    (HI_luc_no + .000001))^-0.2) * HI_SubTime * luc_HDiel * luc_H_ForEff
```

```
LD_luc_PrA = hetDRtwClg * LD_luc_dw * luc_LTd_pA * hetQIO * (((3.51 * LD_luc_dw + .000001) /
    (LD_luc_no + .000001))^-0.2) * LD_SubTime * luc_LDiel * luc_L_ForEff
LD_luc_PrB = hetDRtwClg * LD_luc_dw * luc_LTd_pB * hetQIO * (((3.51 * LD_luc_dw + .000001) /
    (LD_luc_no + .000001))^-0.2) * LD_SubTime * luc_LDiel * luc_L_ForEff
LD_luc_PrC = hetDRtwClg * LD_luc_dw * luc_LTd_pC * hetQIO * (((3.51 * LD_luc_dw + .000001) /
    (LD_luc_no + .000001))^-0.2) * LD_SubTime * luc_LDiel * luc_L_ForEff
LD_luc_PrD = hetDRtwClg * LD_luc_dw * luc_LTd_pD * hetQIO * (((3.51 * LD_luc_dw + .000001) /
    (LD_luc_no + .000001))^-0.2) * LD_SubTime * luc_LDiel * luc_L_ForEff
LS_luc_PrA = hetDRtwClg * LS_luc_dw * luc_LTd_pA * hetQIO * (((3.51 * LS_luc_dw + .000001) /
    (LS_luc_no + .000001))^-0.2) * LS_SubTime * luc_LDiel * luc_L_ForEff
LS_luc_PrB = hetDRtwClg * LS_luc_dw * luc_LTd_pB * hetQIO * (((3.51 * LS_luc_dw + .000001) /
    (LS_luc_no + .000001))^-0.2) * LS_SubTime * luc_LDiel * luc_L_ForEff
LS_luc_PrC = hetDRtwClg * LS_luc_dw * luc_LTd_pC * hetQIO * (((3.51 * LS_luc_dw + .000001) /
    (LS_luc_no + .000001))^-0.2) * LS_SubTime * luc_LDiel * luc_L_ForEff
LS_luc_PrD = hetDRtwClg * LS_luc_dw * luc_LTd_pD * hetQIO * (((3.51 * LS_luc_dw + .000001) /
    (LS_luc_no + .000001))^-0.2) * LS_SubTime * luc_LDiel * luc_L_ForEff

HE_maj_PrA = hetDRtwClg * HE_maj_dw * maj_HTd_pA * hetQIO * (((3.51 * HE_maj_dw + .000001) /
    (HE_maj_no + .000001))^-0.2) * HE_SubTime * maj_HDiel * maj_H_ForEff
HE_maj_PrB = hetDRtwClg * HE_maj_dw * maj_HTd_pB * hetQIO * (((3.51 * HE_maj_dw + .000001) /
    (HE_maj_no + .000001))^-0.2) * HE_SubTime * maj_HDiel * maj_H_ForEff
HE_maj_PrC = hetDRtwClg * HE_maj_dw * maj_HTd_pC * hetQIO * (((3.51 * HE_maj_dw + .000001) /
    (HE_maj_no + .000001))^-0.2) * HE_SubTime * maj_HDiel * maj_H_ForEff
HE_maj_PrD = hetDRtwClg * HE_maj_dw * maj_HTd_pD * hetQIO * (((3.51 * HE_maj_dw + .000001) /
    (HE_maj_no + .000001))^-0.2) * HE_SubTime * maj_HDiel * maj_H_ForEff
HF_maj_PrA = hetDRtwClg * HF_maj_dw * maj_HTd_pA * hetQIO * (((3.51 * HF_maj_dw + .000001) /
    (HF_maj_no + .000001))^-0.2) * HF_SubTime * maj_HDiel * maj_H_ForEff
HF_maj_PrB = hetDRtwClg * HF_maj_dw * maj_HTd_pB * hetQIO * (((3.51 * HF_maj_dw + .000001) /
    (HF_maj_no + .000001))^-0.2) * HF_SubTime * maj_HDiel * maj_H_ForEff
HF_maj_PrC = hetDRtwClg * HF_maj_dw * maj_HTd_pC * hetQIO * (((3.51 * HF_maj_dw + .000001) /
    (HF_maj_no + .000001))^-0.2) * HF_SubTime * maj_HDiel * maj_H_ForEff
HF_maj_PrD = hetDRtwClg * HF_maj_dw * maj_HTd_pD * hetQIO * (((3.51 * HF_maj_dw + .000001) /
    (HF_maj_no + .000001))^-0.2) * HF_SubTime * maj_HDiel * maj_H_ForEff
HI_maj_PrA = hetDRtwClg * HI_maj_dw * maj_HTd_pA * hetQIO * (((3.51 * HI_maj_dw + .000001) /
    (HI_maj_no + .000001))^-0.2) * HI_SubTime * maj_HDiel * maj_H_ForEff
HI_maj_PrB = hetDRtwClg * HI_maj_dw * maj_HTd_pB * hetQIO * (((3.51 * HI_maj_dw + .000001) /
    (HI_maj_no + .000001))^-0.2) * HI_SubTime * maj_HDiel * maj_H_ForEff
HI_maj_PrC = hetDRtwClg * HI_maj_dw * maj_HTd_pC * hetQIO * (((3.51 * HI_maj_dw + .000001) /
    (HI_maj_no + .000001))^-0.2) * HI_SubTime * maj_HDiel * maj_H_ForEff
HI_maj_PrD = hetDRtwClg * HI_maj_dw * maj_HTd_pD * hetQIO * (((3.51 * HI_maj_dw + .000001) /
    (HI_maj_no + .000001))^-0.2) * HI_SubTime * maj_HDiel * maj_H_ForEff
LD_maj_PrA = hetDRtwClg * LD_maj_dw * maj_LTd_pA * hetQIO * (((3.51 * LD_maj_dw + .000001) /
    (LD_maj_no + .000001))^-0.2) * LD_SubTime * maj_LDiel * maj_L_ForEff
LD_maj_PrB = hetDRtwClg * LD_maj_dw * maj_LTd_pB * hetQIO * (((3.51 * LD_maj_dw + .000001) /
    (LD_maj_no + .000001))^-0.2) * LD_SubTime * maj_LDiel * maj_L_ForEff
LD_maj_PrC = hetDRtwClg * LD_maj_dw * maj_LTd_pC * hetQIO * (((3.51 * LD_maj_dw + .000001) /
    (LD_maj_no + .000001))^-0.2) * LD_SubTime * maj_LDiel * maj_L_ForEff
LD_maj_PrD = hetDRtwClg * LD_maj_dw * maj_LTd_pD * hetQIO * (((3.51 * LD_maj_dw + .000001) /
    (LD_maj_no + .000001))^-0.2) * LD_SubTime * maj_LDiel * maj_L_ForEff
LS_maj_PrA = hetDRtwClg * LS_maj_dw * maj_LTd_pA * hetQIO * (((3.51 * LS_maj_dw + .000001) /
    (LS_maj_no + .000001))^-0.2) * LS_SubTime * maj_LDiel * maj_L_ForEff
LS_maj_PrB = hetDRtwClg * LS_maj_dw * maj_LTd_pB * hetQIO * (((3.51 * LS_maj_dw + .000001) /
    (LS_maj_no + .000001))^-0.2) * LS_SubTime * maj_LDiel * maj_L_ForEff
LS_maj_PrC = hetDRtwClg * LS_maj_dw * maj_LTd_pC * hetQIO * (((3.51 * LS_maj_dw + .000001) /
    (LS_maj_no + .000001))^-0.2) * LS_SubTime * maj_LDiel * maj_L_ForEff
LS_maj_PrD = hetDRtwClg * LS_maj_dw * maj_LTd_pD * hetQIO * (((3.51 * LS_maj_dw + .000001) /
    (LS_maj_no + .000001))^-0.2) * LS_SubTime * maj_LDiel * maj_L_ForEff

HU_Shet_PrA = hetDRtwClg * HU_Shet_dw * Shet_HE_pA * hetQIO * (((3.51 * HU_Shet_dw + .000001)
    / (HU_Shet_no + .000001))^-0.2) * HU_SubTime * Shet_HDiel * Shet_H_ForEff
HU_Shet_PrB = hetDRtwClg * HU_Shet_dw * Shet_HE_pB * hetQIO * (((3.51 * HU_Shet_dw + .000001)
    / (HU_Shet_no + .000001))^-0.2) * HU_SubTime * Shet_HDiel * Shet_H_ForEff
HU_Shet_PrC = hetDRtwClg * HU_Shet_dw * Shet_HE_pC * hetQIO * (((3.51 * HU_Shet_dw + .000001)
    / (HU_Shet_no + .000001))^-0.2) * HU_SubTime * Shet_HDiel * Shet_H_ForEff
```

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HU_Shet_PrD  =  hetDRtwCIg * HU_Shet_dw * Shet_HE_pD * hetQIO *  (((3.51 *  HU_Shet_dw + .000001)
    / (HU_Shet_no + .000001))^-0.2) * HU_SubTime * Shet_HDiel * Shet_H_ForEff
HE_Shet_PrA  =  hetDRtwCIg * HE_Shet_dw * Shet_HE_pA * hetQIO *  (((3.51 *  HE_Shet_dw + .000001)
    / (HE_Shet_no + .000001))^-0.2) * HE_SubTime * Shet_HDiel * Shet_H_ForEff
HE_Shet_PrB  =  hetDRtwCIg * HE_Shet_dw * Shet_HE_pB * hetQIO *  (((3.51 *  HE_Shet_dw + .000001)
    / (HE_Shet_no + .000001))^-0.2) * HE_SubTime * Shet_HDiel * Shet_H_ForEff
HE_Shet_PrC  =  hetDRtwCIg * HE_Shet_dw * Shet_HE_pC * hetQIO *  (((3.51 *  HE_Shet_dw + .000001)
    / (HE_Shet_no + .000001))^-0.2) * HE_SubTime * Shet_HDiel * Shet_H_ForEff
HE_Shet_PrD  =  hetDRtwCIg * HE_Shet_dw * Shet_HE_pD * hetQIO *  (((3.51 *  HE_Shet_dw + .000001)
    / (HE_Shet_no + .000001))^-0.2) * HE_SubTime * Shet_HDiel * Shet_H_ForEff
HF_Shet_PrA  =  hetDRtwCIg * HF_Shet_dw * Shet_HF_pA * hetQIO *  (((3.51 *  HF_Shet_dw + .000001)
    / (HF_Shet_no + .000001))^-0.2) * HF_SubTime * Shet_HDiel * Shet_H_ForEff
HF_Shet_PrB  =  hetDRtwCIg * HF_Shet_dw * Shet_HF_pB * hetQIO *  (((3.51 *  HF_Shet_dw + .000001) /
    (HF_Shet_no + .000001))^-0.2) * HF_SubTime * Shet_HDiel * Shet_H_ForEff
HF_Shet_PrC  =  hetDRtwCIg * HF_Shet_dw * Shet_HF_pC * hetQIO *  (((3.51 *  HF_Shet_dw + .000001) /
    (HF_Shet_no + .000001))^-0.2) * HF_SubTime * Shet_HDiel * Shet_H_ForEff
HF_Shet_PrD  =  hetDRtwCIg * HF_Shet_dw * Shet_HF_pD * hetQIO *  (((3.51 *  HF_Shet_dw + .000001)
    / (HF_Shet_no + .000001))^-0.2) * HF_SubTime * Shet_HDiel * Shet_H_ForEff
HI_Shet_PrA  =  hetDRtwCIg * HI_Shet_dw * Shet_HI_pA * hetQIO *  (((3.51 *  HI_Shet_dw + .000001) /
    (HI_Shet_no + .000001))^-0.2) * HI_SubTime * Shet_HDiel * Shet_H_ForEff
HI_Shet_PrB  =  hetDRtwCIg * HI_Shet_dw * Shet_HI_pB * hetQIO *  (((3.51 *  HI_Shet_dw + .000001) /
    (HI_Shet_no + .000001))^-0.2) * HI_SubTime * Shet_HDiel * Shet_H_ForEff
HI_Shet_PrC  =  hetDRtwCIg * HI_Shet_dw * Shet_HI_pC * hetQIO *  (((3.51 *  HI_Shet_dw + .000001) /
    (HI_Shet_no + .000001))^-0.2) * HI_SubTime * Shet_HDiel * Shet_H_ForEff
HI_Shet_PrD  =  hetDRtwCIg * HI_Shet_dw * Shet_HI_pD * hetQIO *  (((3.51 *  HI_Shet_dw + .000001) /
    (HI_Shet_no + .000001))^-0.2) * HI_SubTime * Shet_HDiel * Shet_H_ForEff
HV_Shet_PrA  =  hetDRtwCIg * HV_Shet_dw * Shet_HE_pA * hetQIO *  (((3.51 *  HV_Shet_dw +
    .000001) / (HV_Shet_no + .000001))^-0.2) * HV_SubTime * Shet_HDiel * Shet_H_ForEff
HV_Shet_PrB  =  hetDRtwCIg * HV_Shet_dw * Shet_HE_pB * hetQIO *  (((3.51 *  HV_Shet_dw + .000001)
    / (HV_Shet_no + .000001))^-0.2) * HV_SubTime * Shet_HDiel * Shet_H_ForEff
HV_Shet_PrC  =  hetDRtwCIg * HV_Shet_dw * Shet_HE_pC * hetQIO *  (((3.51 *  HV_Shet_dw + .000001)
    / (HV_Shet_no + .000001))^-0.2) * HV_SubTime * Shet_HDiel * Shet_H_ForEff
HV_Shet_PrD  =  hetDRtwCIg * HV_Shet_dw * Shet_HE_pD * hetQIO *  (((3.51 *  HV_Shet_dw +
    .000001) / (HV_Shet_no + .000001))^-0.2) * HV_SubTime * Shet_HDiel * Shet_H_ForEff
LD_Shet_PrA  =  hetDRtwCIg * LD_Shet_dw * Shet_LTd_pA * hetQIO *  (((3.51 *  LD_Shet_dw +
    .000001) / (LD_Shet_no + .000001))^-0.2) * LD_SubTime * Shet_LDiel * Shet_L_ForEff
LD_Shet_PrB  =  hetDRtwCIg * LD_Shet_dw * Shet_LTd_pB * hetQIO *  (((3.51 *  LD_Shet_dw +
    .000001) / (LD_Shet_no + .000001))^-0.2) * LD_SubTime * Shet_LDiel * Shet_L_ForEff
LD_Shet_PrC  =  hetDRtwCIg * LD_Shet_dw * Shet_LTd_pC * hetQIO *  (((3.51 *  LD_Shet_dw +
    .000001) / (LD_Shet_no + .000001))^-0.2) * LD_SubTime * Shet_LDiel * Shet_L_ForEff
LD_Shet_PrD  =  hetDRtwCIg * LD_Shet_dw * Shet_LTd_pD * hetQIO *  (((3.51 *  LD_Shet_dw +
    .000001) / (LD_Shet_no + .000001))^-0.2) * LD_SubTime * Shet_LDiel * Shet_L_ForEff
LS_Shet_PrA  =  hetDRtwCIg * LS_Shet_dw * Shet_LTd_pA * hetQIO *  (((3.51 *  LS_Shet_dw + .000001)
    / (LS_Shet_no + .000001))^-0.2) * LS_SubTime * Shet_LDiel * Shet_L_ForEff
LS_Shet_PrB  =  hetDRtwCIg * LS_Shet_dw * Shet_LTd_pB * hetQIO *  (((3.51 *  LS_Shet_dw + .000001)
    / (LS_Shet_no + .000001))^-0.2) * LS_SubTime * Shet_LDiel * Shet_L_ForEff
LS_Shet_PrC  =  hetDRtwCIg * LS_Shet_dw * Shet_LTd_pC * hetQIO *  (((3.51 *  LS_Shet_dw + .000001)
    / (LS_Shet_no + .000001))^-0.2) * LS_SubTime * Shet_LDiel * Shet_L_ForEff
LS_Shet_PrD  =  hetDRtwCIg * LS_Shet_dw * Shet_LTd_pD * hetQIO *  (((3.51 *  LS_Shet_dw + .000001)
    / (LS_Shet_no + .000001))^-0.2) * LS_SubTime * Shet_LDiel * Shet_L_ForEff
LV_Shet_PrA  =  hetDRtwCIg * LV_Shet_dw * Shet_LTd_pA * hetQIO *  (((3.51 *  LV_Shet_dw +
    .000001) / (LV_Shet_no + .000001))^-0.2) * LV_SubTime * Shet_LDiel * Shet_L_ForEff
LV_Shet_PrB  =  hetDRtwCIg * LV_Shet_dw * Shet_LTd_pB * hetQIO *  (((3.51 *  LV_Shet_dw +
    .000001) / (LV_Shet_no + .000001))^-0.2) * LV_SubTime * Shet_LDiel * Shet_L_ForEff
LV_Shet_PrC  =  hetDRtwCIg * LV_Shet_dw * Shet_LTd_pC * hetQIO *  (((3.51 *  LV_Shet_dw +
    .000001) / (LV_Shet_no + .000001))^-0.2) * LV_SubTime * Shet_LDiel * Shet_L_ForEff
LV_Shet_PrD  =  hetDRtwCIg * LV_Shet_dw * Shet_LTd_pD * hetQIO *  (((3.51 *  LV_Shet_dw +
    .000001) / (LV_Shet_no + .000001))^-0.2) * LV_SubTime * Shet_LDiel * Shet_L_ForEff


HU_men_PrA  =  menDRtwCIg * HU_men_dw * men_Off_pA * menQIO * (((5.00 *  HU_men_dw + .000001)
    / (HU_men_no + .000001))^-0.2) * HU_SubTime * men_HDiel * men_H_ForEff
HU_men_PrB  =  menDRtwCIg * HU_men_dw * men_Off_pB * menQIO * (((5.00 *  HU_men_dw + .000001) /
    (HU_men_no + .000001))^-0.2) * HU_SubTime * men_HDiel * men_H_ForEff
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HU_men_PrC = menDRtwClg * HU_men_dw * men_Off_pC * menQIO * (((5.00 * HU_men_dw + .000001) /
    (HU_men_no + .000001))^-0.2) * HU_SubTime * men_HDiel * men_H_ForEff
HU_men_PrD = menDRtwClg * HU_men_dw * men_Off_pD * menQIO * (((5.00 * HU_men_dw + .000001)
    / (HU_men_no + .000001))^-0.2) * HU_SubTime * men_HDiel * men_H_ForEff
HE_men_PrA = menDRtwClg * HE_men_dw * men_Msh_pA * menQIO * (((5.00 * HE_men_dw + .000001)
    / (HE_men_no + .000001))^-0.2) * HE_SubTime * men_HDiel * men_H_ForEff
HE_men_PrB = menDRtwClg * HE_men_dw * men_Msh_pB * menQIO * (((5.00 * HE_men_dw + .000001)
    / (HE_men_no + .000001))^-0.2) * HE_SubTime * men_HDiel * men_H_ForEff
HE_men_PrC = menDRtwClg * HE_men_dw * men_Msh_pC * menQIO * (((5.00 * HE_men_dw + .000001)
    / (HE_men_no + .000001))^-0.2) * HE_SubTime * men_HDiel * men_H_ForEff
HE_men_PrD = menDRtwClg * HE_men_dw * men_Msh_pD * menQIO * (((5.00 * HE_men_dw + .000001)
    / (HE_men_no + .000001))^-0.2) * HE_SubTime * men_HDiel * men_H_ForEff
HF_men_PrA = menDRtwClg * HF_men_dw * men_Msh_pA * menQIO * (((5.00 * HF_men_dw + .000001)
    / (HF_men_no + .000001))^-0.2) * HF_SubTime * men_HDiel * men_H_ForEff
HF_men_PrB = menDRtwClg * HF_men_dw * men_Msh_pB * menQIO * (((5.00 * HF_men_dw + .000001) /
    (HF_men_no + .000001))^-0.2) * HF_SubTime * men_HDiel * men_H_ForEff
HF_men_PrC = menDRtwClg * HF_men_dw * men_Msh_pC * menQIO * (((5.00 * HF_men_dw + .000001) /
    (HF_men_no + .000001))^-0.2) * HF_SubTime * men_HDiel * men_H_ForEff
HF_men_PrD = menDRtwClg * HF_men_dw * men_Msh_pD * menQIO * (((5.00 * HF_men_dw + .000001)
    / (HF_men_no + .000001))^-0.2) * HF_SubTime * men_HDiel * men_H_ForEff
HI_men_PrA = menDRtwClg * HI_men_dw * men_Msh_pA * menQIO * (((5.00 * HI_men_dw + .000001) /
    (HI_men_no + .000001))^-0.2) * HI_SubTime * men_HDiel * men_H_ForEff
HI_men_PrB = menDRtwClg * HI_men_dw * men_Msh_pB * menQIO * (((5.00 * HI_men_dw + .000001) /
    (HI_men_no + .000001))^-0.2) * HI_SubTime * men_HDiel * men_H_ForEff
HI_men_PrC = menDRtwClg * HI_men_dw * men_Msh_pC * menQIO * (((5.00 * HI_men_dw + .000001) /
    (HI_men_no + .000001))^-0.2) * HI_SubTime * men_HDiel * men_H_ForEff
HI_men_PrD = menDRtwClg * HI_men_dw * men_Msh_pD * menQIO * (((5.00 * HI_men_dw + .000001) /
    (HI_men_no + .000001))^-0.2) * HI_SubTime * men_HDiel * men_H_ForEff
LD_men_PrA = menDRtwClg * LD_men_dw * men_Off_pA * menQIO * (((5.00 * LD_men_dw + .000001)
    / (LD_men_no + .000001))^-0.2) * LD_SubTime * men_LDiel * men_L_ForEff
LD_men_PrB = menDRtwClg * LD_men_dw * men_Off_pB * menQIO * (((5.00 * LD_men_dw + .000001) /
    (LD_men_no + .000001))^-0.2) * LD_SubTime * men_LDiel * men_L_ForEff
LD_men_PrC = menDRtwClg * LD_men_dw * men_Off_pC * menQIO * (((5.00 * LD_men_dw + .000001) /
    (LD_men_no + .000001))^-0.2) * LD_SubTime * men_LDiel * men_L_ForEff
LD_men_PrD = menDRtwClg * LD_men_dw * men_Off_pD * menQIO * (((5.00 * LD_men_dw + .000001)
    / (LD_men_no + .000001))^-0.2) * LD_SubTime * men_LDiel * men_L_ForEff
LS_men_PrA = menDRtwClg * LS_men_dw * men_Off_pA * menQIO * (((5.00 * LS_men_dw + .000001) /
    (LS_men_no + .000001))^-0.2) * LS_SubTime * men_LDiel * men_L_ForEff
LS_men_PrB = menDRtwClg * LS_men_dw * men_Off_pB * menQIO * (((5.00 * LS_men_dw + .000001) /
    (LS_men_no + .000001))^-0.2) * LS_SubTime * men_LDiel * men_L_ForEff
LS_men_PrC = menDRtwClg * LS_men_dw * men_Off_pC * menQIO * (((5.00 * LS_men_dw + .000001) /
    (LS_men_no + .000001))^-0.2) * LS_SubTime * men_LDiel * men_L_ForEff
LS_men_PrD = menDRtwClg * LS_men_dw * men_Off_pD * menQIO * (((5.00 * LS_men_dw + .000001) /
    (LS_men_no + .000001))^-0.2) * LS_SubTime * men_LDiel * men_L_ForEff

HE_bai_PrA = sciDRtwClg * HE_bai_dw * bai_All_pA * sciQIO * (((5.00 * HE_bai_dw + .000001) /
    (HE_bai_no + .000001))^-0.2) * HE_SubTime * bai_HDiel * bai_H_ForEff
HE_bai_PrB = sciDRtwClg * HE_bai_dw * bai_All_pB * sciQIO * (((5.00 * HE_bai_dw + .000001) /
    (HE_bai_no + .000001))^-0.2) * HE_SubTime * bai_HDiel * bai_H_ForEff
HE_bai_PrC = sciDRtwClg * HE_bai_dw * bai_All_pC * sciQIO * (((5.00 * HE_bai_dw + .000001) /
    (HE_bai_no + .000001))^-0.2) * HE_SubTime * bai_HDiel * bai_H_ForEff
HE_bai_PrD = sciDRtwClg * HE_bai_dw * bai_All_pD * sciQIO * (((5.00 * HE_bai_dw + .000001) /
    (HE_bai_no + .000001))^-0.2) * HE_SubTime * bai_HDiel * bai_H_ForEff
HI_bai_PrA = sciDRtwClg * HI_bai_dw * bai_All_pA * sciQIO * (((5.00 * HI_bai_dw + .000001) / (HI_bai_no
    + .000001))^-0.2) * HI_SubTime * bai_HDiel * bai_H_ForEff
HI_bai_PrB = sciDRtwClg * HI_bai_dw * bai_All_pB * sciQIO * (((5.00 * HI_bai_dw + .000001) / (HI_bai_no
    + .000001))^-0.2) * HI_SubTime * bai_HDiel * bai_H_ForEff
HI_bai_PrC = sciDRtwClg * HI_bai_dw * bai_All_pC * sciQIO * (((5.00 * HI_bai_dw + .000001) / (HI_bai_no
    + .000001))^-0.2) * HI_SubTime * bai_HDiel * bai_H_ForEff
HI_bai_PrD = sciDRtwClg * HI_bai_dw * bai_All_pD * sciQIO * (((5.00 * HI_bai_dw + .000001) / (HI_bai_no
    + .000001))^-0.2) * HI_SubTime * bai_HDiel * bai_H_ForEff
HE_cyn_PrA = sciDRtwClg * HE_cyn_dw * cyn_All_pA * sciQIO * (((5.00 * HE_cyn_dw + .000001) /
    (HE_cyn_no + .000001))^-0.2) * HE_SubTime * cyn_HDiel * cyn_H_ForEff
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HE_cyn_PrB = sciDRtwCIg * HE_cyn_dw * cyn_All_pB * sciQIO * (((5.00 * HE_cyn_dw + .000001) /
    (HE_cyn_no + .000001))^-0.2) * HE_SubTime * cyn_HDiel * cyn_H_ForEff
HE_cyn_PrC = sciDRtwCIg * HE_cyn_dw * cyn_All_pC * sciQIO * (((5.00 * HE_cyn_dw + .000001) /
    (HE_cyn_no + .000001))^-0.2) * HE_SubTime * cyn_HDiel * cyn_H_ForEff
HE_cyn_PrD = sciDRtwCIg * HE_cyn_dw * cyn_All_pD * sciQIO * (((5.00 * HE_cyn_dw + .000001) /
    (HE_cyn_no + .000001))^-0.2) * HE_SubTime * cyn_HDiel * cyn_H_ForEff
HU_lei_PrA = sciDRtwCIg * HU_lei_dw * lei_All_pA * sciQIO * (((5.00 * HU_lei_dw + .000001) /
    (HU_lei_no + .000001))^-0.2) * HU_SubTime * lei_HDiel * lei_H_ForEff
HU_lei_PrB = sciDRtwCIg * HU_lei_dw * lei_All_pB * sciQIO * (((5.00 * HU_lei_dw + .000001) / (HU_lei_no
    + .000001))^-0.2) * HU_SubTime * lei_HDiel * lei_H_ForEff
HU_lei_PrC = sciDRtwCIg * HU_lei_dw * lei_All_pC * sciQIO * (((5.00 * HU_lei_dw + .000001) / (HU_lei_no
    + .000001))^-0.2) * HU_SubTime * lei_HDiel * lei_H_ForEff
HU_lei_PrD = sciDRtwCIg * HU_lei_dw * lei_All_pD * sciQIO * (((5.00 * HU_lei_dw + .000001) /
    (HU_lei_no + .000001))^-0.2) * HU_SubTime * lei_HDiel * lei_H_ForEff
HE_lei_PrA = sciDRtwCIg * HE_lei_dw * lei_All_pA * sciQIO * (((5.00 * HE_lei_dw + .000001) /
    (HE_lei_no + .000001))^-0.2) * HE_SubTime * lei_HDiel * lei_H_ForEff
HE_lei_PrB = sciDRtwCIg * HE_lei_dw * lei_All_pB * sciQIO * (((5.00 * HE_lei_dw + .000001) / (HE_lei_no
    + .000001))^-0.2) * HE_SubTime * lei_HDiel * lei_H_ForEff
HE_lei_PrC = sciDRtwCIg * HE_lei_dw * lei_All_pC * sciQIO * (((5.00 * HE_lei_dw + .000001) / (HE_lei_no
    + .000001))^-0.2) * HE_SubTime * lei_HDiel * lei_H_ForEff
HE_lei_PrD = sciDRtwCIg * HE_lei_dw * lei_All_pD * sciQIO * (((5.00 * HE_lei_dw + .000001) /
    (HE_lei_no + .000001))^-0.2) * HE_SubTime * lei_HDiel * lei_H_ForEff
LD_soc_PrA = sciDRtwCIg * LD_soc_dw * soc_All_pA * sciQIO * (((5.00 * LD_soc_dw + .000001) /
    (LD_soc_no + .000001))^-0.2) * LD_SubTime * soc_LDiel * soc_L_ForEff
LD_soc_PrB = sciDRtwCIg * LD_soc_dw * soc_All_pB * sciQIO * (((5.00 * LD_soc_dw + .000001) /
    (LD_soc_no + .000001))^-0.2) * LD_SubTime * soc_LDiel * soc_L_ForEff
LD_soc_PrC = sciDRtwCIg * LD_soc_dw * soc_All_pC * sciQIO * (((5.00 * LD_soc_dw + .000001) /
    (LD_soc_no + .000001))^-0.2) * LD_SubTime * soc_LDiel * soc_L_ForEff
LD_soc_PrD = sciDRtwCIg * LD_soc_dw * soc_All_pD * sciQIO * (((5.00 * LD_soc_dw + .000001) /
    (LD_soc_no + .000001))^-0.2) * LD_SubTime * soc_LDiel * soc_L_ForEff

{B2 - CRUSTACEAN PREDATION}

HU_PAL_PrA = palDRtwCoIg * HU_PAL_dw * PAL_HE_pA * palQIO * (0.631*((( 3.85 * HU_PAL_dw +
    .000001) / (HU_PAL_no + .000001))^-0.2)) * HU_SubTime * PAL_HDiel * PAL_H_ForEff
HU_PAL_PrB = palDRtwCoIg * HU_PAL_dw * PAL_HE_pB * palQIO * (0.631*((( 3.85 * HU_PAL_dw +
    .000001) / (HU_PAL_no + .000001))^-0.2)) * HU_SubTime * PAL_HDiel * PAL_H_ForEff
HU_PAL_PrC = palDRtwCoIg * HU_PAL_dw * PAL_HE_pC * palQIO * (0.631*((( 3.85 * HU_PAL_dw +
    .000001) / (HU_PAL_no + .000001))^-0.2)) * HU_SubTime * PAL_HDiel * PAL_H_ForEff
HU_PAL_PrD = palDRtwCoIg * HU_PAL_dw * PAL_HE_pD * palQIO * (0.631*((( 3.85 * HU_PAL_dw +
    .000001) / (HU_PAL_no + .000001))^-0.2)) * HU_SubTime * PAL_HDiel * PAL_H_ForEff
HE_PAL_PrA = palDRtwCoIg * HE_PAL_dw * PAL_HE_pA * palQIO * (0.631*((( 3.85 * HE_PAL_dw +
    .000001) / (HE_PAL_no + .000001))^-0.2)) * HE_SubTime * PAL_HDiel * PAL_H_ForEff
HE_PAL_PrB = palDRtwCoIg * HE_PAL_dw * PAL_HE_pB * palQIO * (0.631*((( 3.85 * HE_PAL_dw +
    .000001) / (HE_PAL_no + .000001))^-0.2)) * HE_SubTime * PAL_HDiel * PAL_H_ForEff
HE_PAL_PrC = palDRtwCoIg * HE_PAL_dw * PAL_HE_pC * palQIO * (0.631*((( 3.85 * HE_PAL_dw +
    .000001) / (HE_PAL_no + .000001))^-0.2)) * HE_SubTime * PAL_HDiel * PAL_H_ForEff
HE_PAL_PrD = palDRtwCoIg * HE_PAL_dw * PAL_HE_pD * palQIO * (0.631*((( 3.85 * HE_PAL_dw +
    .000001) / (HE_PAL_no + .000001))^-0.2)) * HE_SubTime * PAL_HDiel * PAL_H_ForEff
HF_PAL_PrA = palDRtwCoIg * HF_PAL_dw * PAL_HIF_pA * palQIO * (0.631*((( 3.85 * HF_PAL_dw +
    .000001) / (HF_PAL_no + .000001))^-0.2)) * HF_SubTime * PAL_HDiel * PAL_H_ForEff
HF_PAL_PrB = palDRtwCoIg * HF_PAL_dw * PAL_HIF_pB * palQIO * (0.631*((( 3.85 * HF_PAL_dw +
    .000001) / (HF_PAL_no + .000001))^-0.2)) * HF_SubTime * PAL_HDiel * PAL_H_ForEff
HF_PAL_PrC = palDRtwCoIg * HF_PAL_dw * PAL_HIF_pC * palQIO * (0.631*((( 3.85 * HF_PAL_dw +
    .000001) / (HF_PAL_no + .000001))^-0.2)) * HF_SubTime * PAL_HDiel * PAL_H_ForEff
HF_PAL_PrD = palDRtwCoIg * HF_PAL_dw * PAL_HIF_pD * palQIO * (0.631*((( 3.85 * HF_PAL_dw +
    .000001) / (HF_PAL_no + .000001))^-0.2)) * HF_SubTime * PAL_HDiel * PAL_H_ForEff
HI_PAL_PrA = palDRtwCoIg * HI_PAL_dw * PAL_HIF_pA * palQIO * (0.631*((( 3.85 * HI_PAL_dw +
    .000001) / (HI_PAL_no + .000001))^-0.2)) * HI_SubTime * PAL_HDiel * PAL_H_ForEff
HI_PAL_PrB = palDRtwCoIg * HI_PAL_dw * PAL_HIF_pB * palQIO * (0.631*((( 3.85 * HI_PAL_dw +
    .000001) / (HI_PAL_no + .000001))^-0.2)) * HI_SubTime * PAL_HDiel * PAL_H_ForEff
HI_PAL_PrC = palDRtwCoIg * HI_PAL_dw * PAL_HIF_pC * palQIO * (0.631*((( 3.85 * HI_PAL_dw +
    .000001) / (HI_PAL_no + .000001))^-0.2)) * HI_SubTime * PAL_HDiel * PAL_H_ForEff
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HI_PAL_PrD  =  palDRtwCoIg * HI_PAL_dw * PAL_HIF_pD * palQIO * (0.631*((( 3.85 *  HI_PAL_dw +
    .000001) / (HI_PAL_no + .000001))^-0.2)) * HI_SubTime * PAL_HDiel * PAL_H_ForEff
LD_PAL_PrA  =  palDRtwCoIg * LD_PAL_dw * PAL_LTd_pA * palQIO * (0.631*((( 3.85 *  LD_PAL_dw +
    .000001) / (LD_PAL_no + .000001))^-0.2)) * LD_SubTime * PAL_LDiel * PAL_L_ForEff
LD_PAL_PrB  =  palDRtwCoIg * LD_PAL_dw * PAL_LTd_pB * palQIO * (0.631*((( 3.85 *  LD_PAL_dw +
    .000001) / (LD_PAL_no + .000001))^-0.2)) * LD_SubTime * PAL_LDiel * PAL_L_ForEff
LD_PAL_PrC  =  palDRtwCoIg * LD_PAL_dw * PAL_LTd_pC * palQIO * (0.631*((( 3.85 *  LD_PAL_dw +
    .000001) / (LD_PAL_no + .000001))^-0.2)) * LD_SubTime * PAL_LDiel * PAL_L_ForEff
LD_PAL_PrD  =  palDRtwCoIg * LD_PAL_dw * PAL_LTd_pD * palQIO * (0.631*((( 3.85 *  LD_PAL_dw +
    .000001) / (LD_PAL_no + .000001))^-0.2)) * LD_SubTime * PAL_LDiel * PAL_L_ForEff
LS_PAL_PrA  =  palDRtwCoIg * LS_PAL_dw * PAL_LTd_pA * palQIO * (0.631*((( 3.85 *  LS_PAL_dw +
    .000001) / (LS_PAL_no + .000001))^-0.2)) * LS_SubTime * PAL_LDiel * PAL_L_ForEff
LS_PAL_PrB  =  palDRtwCoIg * LS_PAL_dw * PAL_LTd_pB * palQIO * (0.631*((( 3.85 *  LS_PAL_dw +
    .000001) / (LS_PAL_no + .000001))^-0.2)) * LS_SubTime * PAL_LDiel * PAL_L_ForEff
LS_PAL_PrC  =  palDRtwCoIg * LS_PAL_dw * PAL_LTd_pC * palQIO * (0.631*((( 3.85 *  LS_PAL_dw +
    .000001) / (LS_PAL_no + .000001))^-0.2)) * LS_SubTime * PAL_LDiel * PAL_L_ForEff
LS_PAL_PrD  =  palDRtwCoIg * LS_PAL_dw * PAL_LTd_pD * palQIO * (0.631*((( 3.85 *  LS_PAL_dw +
    .000001) / (LS_PAL_no + .000001))^-0.2)) * LS_SubTime * PAL_LDiel * PAL_L_ForEff

HU_Scal_PrA  =  ScalDRtwCIg * HU_Scal_dw * Scal_HU_pA * calQIO *  (((3.70 *  HU_Scal_dw + .000001) /
    (HU_Scal_no + .000001))^-0.29) * HU_SubTime * Scal_HDiel * Scal_H_ForEff
HU_Scal_PrB  =  ScalDRtwCIg * HU_Scal_dw * Scal_HU_pB * calQIO *  (((3.70 *  HU_Scal_dw + .000001) /
    (HU_Scal_no + .000001))^-0.29) * HU_SubTime * Scal_HDiel * Scal_H_ForEff
HU_Scal_PrC  =  ScalDRtwCIg * HU_Scal_dw * Scal_HU_pC * calQIO *  (((3.70 *  HU_Scal_dw + .000001) /
    (HU_Scal_no + .000001))^-0.29) * HU_SubTime * Scal_HDiel * Scal_H_ForEff
HU_Scal_PrD  =  ScalDRtwCIg * HU_Scal_dw * Scal_HU_pD * calQIO *  (((3.70 *  HU_Scal_dw + .000001) /
    (HU_Scal_no + .000001))^-0.29) * HU_SubTime * Scal_HDiel * Scal_H_ForEff
HE_Scal_PrA  =  ScalDRtwCIg * HE_Scal_dw * Scal_HE_pA * calQIO *  (((3.70 *  HE_Scal_dw + .000001) /
    (HE_Scal_no + .000001))^-0.29) * HE_SubTime * Scal_HDiel * Scal_H_ForEff
HE_Scal_PrB  =  ScalDRtwCIg * HE_Scal_dw * Scal_HE_pB * calQIO *  (((3.70 *  HE_Scal_dw + .000001) /
    (HE_Scal_no + .000001))^-0.29) * HE_SubTime * Scal_HDiel * Scal_H_ForEff
HE_Scal_PrC  =  ScalDRtwCIg * HE_Scal_dw * Scal_HE_pC * calQIO *  (((3.70 *  HE_Scal_dw + .000001) /
    (HE_Scal_no + .000001))^-0.29) * HE_SubTime * Scal_HDiel * Scal_H_ForEff
HE_Scal_PrD  =  ScalDRtwCIg * HE_Scal_dw * Scal_HE_pD * calQIO *  (((3.70 *  HE_Scal_dw + .000001) /
    (HE_Scal_no + .000001))^-0.29) * HE_SubTime * Scal_HDiel * Scal_H_ForEff
HF_Scal_PrA  =  ScalDRtwCIg * HF_Scal_dw * Scal_HIF_pA * calQIO *  (((3.70 *  HF_Scal_dw + .000001) /
    (HF_Scal_no + .000001))^-0.29) * HF_SubTime * Scal_HDiel * Scal_H_ForEff
HF_Scal_PrB  =  ScalDRtwCIg * HF_Scal_dw * Scal_HIF_pB * calQIO *  (((3.70 *  HF_Scal_dw + .000001) /
    (HF_Scal_no + .000001))^-0.29) * HF_SubTime * Scal_HDiel * Scal_H_ForEff
HF_Scal_PrC  =  ScalDRtwCIg * HF_Scal_dw * Scal_HIF_pC * calQIO *  (((3.70 *  HF_Scal_dw + .000001) /
    (HF_Scal_no + .000001))^-0.29) * HF_SubTime * Scal_HDiel * Scal_H_ForEff
HF_Scal_PrD  =  ScalDRtwCIg * HF_Scal_dw * Scal_HIF_pD * calQIO *  (((3.70 *  HF_Scal_dw + .000001) /
    (HF_Scal_no + .000001))^-0.29) * HF_SubTime * Scal_HDiel * Scal_H_ForEff
HI_Scal_PrA  =  ScalDRtwCIg * HI_Scal_dw * Scal_HIF_pA * calQIO *  (((3.70 *  HI_Scal_dw + .000001) /
    (HI_Scal_no + .000001))^-0.29) * HI_SubTime * Scal_HDiel * Scal_H_ForEff
HI_Scal_PrB  =  ScalDRtwCIg * HI_Scal_dw * Scal_HIF_pB * calQIO *  (((3.70 *  HI_Scal_dw + .000001) /
    (HI_Scal_no + .000001))^-0.29) * HI_SubTime * Scal_HDiel * Scal_H_ForEff
HI_Scal_PrC  =  ScalDRtwCIg * HI_Scal_dw * Scal_HIF_pC * calQIO *  (((3.70 *  HI_Scal_dw + .000001) /
    (HI_Scal_no + .000001))^-0.29) * HI_SubTime * Scal_HDiel * Scal_H_ForEff
HI_Scal_PrD  =  ScalDRtwCIg * HI_Scal_dw * Scal_HIF_pD * calQIO *  (((3.70 *  HI_Scal_dw + .000001) /
    (HI_Scal_no + .000001))^-0.29) * HI_SubTime * Scal_HDiel * Scal_H_ForEff
LD_Scal_PrA  =  ScalDRtwCIg * LD_Scal_dw * Scal_LTd_pA * calQIO *  (((3.70 *  LD_Scal_dw + .000001) /
    (LD_Scal_no + .000001))^-0.29) * LD_SubTime * Scal_LDiel * Scal_L_ForEff
LD_Scal_PrB  =  ScalDRtwCIg * LD_Scal_dw * Scal_LTd_pB * calQIO *  (((3.70 *  LD_Scal_dw + .000001) /
    (LD_Scal_no + .000001))^-0.29) * LD_SubTime * Scal_LDiel * Scal_L_ForEff
LD_Scal_PrC  =  ScalDRtwCIg * LD_Scal_dw * Scal_LTd_pC * calQIO *  (((3.70 *  LD_Scal_dw + .000001) /
    (LD_Scal_no + .000001))^-0.29) * LD_SubTime * Scal_LDiel * Scal_L_ForEff
LD_Scal_PrD  =  ScalDRtwCIg * LD_Scal_dw * Scal_LTd_pD * calQIO *  (((3.70 *  LD_Scal_dw + .000001) /
    (LD_Scal_no + .000001))^-0.29) * LD_SubTime * Scal_LDiel * Scal_L_ForEff
LS_Scal_PrA  =  ScalDRtwCIg * LS_Scal_dw * Scal_LTd_pA * calQIO *  (((3.70 *  LS_Scal_dw + .000001) /
    (LS_Scal_no + .000001))^-0.29) * LS_SubTime * Scal_LDiel * Scal_L_ForEff
LS_Scal_PrB  =  ScalDRtwCIg * LS_Scal_dw * Scal_LTd_pB * calQIO *  (((3.70 *  LS_Scal_dw + .000001) /
    (LS_Scal_no + .000001))^-0.29) * LS_SubTime * Scal_LDiel * Scal_L_ForEff
```

LS_Scal_PrC = ScalDRtwClg * LS_Scal_dw * Scal_LTd_pC * calQIO * (((3.70 * LS_Scal_dw + .000001) / (LS_Scal_no + .000001))^-0.29) * LS_SubTime * Scal_LDiel * Scal_L_ForEff
LS_Scal_PrD = ScalDRtwClg * LS_Scal_dw * Scal_LTd_pD * calQIO * (((3.70 * LS_Scal_dw + .000001) / (LS_Scal_no + .000001))^-0.29) * LS_SubTime * Scal_LDiel * Scal_L_ForEff

HU_Lcal_PrA = LcalDRtwClOg * HU_Lcal_dw * Lcal_HU_pA * calQIO * (1.950* (((4.00 * HU_Lcal_dw + .000001) / (HU_Lcal_no + .000001))^-0.29)) * HU_SubTime * Lcal_HDiel * Lcal_H_ForEff
HU_Lcal_PrB = LcalDRtwClOg * HU_Lcal_dw * Lcal_HU_pB * calQIO * (1.950* (((4.00 * HU_Lcal_dw + .000001) / (HU_Lcal_no + .000001))^-0.29)) * HU_SubTime * Lcal_HDiel * Lcal_H_ForEff
HU_Lcal_PrC = LcalDRtwClOg * HU_Lcal_dw * Lcal_HU_pC * calQIO * (1.950* (((4.00 * HU_Lcal_dw + .000001) / (HU_Lcal_no + .000001))^-0.29)) * HU_SubTime * Lcal_HDiel * Lcal_H_ForEff
HU_Lcal_PrD = LcalDRtwClOg * HU_Lcal_dw * Lcal_HU_pD * calQIO * (1.950* (((4.00 * HU_Lcal_dw + .000001) / (HU_Lcal_no + .000001))^-0.29)) * HU_SubTime * Lcal_HDiel * Lcal_H_ForEff
HE_Lcal_PrA = LcalDRtwClOg * HE_Lcal_dw * Lcal_HE_pA * calQIO * (1.950* (((4.00 * HE_Lcal_dw + .000001) / (HE_Lcal_no + .000001))^-0.29)) * HE_SubTime * Lcal_HDiel * Lcal_H_ForEff
HE_Lcal_PrB = LcalDRtwClOg * HE_Lcal_dw * Lcal_HE_pB * calQIO * (1.950* (((4.00 * HE_Lcal_dw + .000001) / (HE_Lcal_no + .000001))^-0.29)) * HE_SubTime * Lcal_HDiel * Lcal_H_ForEff
HE_Lcal_PrC = LcalDRtwClOg * HE_Lcal_dw * Lcal_HE_pC * calQIO * (1.950* (((4.00 * HE_Lcal_dw + .000001) / (HE_Lcal_no + .000001))^-0.29)) * HE_SubTime * Lcal_HDiel * Lcal_H_ForEff
HE_Lcal_PrD = LcalDRtwClOg * HE_Lcal_dw * Lcal_HE_pD * calQIO * (1.950* (((4.00 * HE_Lcal_dw + .000001) / (HE_Lcal_no + .000001))^-0.29)) * HE_SubTime * Lcal_HDiel * Lcal_H_ForEff
HF_Lcal_PrA = LcalDRtwClOg * HF_Lcal_dw * Lcal_HIF_pA * calQIO * (1.950* (((4.00 * HF_Lcal_dw + .000001) / (HF_Lcal_no + .000001))^-0.29)) * HF_SubTime * Lcal_HDiel * Lcal_H_ForEff
HF_Lcal_PrB = LcalDRtwClOg * HF_Lcal_dw * Lcal_HIF_pB * calQIO * (1.950* (((4.00 * HF_Lcal_dw + .000001) / (HF_Lcal_no + .000001))^-0.29)) * HF_SubTime * Lcal_HDiel * Lcal_H_ForEff
HF_Lcal_PrC = LcalDRtwClOg * HF_Lcal_dw * Lcal_HIF_pC * calQIO * (1.950* (((4.00 * HF_Lcal_dw + .000001) / (HF_Lcal_no + .000001))^-0.29)) * HF_SubTime * Lcal_HDiel * Lcal_H_ForEff
HF_Lcal_PrD = LcalDRtwClOg * HF_Lcal_dw * Lcal_HIF_pD * calQIO * (1.950* (((4.00 * HF_Lcal_dw + .000001) / (HF_Lcal_no + .000001))^-0.29)) * HF_SubTime * Lcal_HDiel * Lcal_H_ForEff
HI_Lcal_PrA = LcalDRtwClOg * HI_Lcal_dw * Lcal_HIF_pA * calQIO * (1.950* (((4.00 * HI_Lcal_dw + .000001) / (HI_Lcal_no + .000001))^-0.29)) * HI_SubTime * Lcal_HDiel * Lcal_H_ForEff
HI_Lcal_PrB = LcalDRtwClOg * HI_Lcal_dw * Lcal_HIF_pB * calQIO * (1.950* (((4.00 * HI_Lcal_dw + .000001) / (HI_Lcal_no + .000001))^-0.29)) * HI_SubTime * Lcal_HDiel * Lcal_H_ForEff
HI_Lcal_PrC = LcalDRtwClOg * HI_Lcal_dw * Lcal_HIF_pC * calQIO * (1.950* (((4.00 * HI_Lcal_dw + .000001) / (HI_Lcal_no + .000001))^-0.29)) * HI_SubTime * Lcal_HDiel * Lcal_H_ForEff
HI_Lcal_PrD = LcalDRtwClOg * HI_Lcal_dw * Lcal_HIF_pD * calQIO * (1.950* (((4.00 * HI_Lcal_dw + .000001) / (HI_Lcal_no + .000001))^-0.29)) * HI_SubTime * Lcal_HDiel * Lcal_H_ForEff
LD_Lcal_PrA = LcalDRtwClOg * LD_Lcal_dw * Lcal_LTd_pA * calQIO * (1.950* (((4.00 * LD_Lcal_dw + .000001) / (LD_Lcal_no + .000001))^-0.29)) * LD_SubTime * Lcal_LDiel * Lcal_L_ForEff
LD_Lcal_PrB = LcalDRtwClOg * LD_Lcal_dw * Lcal_LTd_pB * calQIO * (1.950* (((4.00 * LD_Lcal_dw + .000001) / (LD_Lcal_no + .000001))^-0.29)) * LD_SubTime * Lcal_LDiel * Lcal_L_ForEff
LD_Lcal_PrC = LcalDRtwClOg * LD_Lcal_dw * Lcal_LTd_pC * calQIO * (1.950* (((4.00 * LD_Lcal_dw + .000001) / (LD_Lcal_no + .000001))^-0.29)) * LD_SubTime * Lcal_LDiel * Lcal_L_ForEff
LD_Lcal_PrD = LcalDRtwClOg * LD_Lcal_dw * Lcal_LTd_pD * calQIO * (1.950* (((4.00 * LD_Lcal_dw + .000001) / (LD_Lcal_no + .000001))^-0.29)) * LD_SubTime * Lcal_LDiel * Lcal_L_ForEff
LS_Lcal_PrA = LcalDRtwClOg * LS_Lcal_dw * Lcal_LTd_pA * calQIO * (1.950* (((4.00 * LS_Lcal_dw + .000001) / (LS_Lcal_no + .000001))^-0.29)) * LS_SubTime * Lcal_LDiel * Lcal_L_ForEff
LS_Lcal_PrB = LcalDRtwClOg * LS_Lcal_dw * Lcal_LTd_pB * calQIO * (1.950* (((4.00 * LS_Lcal_dw + .000001) / (LS_Lcal_no + .000001))^-0.29)) * LS_SubTime * Lcal_LDiel * Lcal_L_ForEff
LS_Lcal_PrC = LcalDRtwClOg * LS_Lcal_dw * Lcal_LTd_pC * calQIO * (1.950* (((4.00 * LS_Lcal_dw + .000001) / (LS_Lcal_no + .000001))^-0.29)) * LS_SubTime * Lcal_LDiel * Lcal_L_ForEff
LS_Lcal_PrD = LcalDRtwClOg * LS_Lcal_dw * Lcal_LTd_pD * calQIO * (1.950* (((4.00 * LS_Lcal_dw + .000001) / (LS_Lcal_no + .000001))^-0.29)) * LS_SubTime * Lcal_LDiel * Lcal_L_ForEff

C_Parameters_=X{XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX}

{C1 - Predator Daily Rations. The ration is specific for a 1 gram (wet weight) animal feeding at 20 degrees Celsius, with the exception of Palaemonetes, which is for an 0.1 gram (wet weight) animal and for large crabs (_Lcal_), which is for a 10.0 gram (wet weight) animal.}

genDRtwClg = 0.12 {mean of all documented values below}
hetDRtwClg = 0.162 {modified from Weisberg et al 1981 and Weisberg and Lotrich 1982}

```
menDRtwCIg = genDRtwCIg
sciDRtwCIg = 0.069 {modified from Brooks 1985 for B. chrysoura}
ScalDRtwCIg = 0.142 {value for Lcal (below) extrapolated to smaller crabs using Laird and Haefner 1976}
LcalDRtwCIOg = 0.079 {method of Elliott and Perrson 1978 applied to data from Ryer 1987}
palDRtwCoIg = 0.127 {modified from Morgan 1980 and Wood 1967}

{C2 - Predator Q10 equations, temperature range of 18 to 32 degrees C. These are set up to
produce a value of 1.0 at 20 degrees Celsius. A Q10 value of 2.0 (genQIO) is used in the absence
of other information.}

genQIO = 0.2500 * (10^(0.0301*Temp)) {Q10 = 2.0 for temperature range, estimated from the
    documented values below and from Winberg 1960}
hetQIO = 0.2630 * (10^(0.0290*Temp)) {Q10 = 1.95 for temperature range, modified from Nichols 1931}
menQIO = genQIO
sciQIO = 0.3420 * (10^(0.0233*Temp)) {Q10 = 1.71 for temperature range, extrapolated from Brooks
    1985 for B. chrysoura}
calQIO = 0.6104 * (10^(0.0107*Temp)) {Q10 = 1.28 for temperature range, modified from Laird and
    Haefner 1976 and Eggleston 1990}
palQIO = 0.3764 * (10^(0.0212*Temp)) {Q10 = 1.63 for temperature range, estimated from Welsh 1975}


{C3 - Diel feeding. A value of 1.0 indicates equal feeding during day and night. The fraction
of time during daylight that is available to a daytime feeder for feeding can be calculated as
(DayLength/24). In practice, since consumption is calculated as a daily ration averaged over
24 hours, this calculation is of very little consequence to the final results
for an individual fish. The diel factor does affect habitat-specific daily ration over a
24 hour time period. This is because the relative extent to which each habitat is flooded during
the peak feeding time might change from day to day given different tide/daylength combinations.
This is included in the model but does not greatly affect the overall results.}

FLT_HDiel = 1.0 {No diel cycle assumed in absence of other information}
FLT_LDiel = 1.0 {No diel cycle assumed in absence of other information}
gbo_HDiel = 1.0 {No diel cycle assumed in absence of other information}
gbo_LDiel = 1.0 {No diel cycle assumed in absence of other information}
str_HDiel = 1.0 {No diel cycle assumed in absence of other information}
Str_LDiel = 1.0 {No diel cycle assumed in absence of other information}
Shet_HDiel = MIN(((2 * (Day_HT))/(Day_HT + Nite_HT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 1.25) {Primarily daytime feeders, based on Weisberg et al 1981 and
    on gut analyses from this study}
Shet_LDiel = MAX(((2 * (Day_LT))/(Nite_LT + Day_LT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 0.75) {Primarily daytime feeders, based on Weisberg et al 1981 and
    on gut analyses from this study}
Lhet_HDiel = MIN(((2 * (Day_HT))/(Day_HT + Nite_HT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 1.25) {Primarily daytime feeders, based on Weisberg et al 1981
    and on gut analyses from this study}
Lhet_LDiel = MAX(((2 * (Day_LT))/(Nite_LT + Day_LT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 0.75) {Primarily daytime feeders, based on Weisberg et al 1981
    and on gut analyses from this study}
luc_HDiel = MIN(((2 * (Day_HT))/(Day_HT + Nite_HT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 1.25) {Assumed similar to F. heteroclitus}
luc_LDiel = MAX(((2 * (Day_LT))/(Nite_LT + Day_LT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 0.75) {Assumed similar to F. heteroclitus}
maj_HDiel = MIN(((2 * (Day_HT))/(Day_HT + Nite_HT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 1.25) {Assumed similar to F. heteroclitus}
maj_LDiel = MAX(((2 * (Day_LT))/(Nite_LT + Day_LT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 0.75) { {Assumed similar to F. heteroclitus}
men_HDiel = MIN(((2 * (Day_HT))/(Day_HT + Nite_HT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 1.25) {Primarily daytime feeders based on gut analyses from this
    study}
men_LDiel = MAX(((2 * (Day_LT))/(Nite_LT + Day_LT))/(((Day_HT)/(Day_HT + Nite_HT)) +
    ((Day_LT)/(Nite_LT + Day_LT))), 0.75) {Primarily daytime feeders based on gut analyses from this
    study}
bai_HDiel = 1.0 {No diel cycle assumed in absence of other information}
bai_LDiel = 1.0 {No diel cycle assumed in absence of other information}
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cyn_HDiel  =  1.0 {No diel cycle assumed in absence of other information}
cyn_LDiel  =  1.0 {No diel cycle assumed in absence of other information}
lei_HDiel  =  1.0 {No diel cycle assumed in absence of other information}
lei_LDiel  =  1.0 {No diel cycle assumed in absence of other information}
soc_HDiel  =  1.0 {No diel cycle assumed in absence of other information}
soc_LDiel  =  1.0 {No diel cycle assumed in absence of other information}
Scal_HDiel  =  1.0 {No diel cycle in marshes, Ryer 1987}
Scal_LDiel  =  1.0 {No diel cycle in marshes, Ryer 1987}
Lcal_HDiel  =  1.0  {No diel cycle in marshes, Ryer 1987}
Lcal_LDiel  =  1.0 {No diel cycle in marshes, Ryer 1987}
PAL_HDiel  =  1.0 {No diel cycle assumed in absence of other information}
PAL_LDiel  =  1.0 {No diel cycle assumed in absence of other information}

{C4 - Tidal Foraging Efficiency. Many cyprinodonts have been shown to feed more actively at
high tide versus low tide. Gut fullness data from this study was used to determine the extent
of this preference for marsh dependent species. Values of 1.0 for both _H_ and _L_ indicate
equal feeding at both tides. If values other than 1.0 are chosen, further calculations may be
required in order to maintain the daily ration of each predator. }

FLT_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
FLT_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
gbo_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
gbo_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
str_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
str_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
Shet_H_ForEff =  1.111*(2.0/((2*HE_Subtime* 1.111) + ((1 - HE_Subtime) *.9*2)))  {based on gut
    content analyses from this study}
Shet_L_ForEff =  .9*(2.0/((2*HE_Subtime* 1.111) + ((1 - HE_Subtime) *.9*2)))  {based on gut content
    analyses from this study}
Lhet_H_ForEff =  1.111*(2.0/((2*HE_Subtime* 1.111) + ((1 - HE_Subtime) *.9*2)))  {based on gut
    content analyses from this study}
Lhet_L_ForEff =  .9*(2.0/((2*HE_Subtime* 1.111) + ((1 - HE_Subtime) *.9*2)))  {based on gut content
    analyses from this study}
luc_H_ForEff =  1.0  {No tidal feeding cycle assumed due to insufficient information in gut analyses, this
    study}
luc_L_ForEff =  1.0  {No tidal feeding cycle assumed due to insufficient information in gut analyses, this
    study}
maj_H_ForEff =  1.0  {No tidal feeding cycle, Werme 1981}
maj_L_ForEff =  1.0  {No tidal feeding cycle, Werme 1981}
men_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
men_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
bai_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
bai_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
cyn_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
cyn_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
lei_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
lei_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
soc_H_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
soc_L_ForEff =  1.0  {No tidal feeding cycle assumed in absence of other information}
Scal_H_ForEff =  1.2*(2.0/((HE_Subtime*1.2*2) + ((1 - HE_Subtime) * 0.833 *2)))  {based on gut content
    analyses from this study, also from Ryer 1987, Laughlin 1982}
Scal_L_ForEff =  0.833*(2.0/((HE_Subtime* 1.2 *2) + ((1 - HE_Subtime) * 0.833 *2)))  {based on gut
    content analyses from this study, also from Ryer 1987, Laughlin 1982}
Lcal_H_ForEff =  1.3*(2.0/((HE_Subtime* 1.3 *2) + ((1 - HE_Subtime) * 0.770*2)))  {based on gut
    content analyses from this study, also from Ryer 1987, Laughlin 1982}
Lcal_L_ForEff =  0.770*(2.0/((HE_Subtime* 1.3 *2) + ((1 - HE_Subtime) * 0.770 *2)))  {based on gut
    content analyses from this study, also from Ryer 1987, Laughlin 1982}
PAL_H_ForEff =  1.0 {No tidal feeding cycle assumed due to insufficient information in gut analyses, this
    study}
PAL_L_ForEff =  1.0 {No tidal feeding cycle assumed due to insufficient information in gut analyses, this
    study}

{C5 - Fraction of predator diet that is each prey. This is entered separately for each prey when
information about that prey is desired. A list of values for each predator x habitat x prey
```

combination is provided separately from this model. The list is derived from means of data obtained in the gut content study associated with this project. A value of 0 indicates that the predator does not eat the particular prey, while a value of 1.0 indicates that the entire diet of that predator is the single prey.}

{PREY A = INSERT GUT VALUES}

FLT_HTd_pA =
FLT_LTd_pA =
gbo_All_pA =
str_All_pA =
Shet_HE_pA =
Shet_HF_pA =
Shet_HI_pA =
Shet_LTd_pA =
Lhet_HE_pA =
Lhet_HF_pA =
Lhet_HI_pA =
Lhet_LTd_pA =
luc_HU_pA = luc_LTd_pA
luc_HE_pA =
luc_HIF_pA =
luc_LTd_pA =
maj_HTd_pA =
maj_LTd_pA =
men_Msh_pA =
men_Off_pA =
bai_All_pA =
cyn_All_pA =
lei_All_pA =
soc_All_pA =
Scal_HU_pA =
Scal_HE_pA =
Scal_HIF_pA =
Scal_LTd_pA =
Lcal_HU_pA =
Lcal_HE_pA =
Lcal_HIF_pA =
Lcal_LTd_pA =
PAL_HE_pA =
PAL_HIF_pA =
PAL_LTd_pA =

{PREY B = INSERT GUT VALUES}

FLT_HTd_pB =
FLT_LTd_pB =
gbo_All_pB =
str_All_pB =
Shet_HE_pB =
Shet_HF_pB =
Shet_HI_pB =
Shet_LTd_pB =
Lhet_HE_pB =
Lhet_HF_pB =
Lhet_HI_pB =
Lhet_LTd_pB =
luc_HU_pB = luc_LTd_pB
luc_HE_pB =
luc_HIF_pB =
luc_LTd_pB =
maj_HTd_pB =
maj_LTd_pB =
men_Msh_pB =

men_Off_pB =
bai_All_pB =
cyn_All_pB =
lei_All_pB =
soc_All_pB =
Scal_HU_pB =
Scal_HE_pB =
Scal_HIF_pB =
Scal_LTd_pB =
Lcal_HU_pB =
Lcal_HE_pB =
Lcal_HIF_pB =
Lcal_LTd_pB =
PAL_HE_pB =
PAL_HIF_pB =
PAL_LTd_pB =

{PREY C = INSERT GUT VALUES}

FLT_HTd_pC =
FLT_LTd_pC =
gbo_All_pC =
str_All_pC =
Shet_HE_pC =
Shet_HF_pC =
Shet_HI_pC =
Shet_LTd_pC =
Lhet_HE_pC =
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Lhet_HI_pC =
Lhet_LTd_pC =
luc_HU_pC = luc_LTd_pC
luc_HE_pC =
luc_HIF_pC =
luc_LTd_pC =
maj_HTd_pC =
maj_LTd_pC =
men_Msh_pC =
men_Off_pC =
bai_All_pC =
cyn_All_pC =
lei_All_pC =
soc_All_pC =
Scal_HU_pC =
Scal_HE_pC =
Scal_HIF_pC =
Scal_LTd_pC =
Lcal_HU_pC =
Lcal_HE_pC =
Lcal_HIF_pC =
Lcal_LTd_pC =
PAL_HE_pC =
PAL_HIF_pC =
PAL_LTd_pC =

{PREY D = INSERT GUT VALUES}

FLT_HTd_pD =
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gbo_All_pD =
str_All_pD =
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Shet_HF_pD =

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Shet_HI_pD  =
Shet_LTd_pD  =
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Lhet_HF_pD  =
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Lhet_LTd_pD  =
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luc_HE_pD  =
luc_HIF_pD  =
luc_LTd_pD  =
maj_HTd_pD  =
maj_LTd_pD  =
men_Msh_pD  =
men_Off_pD  =
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PAL_HE_pD  =
PAL_HIF_pD  =
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                        END OF MODEL version 6-98
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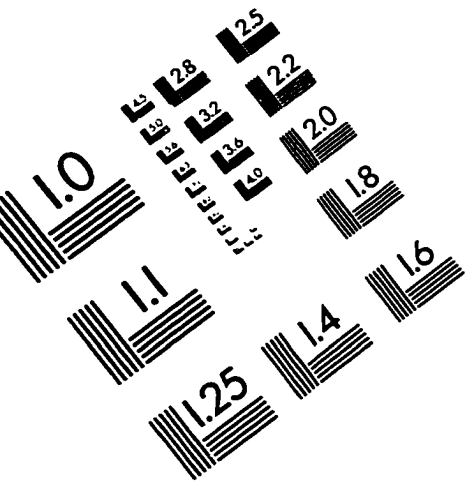
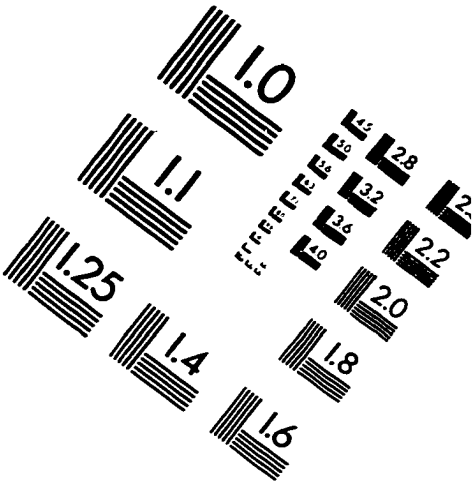
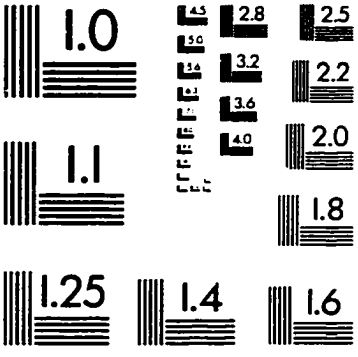
VITA

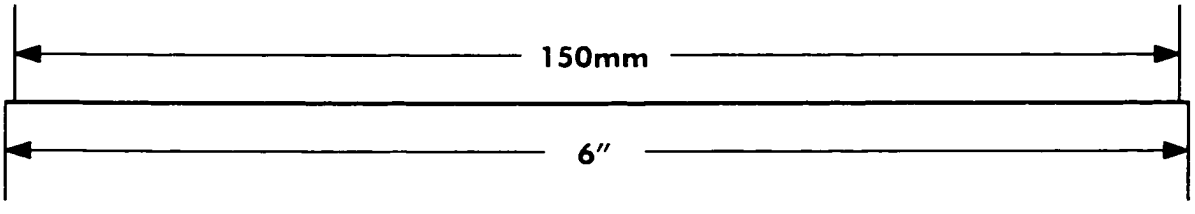
Giancarlo Cicchetti was born in Italy in 1964. He moved with his family to the United States in 1966, and has lived in various parts of the country. He graduated from Harvard University in 1986 with a BA in Biology. In 1987, Giancarlo married Jennifer Sternick. The couple moved to Maine where Jennifer attended the University of Maine School of Law and Giancarlo taught Biology in high school. In 1993, Giancarlo enrolled in a degree program at the Virginia Institute of Marine Science. Giancarlo and Jennifer's 2 children, Nicholas and Paul, were born while Giancarlo was a graduate student.

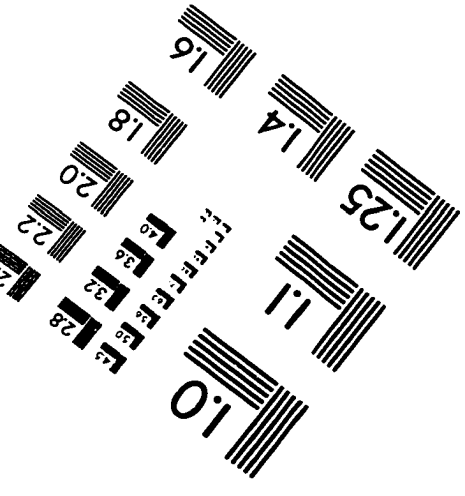
IMAGE EVALUATION TEST TARGET (QA-3)

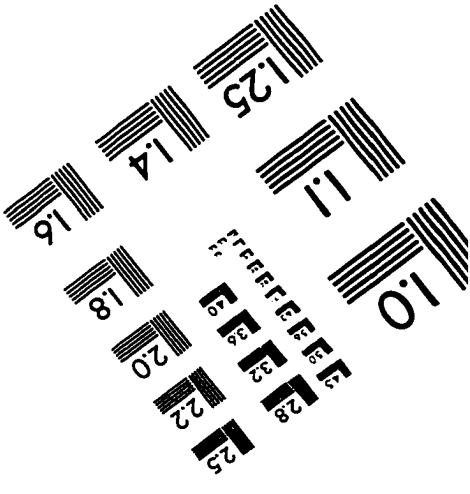












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