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AN ECOLOGICAL ANALYSIS of NAUSET MARSH

Cape Cod National Seashore

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AN ECOLOGICAL ANALYSIS OF NAUSET MARSH - Cape Cod National Seashore -

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Use of Salt-Marsh Peat Reefs by Small Juvenile Lobsters on Cape Cod, Massachusetts

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ABSTRACT: The habitats utilized by small juvenile (<40 mm carapace length, CL) lobsters (Homarus americanus) are poorly known. We discovered and studied an undescribed juvenile lobster habitat in Nauset Marsh, Cape Cod. Juvenile lobsters ($\bar{X} = 26.7$ mm carapace length, 6 to 72 mm, n = 38) were collected from suction samples primarily in "peat reef" habitats during the period from August 1985 through October 1986. The reefs consisted of large blocks of Spartina alterniflora peat that had separated from the marsh surface and fallen into adjacent subtidal marsh channels. The smallest lobsters (6 to 7 mm CL) were collected from peat reefs in October 1985, and April and July 1986. In these habitats, juvenile lobster density averaged 2.5 individuals m⁻¹ (range 0-5.7) in suction samples. Peat reef habitats occur in other salt marshes in the northeastern United States and may be an important nursery habitat for small juvenile lobsters.

Introduction

The fishery for American lobster (Homarus americanus) is among the most valuable in the United States. Despite the economic importance and numerous studies of this species (Cobb and Phillips 1980; International Workshop on Lobster Recruitment 1986), little is known of the biology of small juvenile lobsters (<40 mm carapace length, CL) or their habitat. Field observations in nature are few and the general absence of the post-planktonic, benthic juveniles in field collections is a longstanding enigma (Cobb 1986). In a few instances small juveniles have been collected by scuba divers in hard bottom habitats (Cooper et al. 1975; Bernstein and Campbell 1983: Elner and Hamet 1984) and observed in mud substrates (Cooper and Uzmann 1980). The purpose of this paper is to describe a salt marsh habitat utilized by small juvenile lobsters in a Cape Cod estuary.

Study Site

The Nauset Marsh study site is a Spartina alterniflora-dominated marsh system located behind barrier beaches and connected through an inlet to the Atlantic Ocean at approximately 41°49'N on Cape Cod, Massachusetts. The system has a maximum depth of 6 m and a tidal range of 2 m. During the period of study, temperature varied from 0 to

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Fig. 1. Diagramatic cross section through typical salt marsh channel showing peat reefs.

23 °C and salinity from 24 to 35‰. Lobsters are common and a small pot fishery exists.

Methods

Sampling was conducted in representative Nauset Marsh habitats as part of a larger study of fish and shellfish habitat utilization from August 1985 through October 1986. Preliminary underwater observations suggested that peat reefs in marsh creek channels supported juvenile and adult lobsters.

Peat reefs, as here described, consist of large (up to 5 to 7 m long), irregular blocks of salt marsh peat that break off from the marsh surface and fall into adjacent marsh creek channels (Fig. 1). After the blocks of marsh peat fall into the creek (a process common to other New England salt marshes (Redfield 1972)), the Spartina may continue to grow on that portion above mean low water. Spartina that is deposited subtidally decays and eventually the surface of the peat becomes densely covered with algae (e.g., Codium fragile, Enteromorpha spp., Ulva lactuca) and is colonized by invertebrates. Common macroinvertebrates of the reefs include juvenile and adult lobster, green crab (Carcinus maenas), rock crab (Cancer irroratus), spider crab (*Libinia* sp.), and rarely, mud crab (*Neopanope sayi*). Fishes frequently found in and around the reef include cunner (Tautogolabrus adspersus), American eel (Anguilla rostrata), and occasionally, rock gunnel (Pholis gunnellus), white hake (Urophycis tenuis), radiated shanny (Ulvaria subbifurcata), pollock (Pollachius virens) and grubby (Myoxocephalus aenaeus). Often there were two or three horizons of peat reefs at the same location and these were separated by distinct, usually narrow, sand channels where the creek bottom substrate is exposed (Fig. 1). Peat reefs occur along the margins of the deepest marsh creek channels throughout Nauset Marsh. These structures are much larger and are distributed in deeper water than the ice-rafted salt marsh peat

described by Hardick-Witman (1985, 1986), although both originate from the same material.

In most habitats (eelgrass, intertidal sand, intertidal macroalgal mud flat and marsh pools), quantitative suction sampling in depths less than 1 m (modified from Zimmerman and Minello 1984, Zimmerman et al. 1984) began with the deployment of a cylinder that enclosed 0.85 m² of the bottom and the water column above (n = 56). The contents of the cylinder and the surface of the substrate were sucked up with a gasoline-powered pump and passed through a 0.5-mm mesh bag. At all locations where the large cylinder was used, the contents of the mesh bag were preserved in 10% formalin, washed and later sorted in the laboratory. Peat reefs were sampled by hookah-assisted divers who randomly placed a smaller cylinder over 0.13 m² of peat reef surface and the suction sampler was used to pump out the contents (n = 13). On some occasions suction samples covered an undetermined area (qualitative samples) of peat reef to determine presence of juvenile lobsters. Suction sampling at peat reef habitats was conducted at seven different locations in Nauset Marsh during August and October 1985, and April, June, July, August, and October 1986. For all peat reef collections, the sample was sorted for juvenile lobsters shortly after collection. Each lobster captured was measured to the nearest millimeter carapace length (CL, the distance from posterior rim of eye socket to posterior edge of carapace along the dorsal midline).

Results

Juvenile lobsters were only collected in peat reef habitats. The qualitative and quantitative suction samples found small juveniles (6–72 mm CL, mean CL = 26.7, n = 38) in burrows in most peat reef collections. Density of small juvenile lobster (<40 mm CL) ranged from 0 to 5.7 individuals m^{-2} . In one frequently sampled marsh creek channel, small juvenile lobsters were present in samples in August (mean CL = 41.4 mm, n = 10) and October (mean CL = 41.4 mm, n = 10)CL = 18.0, n = 10) 1985, and April (mean CL =9.5, n = 2), June (mean CL = 30.5, n = 7), and October (mean CL = 24.0, n = 3) 1986. At the same site during June and October 1986 mean density was 3.3 m^{-2} (1.57 SD, n = 4 samples) and 2.5 m^{-2} (2.07 SD, n = 3), respectively. Mean density of small juvenile lobsters for all quantitative peat reef suction samples in all peat reef habitats was 2.1 m⁻² (n = 13). These are underestimates of juvenile lobster density because on at least two occasions a lobster escaped over the rim of the cylinder while suction sampling.

Small juveniles (<40 mm CL) were present in peat reef samples at all collection periods. The oc-

currence of the smallest individuals (6-7 mm CL) also spanned most seasons, including collections in October 1985, and April and July 1986. Visual observations while diving indicated that peat reefs were used by a wide size range of lobsters. Typically, larger lobsters (>40 mm CL) were found in extensive burrows, some almost 1 m deep, at the base of the peat reef. Often these burrows had another entrance, on the opposite side of the reef. The largest and most obvious opening always faced the center of the marsh creek channel and frequently had a mound of substrate immediately outside the entrance. The smaller lobsters appeared to have burrows distributed on the outer surface of the peat reef, although these were often difficult to detect visually because of the dense algal growth. Most small juveniles (<40 mm CL) were collected on this surface. Often the most extensively burrowed reefs, with what appeared to be the largest lobster populations, were those found deepest in the channels. The peat in these reefs was less firm and much more porous than in the shallower reefs nearer the marsh surface. On one occasion three small lobsters (15, 22, and 27 mm CL) were collected by hand when small peripheral chunks of peat (0.2-0.4 m largest dimension) that were resting on the bottom of the channel were turned over to reveal burrows under the peat.

Discussion

Our discovery of small juvenile lobsters in salt marsh peat reefs demonstrates the potential nursery role these habitats might play in the ecology of inshore lobster populations. The smallest juvenile lobsters (6-7 mm CL) collected from peat reefs are typical of lobsters that have recently left the plankton and begun a benthic existence (Stage IV and older; Herrick 1911; Scarrat 1973). Previous laboratory studies of habitat utilization (Pottle and Elner 1982; Botero and Atema 1982; Roach 1983; Barshaw 1987) have not tested peat reefs as potential juvenile habitats. Smaller juveniles (at least some less than 40 mm CL) have been reported to occupy rocky (Cooper et al. 1975; Bernstein and Campbell 1983: Elner and Hamet 1984) and mud substrates (Cooper and Uzmann 1977). In our Nauset Marsh study sites the small juvenile lobsters were only collected in peat reefs, although a few larger lobster were collected by trawl in eelgrass (unpublished data, authors of this paper) and over mud and sand substrate. In addition, our collections from peat reefs provide quantitative determinations of densities (mean 2.1 m⁻², range 0-5.7) that are much greater than previously reported. Actual determinations of lobster density (presumably juvenile and adult) range from 0.09 to 0.35 lobsters m⁻² in Narragansett Bay rocky bottom

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habitat (Cobb 1971: Cobb et al. 1986) and 0.04 to 0.12 m⁻² for a sand substrate with rock outcrops near Boothbay, Maine (Cooper et al. 1975). Other studies based primarily on smaller juveniles have found mean densities of 0.11 m⁻² (modal carapace length = 58 mm, range 10-65 mm, Bernstein and Campbell 1983) and 0.0-0.24 m⁻² (mean carapace length = 45 mm, range 20-132 mm, Elner and Hamet 1984). Densities of juveniles in mud substrates have been reported to be 1-20 m⁻². These are based on visual estimates, presumably of burrows (Cooper, unpublished data, in Cooper and Uzmann 1977).

The general significance of salt marsh peat reefs as habitat for the smallest benthic juvenile lobsters in other areas is unknown. However, salt marsh with a fibrous peat substrate ranges from Maine to southern New Jersey (Chapman 1960) and we as-sume that peat reef habitat may have a simillar distribution. The abundance of the smallest juvenile lobsters in peat reefs, however, could vary geographically. Recently, Lavalli and Barshaw (1986) have shown, in the laboratory, that mud crabs (Neopanope sayi) and cunner (Tautogolabrus adspersus) can prey upon postlarval lobsters and that predation by the former may be an important source of mortality. During our extensive sampling in Nauset Marsh we seldom encountered mud crabs in any habitat. Assuming that predation by mud crabs occurs under natural conditions, we suggest that utilization of peat reefs by small juvenile lobsters may not be as common to the south, where mud crabs are abundant (Williams 1984). Despite this potential source of mortality, salt marsh peat reefs may have special significance as lobster habitat because all benthic stages of lobster can utilize them, based on our observations in Nauset Marsh.

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ABSTRACT

The habitats utilized by early juvenile lobsters, <u>Homarus americanus</u>, are poorly known. However, high densities of juvenile lobsters (< 40 mm CL) were recently observed in salt marsh peat reefs on Cape Cod, Massachusetts. To assess the quality of peat reef habitat, peat was compared to two other substrates (rocks and sand, previously determined to be good and poor habitats, respectively) using two measures of habitat quality, time to settling and survival from predation. In each treatment late Stage IV (settling stage) lobsters were placed into tanks with peat, rock and sand substrates for two days and allowed to settle and build burrows. Juvenile lobsters settled into rocks and peat quickly, but delayed settling into sand, suggesting that the former two were preferred habitats.

Fish (<u>Tautogolabrus adspersus</u>) and green crabs (<u>Carcinus maenas</u>) predators were then added to each treatment except for predator free controls. No significant differences were found in lobster survival when predators were introduced into the habitats two days before or after the lobsters. Rocks provided significantly more protection from fish than either peat or sand, and peat provided significantly more protection than sand. Similarly, rocks provided significantly more protection from crabs than peat or sand. The relationship between peat and sand, however, was not consistent with crabs as the predator. Although Stage IV lobsters chose to settle in peat as quickly as in rock habitats, rocks provided better protection from predation. The refuge value of peat in these experiments varied with type of predator.

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INTRODUCTION

Several recent experiments have examined the role of various substrates as refuges for postlarval American lobsters. Of the substrates tested, rock has consistently provided the most protection, with eelgrass and mud providing better protection than sand (Roach, 1983; Lavalli and Barshaw, 1986; Barshaw and Lavalli, In review). Using artificial substrates Johns and Mann (1987) tested bricks and bricks with varying amounts of macro-algae as refuge from fish predators for early juvenile lobsters. They found a positive relationship between the number of algae plants and protection.

While researchers have had a long standing difficulty finding the post-planktonic benthic juvenile lobsters in the field (Cobb, 1986). Recently, Richard Wahle (Personal Communication, University of Maine, Darling Center, Walpole, Maine 04573) has found densities up to $20/m^2$ of small juvenile lobsters in cobble substrates in Maine. Also, on Cape Cod, Massachusetts, Able et al. (In press) have found high densities (range 0 -5.7 individuals / m^2 , mean 2.5) of early juvenile lobsters (<40 mm CL) consistently in a previously untested and undescribed habitat - salt marsh 'peat reefs'. These consist of large (up to 5-7 m long), irregular blocks of salt marsh peat and living marsh plants that break off from the marsh surface and fall into adjacent marsh creek channels. Green crabs (<u>Carcinus maenas</u>) and the fish, cunners (<u>Tautogolabrus adspersus</u>) are some of the most abundant potential lobster predators found in this habitat (Able et al. In press).

The purpose of this study was to compare peat reef as juvenile lobster habitat to two other substrates: rocks and sand, previously determined to be good and poor habitats, respectively (Botero and Atema, 1982; Lavalli and Barshaw, 1986; Barshaw and Lavalli, In review;). These comparisons were based on two measures of habitat quality; time to settling and protection against two different types of predators, green crabs and cunners.

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METHODS

Thirty two replicate tanks (0.6 m wide, 0.8 m long, 0.6 m deep) were supplied with flowing, ambient, unfiltered sea water. The tanks contained either sand (10 cm deep), rock (0.1 - 20 cm diameter, 12 cm deep) over a base of sand, or peat reef (5 - 30 cm deep) substrates also over a base of sand. The rocks were collected from subtidal areas in Woods Hole, Massachusetts while the peat reef was collected near the Rutgers University Marine Field Station, Tuckerton, New Jersey. Care was taken to make sure that the bioeroded surface of the peat was exposed in the tanks. After being placed into the tanks the peat was covered with fresh water for 48 hours to kill any macroinvertebrates and fishes that might be living inside. After the 48 hour period all dead animals were removed, the fresh water was drained and the substrates were exposed to running sea water for one week. For the first series of experiments (Run 1) 14 tanks were designated as predator free controls (5, 5, and 4 tanks containing peat, rocks, and sand, respectively). The 18 experimental tanks were divided evenly between the three substrates and two predator species, so that there were 6 tanks of each substrate, 3 with green crabs and 3 with cunners as predators.

After the one week acclimation period, 10 (= $20.8/m^2$) late Stage IV lobsters (reared at the Marthas Vineyard, Massachusetts, Lobster Hatchery) were placed into each of the tanks in Run 1. While this density is high, it falls within the limits of natural densities: for example, Richard Wahle found up to $20/m^2$ in cobble in Maine (Personal Communication), and densities of juveniles in mud substrates have been reported to be $1 - 20/m^2$ based on visual estimates, presumably of burrows (as Cooper, unpublished data, in Cooper and Uzmann, 1977). After release into the tanks lobsters were given two days to settle and build burrows. During this period lobsters were fed daily with frozen brine shrimp. After two days we stopped feeding

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and introduced the predators. Either three cunners $(=6.2/m^2, 55-120 \text{ mm}$ total length, TL) or five green crabs $(=10.4/m^2, 35-65 \text{ mm} \text{ carapace width}, CW)$ were placed into each of the experimental tanks. The predators were allowed four days to prey upon lobsters after which time the predators were removed and the substrates sorted to determine the number of surviving lobsters. Censuses were taken on the number of lobsters that were still swimming in the water column, i.e. were not walking on or burrowed in the substrate, four times daily for the six days of each run. A census took approximately one minute per tank.

Run 2 was similar to Run 1, except that because we found no significant differences between the controls of each substrate in Run 1 and no differences were found between controls of different substrates in similar previous experiments (Barshaw and Lavalli, In review), we eliminated the peat and rock controls. Thus, in Run 2 we had four sand controls; the remaining 28 tanks were than divided between the three substrates and two predators as follows: fish - 6, 6 and 3 tanks of peat, rock and sand respectively; crabs - 5, 5, and 3 tanks of peat, rocks and respectively.

Run 3 had the same arrangement of substrates and predators as in Run 2 but, to test the effect of prior residence, the predators were introduced into the tanks before the lobsters. The predators were given two days to acclimate after which 10 lobsters were placed in each tank. Interactions between lobsters and predators in each tank were observed for ten minutes after the lobsters were introduced into each tank. The lobsters remained in the tanks for four days. After this period substrates were sorted for surviving lobsters as in previous runs.

The census data were analyzed with a 2-way ANOVA testing for the effects of both time since lobster introduction and substrate type, on the number of lobsters remaining in the water column. The survival data were analyzed for

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differences between runs and between substrate types using contingency tables analyzed with Chi-square tests.

These experiments were carried out at the Rutgers University Marine Field Station, Tuckerton, New Jersey from July 1 - August 21, 1987. Water temperature and salinity ranged from 22-28° C and 24-29°/oo respectively, during this period.

RESULTS

Time To Settling

In these experiments lobsters appeared to prefer rock and peat substrates more than sand as indicated by the quickness with which they settled into the former two substrates. There were no significant differences in the time to settling between Run 1 and Run 2 so these data were combined (Students T-test p > 0.1). A significantly greater number of lobsters remained swimming in the sand substrate than in either the peat or rock substrates (Fig.1, 2-way ANOVA, p < .001; Students-Newman-Keuls test, p < .05). Although, there were significantly fewer lobsters swimming over the sand substrate after eight hours than before or afterwards (Fig.1, 2-way ANOVA, p < .001, S-N-K test, p< .05). There was no significant difference between the number of lobsters swimming in peat versus rock.

Survival

Lobster survival was greatest in predator free controls, but survival from predators varied, sometimes inconsistently, between substrates and type of predators. Greater numbers of lobsters survived in the predator free controls than in any of the treatments with predators (Fig. 2, Table 1). There were no significant differences between the number of lobsters surviving in the controls of different substrates so these data from Run 1

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were combined for subsequent analyses. There was also no significant difference between the number of lobsters surviving in the sand controls of the three runs.

With fish as predators lobster survival was consistent between runs for all three substrates, however, survival varied significantly between substrates within a run (Table 1). Survival was greatest in the controls followed by rocks then peat. No lobster survived in the sand (Fig. 2, Table 1). With green crabs as the predators, there were differences between runs, for some substrates (Fig. 2, Table 1). There were no significant differences between lobster survival in rocks among the three runs. However, greater numbers of lobsters survived in the peat substrate in Run 3 than in either Run 1 or Run 2. Also, a greater number of lobsters survived in sand in Run 2 and Run 3 than survived in sand in Run 1 . Rocks always provided significantly better protection against the crabs than either sand or peat. In Run 2 and Run 3 there were no significant differences in lobster survival between the rock substrates and the predator-free controls. There were no significant differences between lobster survival in the peat or sand substrate in either Run 1 or Run 3; however, in Run 2 a greater number of lobsters survived in the sand than in the peat (Fig. 2, Table 1).

DISCUSSION

These experiments were not designed to provide data on the absolute predation rate lobsters experience in the field, rather they were designed to provide relative comparisons of habitat quality based on two indicators, time to settle and relative predation rate in each habitat. We assume that a short settling time is indicative of a positive response to a habitat while delayed settling represents a negative response. Some evidence that Stage IV

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lobsters continue swimming over unsuitable substrates was collected by Cobb et al. (1983) and Botero and Atema (1982). The absolute predation rate in nature could vary due to three important factors. 1) the density of predators and lobsters are usually lower in nature (Able et al., In Press; Richard Wahle, Personal Communication; Richard Cooper, unpublished data) than in these experiments; 2) the density of predators in nature would vary from one substrate to another; 3) there likely would be higher order interactions between cunners and green crabs and their predators, thus altering their behavior.

Our results for the sand and rock substrates (Fig.1, Table 1) are consistent with previous experiments which also show that small juvenile lobsters delay settling into sand while quickly settling into rocks (Botero and Atema, 1982, Barshaw and Bryant-Rich, in review; Barshaw and Lavalli, in review). By this measure peat appears to be a preferred habitat (Fig.1, Table 1) although there was a tendency toward quicker settling into rocks (i.e. almost immediate settlement).

Lobster survival varied with type of predators which presumably reflected differences in predator behavior in different habitats. When cunners were the predators the survival data mirrored the ranking for the settling data, i.e. lobsters were best protected in rocks, while peat reef provided intermediate protection and sand provided no protection (Fig. 1). These data were consistent for all three runs of the experiment.

When green crabs were used as predators, rocks still provided the best protection. In previous experiments with mud crabs, <u>Neopanope sayi</u>, as predators, using the same size rocks, (Lavalli and Barshaw, 1986; Barshaw and Lavalli, In Review) juvenile lobsters of the same stage suffered high mortalities. However, the green crabs used in these trials were larger (35 -65 mm CW) than the mud crabs (11 - 25 mm CW) used in the previous

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experiments, and thus may not have been able to enter small burrows or interstices between the rocks that could be occupied by a small juvenile lobster. Roach (1983) also found that large crabs (<u>Cancer irroratus</u>) were unable to prey upon lobsters occupying rock habitats.

Peat did not provide better protection relative to sand when green crabs were used as predators, and, in Run 2 more lobsters survived in the sand than in the peat substrates. The ability of green crabs to burrow readily into peat was evident in our field collection for individuals of this species. Also, during the experiments crabs were observed making tunnels and ripping up the peat. Thus, green crabs are quite capable of digging juvenile lobsters out of their burrows.

An unexpected result from this experiment was that the occurrence of predators in the substrates prior to introduction of lobsters (Run 3) did not decrease survival. Intuitively it would seem that while the lobsters were building their burrows they would be especially vulnerable; however, our results do not support this hypothesis.

The observation that time to settle consistently ranks substrates in the same order and that, at least with fish as predators, those substrates in which lobsters settle fastest are the same in which they have the highest survival rate, suggests that these tests are useful indicators of habitat quality. Overall, by these two measures, peat reef was found to rank intermediate between rocks and sand. However, with green crabs as predators there was a clear indication that rocks were the substrate of highest rank with peat and sand far behind.

Our study combined with the Able et al. (In Press) field survey emphasizes that early juvenile lobsters are flexible in their choice of habitat and while they may choose the best available substrate, they are capable of burrowing and surviving in rock and peat substrates. The

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cumulative observations of these and others (Botero and Atema, 1982; Roach, 1983; Lavalli and Barshaw, 1986; Barshaw and Lavalli, In review) indicate that rock habitat provides the best protection, but size and behavior of the predator are important parameters affecting the survival of juvenile lobsters in different habitats.

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We thank our friends and colleagues at the Rutgers University Marine Field Station, all of whom helped at some point during the labor intensive portions of the experiment. Special thanks go to Jeanette Bowers, Byungja Marciante and Elizabeth Semple who helped collect the substrates, take censuses and sort for the juvenile lobsters. Mike Syslo and Kevin Johnson from the Massachusetts State Lobster Hatchery, Marthas Vineyard, and Andrew Paterson from the Cutler Marine Hatchery, Cutler, Maine provided Stage IV lobsters. Financial support was provided by the National Park Service, Cooperative Research Unit, and the Center for Coastal and Environmental Studies, Rutgers University.

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Table 1: Differences in lobster survival between the four treatments (predator free controls = C, rocks = R, peat = P, and sand = S) and the two types of predators (fish, cunners, <u>Tautogolabrus adspersus</u>, and crabs, <u>Carcinus maenas</u>) based on Chi-squared tests.

| | RUN 1 | RUN 2 | RUN 3 | BETWEEN RUNS |
|--------------|-------------------------------|-------------------------------|------------------------------|--|
| FISH p < | C > R > P > S .01 .01 .001 | C > R > P > S .05 .001 .01 | C > R > P > S .01 .05 .01 | NO DIFFERENCES |
| CRABS p < | C > R > P,S .05 .001 | C,R > S > P .001 .05 | C,R > P,S .001 | P _{Run#3} > P _{Run#1,2} .05 |
| | | | | $S_{P_{11}}/2 \rightarrow S_{P_{11}}/1$ |

.05

Figure Legend

- Fig. 1. Average number of juvenile lobsters (n=10 per tank) swimming over sand, peat reef and rock substrates during the first 44 hours of the experiment (before predators were introduced). Sand vs. Peat and Rock, p < .001.</p>
- Fig. 2. Percent of lobsters surviving predation by cunners, <u>Tautogolabrus</u> <u>adspersus</u>, and green crabs, <u>Carcinus maenas</u>, in three different substrates. In Run 3 the predators were introduced before the lobsters. * indicates survival of lobsters in the sand tanks with fish predators was zero.

FIGURE 1







Predator Regime

White hake, <u>Urophycis tenuis</u>, in the Gulf of Maine: spawning seasonality, habitat use and growth in young-of-the-year, and relationships to the Scotian Shelf population.

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White hake, <u>Urophycis tenuis</u>, in the Gulf of Maine: spawning seasonality, habitat use and growth in young-of-the-year, and relationships to the Scotian Shelf population.

ABSTRACT

Our interpretation of the pattern of white hake spawning seasonality, habitat use and growth of young-of-the-year in the Gulf of Maine-Georges Bank area is based on analyses of extensive collections of eggs and larvae, pelagic-juveniles, and firstdemersal juveniles. Comparisons are made with studies conducted in Canadian waters. Eggs or larvae of U. tenuis are not found at any time in the study area. During four consecutive years (1984-1987) pelagic-juveniles appeared in Gulf of Maine-Georges Bank collections in May-June, and size distributions indicate a shoreward migration with growth. Recruitment to nearshore areas was detected in June-July and the rate of growth for demersal juveniles was calculated to average 1.02 mm/day in the first summer. Young-of-the-year remain spatially segregated from 1+ fish and both groups are segregated from the adult population. Well-documented spawning of this species during August-September on the Scotian Shelf does not appear to influence the Gulf of Maine population and instead appears to involve a separate stock with a different spawning schedule. It is concluded that spawning which results in recruitment to nearshore areas of Gulf of Maine and Southern New England occurs in continental slope

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regions south of Scotian Shelf, Georges Bank and Southern New England during early spring and that this spawning event also provides pelagic-juveniles to the Scotian Shelf prior to the onset of local spawning there. Future studies should address the relationship between these slope populations and those occurring in deeper basins in the Gulf of Maine.

INTRODUCTION

The western North Atlantic hake, <u>Urophycis tenuis</u> (Mitchill), is morphologically similar in all ontogenetic stages to its congener, <u>U. chuss</u> (Walbaum), and is often misidentified. Treatments of its biology and life history are often avoided because of this similarity (i.e. Bigelow and Schroeder 1953; Leim and Scott 1966). <u>Urophycis tenuis</u> is found over the continental shelf edge, deeper basins in the Gulf of Maine, and submarine canyons along the continental slope (Bigelow and Schroeder 1953; Musick 1974; Cooper et al. 1987). Both hake species have pelagic eggs and larvae followed by a pelagic-juvenile stage and then a first-demersal juvenile stage. On the Scotian Shelf they are sympatric during the pelagic-juvenile stage although some diel periodicity in availability to sampling gear is apparent (Markle <u>et al.</u> 1982).

The first-demersal stage of <u>U</u>. <u>tenuis</u> is poorly documented and not well understood. While we do not refute the claim, often repeated in the literature, that young-of-the-year <u>U</u>. <u>tenuis</u> occupy nearshore shallows, we find little published data to document the claim. Most reports are obscure or lack details, but do provide the necessary background to justify further sampling effort. Bigelow and Schroeder (1953), while not able to distinguish between young of <u>U</u>. <u>tenuis</u> and <u>U</u>. <u>chuss</u>, commented on the presence of young hakes in eelgrass beds in the vicinity of Woods Hole. Nichols and Breder (1927) reported <u>U</u>. <u>tenuis</u>

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specimens 59-66 mm SL "collected in shallow water at the shore" during May near Shark River, New Jersey. MacDonald <u>et al</u>. (1984) reported on the seasonal occurrence of young <u>U</u>. <u>tenuis</u> in the Bay of Fundy. Markle <u>et al</u>. (1982) related the occurrence of pelagic-juveniles on Scotian Shelf to the occurrence of young demersal juveniles in the Bay of Fundy and described age-length relationships for two year classes within that bay. With the exception of Bigelow and Schroeder's (1953) brief comment, however, these reports have not provided details of <u>U</u>. <u>tenuis</u> habitats nor have age estimates been based on techniques other than length-frequency inferences. There have also been no attempts to establish spawning seasonality based on these collections.

Maturity studies in the Gulf of Maine have failed to clearly define spawning seasonality and investigators have been frustrated by a scarcity of ripe specimens (Burnett <u>et al</u>. 1984). This has prompted some investigators to suggest that the Gulf of Maine population demonstrates weak, aperiodic, and protracted spawning and that the population is sustained by recruits from the Scotian Shelf (i.e. Musick 1969). A report that in Gulf of Maine specimens examined, only 7% of males and less than 2% of females were in a ripe condition (Burnett <u>et al</u>. 1984) supports that suggestion.

Confusion concerning spawning seasonality is due partly to past difficulties in identifying the hake species and partly to the fact that authors studying <u>U</u>. <u>tenuis</u> have applied different

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criteria to the establishment of spawning seasons. Reports range from midsummer in the southern Gulf of St. Lawrence, Grand Bank, and Gulf of Maine (Lambert and Ware 1984; Petrov 1973; Sumner <u>et</u> <u>al</u>. 1913), to summer-early fall on Scotian Shelf (Markle <u>et al</u>. 1982), fall-winter on Scotian Shelf (Musick 1969) and winterearly spring in northeastern Gulf of St. Lawrence (Markle <u>et al</u>. 1982) and Bay of Fundy (Battle MS 1951).

The purposes of the present study are to describe the firstyear life history of U. tenuis and to evaluate earlier studies concerning spawning seasonality and the relationships between Scotian Shelf and Gulf of Maine populations based on the early stages. This can be accomplished because materials including pelagic-juveniles and young demersal stages are available and identification problems which confounded earlier investigators have been resolved (Musick 1973; Methven 1985). The study is particularly pertinent because commercial landings of U. tenuis are presently at the highest level since the late 1940's (Burnett et al. 1984). Most U.S. landings (79% of total, 1970-1983) have been from catches made in western Gulf of Maine (Burnett et al. 1984). Some of these landings are a by-catch of other fisheries, but there is directed effort toward U. tenuis (a gill-net fishery), and continued decline of other groundfish species might add momentum to this trend.

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MATERIALS AND METHODS

SOURCES OF STUDY MATERIAL: Lengths and meristic characters of all hakes examined for this study are documented elsewhere (Fahay 1987). Eggs, larvae, and pelagic-juveniles of <u>U</u>. <u>tenuis</u> were collected on NMFS (National Marine Fisheries Service) MARMAP (Marine Resources Monitoring, Assessment and Prediction) cruises in the Gulf of Maine and/or Georges Bank during 1984-1987. We examined demersal juvenile (including inquiline) hakes of all species less than 100 mm TL collected during NMFS bottom trawl and scallop survey cruises during fall 1985 and spring 1986 (Table 1).

Pelagic-juvenile <u>U</u>. <u>tenuis</u> were also collected from seabirds at Matinicus Rock, Maine. Nesting Atlantic puffins (<u>Fratercula</u> <u>arctica</u>) and Arctic terns (<u>Sterna paradisaea</u>) were mist-netted as they returned to nests carrying fish prey for nestlings. As these adults hit the net they dropped loads of fishes from their bills and research associates involved with the "Fratercula" project (National Audubon Society) collected them. The term "fish load" refers to a sample of fish prey from one bird on a single collection date.

A series of first-demersal juvenile hakes was collected in the Damariscotta River, Maine, incidental to a study of trophic relationships among larval cottids (Laroche 1982). These collections were made with a Blake trawl with a 1.3-m mouth width. Netting was 2.5 cm stretched mesh with a 0.64 cm

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stretched mesh liner. Sampling in this study was conducted during every month (except February) between July 1972 and June 1974. Much of this material was lost in a fire in 1985. The surviving material is reported on here.

The Massachusetts Nearshore Trawling Program retained all hakes less than 100 mm TL collected in coastal waters during survey cruises in fall, 1985 and spring, 1986. Only one station (Station 54 of "Gloria Michelle" Cruise 8592, September 12, 1985, 8 m depth, south of West Tisbury Great Pond, Martha's Vineyard) during those two cruises yielded small hakes (n=60). Thirty were examined (£0).

A habitat-specific study in the 945-hectare Nauset Marsh system (Cape Cod National Seashore) included sampling with a 4.8m otter trawl (Heck <u>et al</u>. in review). The marsh complex is composed of a number of distinct habitats including salt marsh (35% of the system), intertidal mudflats (12%), and sandflats (11%). Freshwater wetlands, mussel bars, and eelgrass (<u>Zostera</u> <u>marina</u>) beds are also included and the latter beds comprise 6% of the total area. Sampling was directed toward these habitats and a basin characterized seasonally by the presence of drift algae (<u>Gracilaria verrucosa</u>). Four replicate 2-min tows were made at each site during each sampling period. Hakes collected during this study were identified in the field, measured, and frozen for later removal of otoliths and stomachs.

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DIAGNOSTIC CHARACTERS: Adult and juvenile specimens examined for this study were identified on the basis of numbers of epibranchial gill rakers, total caudal fin rays, and precaudal and caudal vertebrae (Table 2). Pelagic-juveniles were identified on the basis of melanistic pigment on the pelvic fin membranes (absent in U. regia, usually present in other species), total caudal fin rays (examined by X-ray or after briefly staining with alizarin red), and vertebral counts (examined by Xray). Total caudal fin rays in pelagic-juveniles can also be accurately counted microscopically with polarized light. Counts thus obtained were verified by radiographs. Larvae larger than 8.0 mm SL were identified by total caudal fin ray counts, combined with the presence/absence of pelvic fin melanin, while larvae smaller than 8.0 mm SL were identified by pigment characters (Methven 1985). In this study, certain larvae are designated as "<u>Urophycis</u> sp.". These do not include <u>U</u>. <u>tenuis</u>. Workers are presently unable to specifically identify hake eggs, and early-stage egg identifications are tentative because of possible confusion with the eggs of Peprilus triacanthus (Stromateidae).

LIFE HISTORY STAGE TERMINOLOGY: Transition from the larval to pelagic-juvenile stage is not well-defined. The arbitrary terms used herein refer as much to collection gear as to state of development. "Larvae" include those specimens collected in a 61cm bongo net which sampled in double-oblique fashion from surface

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to bottom or 200 m, whichever was less. "Pelagic-juveniles" include all specimens from two sampling gears. "Neuston Net" (Table 1) refers to the second of three neuston samplers described by Bartlett and Haedrich (1968) equipped with 1.7 mm mesh. This sampler was towed at 3.5 knots on the surface at selected stations during MARMAP cruises. "MOCNESS" refers to a 10 m² multiple-net opening-closing device with 3.0 mm mesh which sampled discrete depth strata (including the surface) at 2 knots. The term "first-demersal juvenile" refers to the initial bottom stage of hakes, after descent from the epipelagic zone, and is used interchangeably with "young-of-the-year" in this paper to include fishes residing during their first summer in nearshore areas.

Larvae reported on here are deposited in the collections of the American Museum of Natural History or the Sandy Hook Laboratory (NMFS,NEFC). Eggs and older stages of hakes are lodged either at the Sandy Hook Laboratory or the Marine Field Station, Rutgers University, Tuckerton, New Jersey.

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RESULTS AND COMPARISONS WITH OTHER STUDIES

EGGS AND LARVAE: In the Georges Bank-Gulf of Maine study area, eggs of <u>Urophycis</u> sp. are temporally restricted to summer and fall and co-occur with larval <u>U</u>. <u>chuss</u> or <u>U</u>. <u>regia</u>. Cruises during the first six months of 1984-1986 collected almost no <u>Urophycis</u> sp. eggs in the Georges Bank-Gulf of Maine area (Table 3). Identifications of middle- and late-stage eggs of <u>Urophycis</u> sp. are restricted to one egg in April 1984 (Gulf of Maine) and four eggs in May 1984 (Georges Bank).

Reports of collections of <u>U</u>. <u>tenuis</u> eggs are limited to southern Gulf of St. Lawrence in August and September (Markle and Frost 1985) while eggs collected on Scotian Shelf in August and September were assumed to include both <u>U</u>. <u>tenuis</u> and <u>U</u>. <u>chuss</u> (Markle <u>et al</u>. 1982).

Larvae also rarely occur in our collections in the study area during the first six months of the year (Table 3) and other studies document the absence of <u>Urophycis</u> sp. larvae during the winter in Georges Bank-Gulf of Maine waters (Colton and St. Onge 1974, Bolz <u>et al</u>. 1981, Townsend 1984). The possibility that <u>U</u>. <u>tenuis</u> spawns in nearshore waters and that the eggs and larvae thus escape detection by deeper water surveys seems remote. Twice-monthly sampling during two years in the coastal area in and around Sheepscot Estuary, Maine, produced no hake eggs or larvae (Chenoweth 1973). Nor were hake larvae collected by Laroche (1982) who sampled several locations within the

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Damariscotta River estuary on 14 collection dates from January through May 1973 and 7 dates from February through April 1974.

Larval <u>U</u>. <u>tenuis</u> were also absent from collections during 1984-1985 on Georges Bank or in the Gulf of Maine from July through December (Table 3). Nor were <u>U</u>. <u>tenuis</u> larvae collected with a variety of collecting gear during the Nauset Marsh study, from April through December of two years (1986-1987).

On the Scotian Shelf, no larvae were collected during the earliest sampling period reported, mid-May to mid-July (Markle <u>et</u> <u>al</u>. 1982). Larvae (assumed by these authors to include both <u>U</u>. <u>tenuis</u> and <u>U</u>. <u>chuss</u>) were abundant on Scotian Shelf during August and September.

Small <u>U</u>. <u>tenuis</u> larvae have been collected in early June within a Gulf Stream warm core ring located seaward of the southern Scotian Shelf and southeast of the eastern tip of Georges Bank (Wroblewsky and Cheney 1984). A more detailed discussion of this material is contained in the following section.

PELAGIC-JUVENILES: Two generalizations can be made concerning 1984-1987 collections of pelagic-juvenile <u>U</u>. <u>tenuis</u> in Georges Bank-Gulf of Maine waters: 1) their initial occurrences are restricted temporally to May-June; and 2) they are capable of avoiding a net during daylight, regardless of the depths sampled.

Pelagic-juvenile <u>U</u>. <u>tenuis</u> were distributed evenly over the Gulf of Maine and Georges Bank during May-June (Table 4) but the

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smallest of these (<30 mm TL) were collected near the continental shelf edge and the largest (>60 mm TL) were collected nearer to the coast (Fig. 1). Nocturnal vulnerability to collecting gear in the epipelagic zone by <u>U</u>. <u>tenuis</u> pelagic-juveniles (Markle <u>et</u> <u>al</u>. 1982) is suggested in data from MARMAP collections. While not all night tows collected <u>U</u>. <u>tenuis</u>, nearly all successful tows occurred at night. Whether the lack of pelagic-juveniles in day collections is due to net avoidance or reflects a diel vertical migration behavior is in part demonstrated by MOCNESS collections and seabird feeding studies.

<u>Urophycis tenuis</u> pelagic-juveniles are not abundant in 10m² MOCNESS collections directed at young-of-the-year gadids (<u>Gadus</u> <u>morhua</u> and <u>Melanogrammus aeglefinus</u>), either because of tow speed or timing and location of sampling (G. Lough, NMFS, NEFC, pers. commun.). Nevertheless, in 1986, 18 pelagic-juvenile <u>U</u>. <u>tenuis</u> (31-69 mm SL) were collected at a 48-hour station, sampled every 6 hours (Fig. 2). There are no correlations between fish size and depth, time of capture and depth, or time of capture and fish size. What is apparent from this meager evidence is that regardless of all other variables, <u>U</u>. <u>tenuis</u> pelagic-juveniles are susceptible to capture at all depths (including near-surface) at night, indicating they are capable of avoiding even the largest nets during daylight, and also suggesting that they may occur meso- as well as epipelagically.

Data from seabird feeding studies add to our knowledge of \underline{U} . <u>tenuis</u> distribution in the water column. The Atlantic puffin is

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a diving bird that is likely to collect prey at any depth from the surface to a maximum of about 50 m (Piatt and Nettleship 1985) and we limit the utility of the puffin prey data to confirmation of the seasonality of occurrences. During studies at Matinicus Rock, ME, in summer of 1987, U. tenuis pelagicjuveniles occurred in 96% of 266 puffin fish loads examined from June 13 through July 5 (S. Kress, NAS, pers. commun.) The Arctic tern, however, captures prey only at the surface and only during the day. <u>Urophycis</u> tenuis pelagic-juveniles occurred in 68% of 868 tern fish loads (S. Kress, pers. commun.). Lengths and seasonal occurrences of these collections are in synchrony with the puffin captures and also indicate strongly that U. tenuis pelagic-juveniles occur at the surface during the day and that their absence in daytime neuston collections is due to net avoidance.

Previous reports of collections of pelagic-juvenile <u>U</u>. <u>tenuis</u> are limited. Marak and Colton (1961) and Marak <u>et al</u>. (1962a, 1962b) report on the results of collections made by a surface-towed meter net during the spring (February through June) of 1953, 1955 and 1956. Although the date of first occurrence varies somewhat between years (late April to mid-May) the lack of captures in earlier months corresponds with our observations in 1984-1987. The size distributions (Fig. 3) are similar to our recent collections, with smaller sizes occurring over the continental edge and larger sizes nearer the coast. Musick (1969) also analyzed these data and demonstrated a monthly (late

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April through June) progression of pelagic-juvenile occurrences from the shelf-edge shoreward.

Collections of pelagic-juvenile U. tenuis on the Scotian Shelf (Markle et al. 1982) showed patterns which relate to our observations on Georges Bank and Gulf of Maine. During May and June, pelagic-juveniles were more abundant on the northeast part of the shelf and collections there consisted of smaller individuals than on the southwest part. In the following sampling period (June-July) this was reversed, with smaller individuals occurring in greater abundance on the southwest part. Mean lengths of all Scotian Shelf pelagic-juveniles decreased between May and September while total numbers increased. Based largely on this evidence, the absence of larvae in May-June, and limited maturity data, Markle et al. (1982) concluded that the earliest occurring (and largest) pelagic-juveniles on the Scotian Shelf were the product of upstream spawning, tentatively identified as occurring in the northeast Gulf of St. Lawrence or Laurentian Channel. The influx of smaller individuals later in the season (August and September) was attributed to local spawning.

<u>Urophycis tenuis pelagic-juveniles from Georges Bank-Gulf of</u> Maine are similar in size to May-June material collected on Scotian Shelf. Length (mm SL) mean and range for 1984-1987 are 35.8 and 15.1-63.8, respectively. Scotian Shelf values for May-June were 37.7 and 19-59 (Markle <u>et al</u>. 1982). Based on these data we suggest that the material collected from Georges Bank-

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Gulf of Maine originates from the same spawning source, and during the same time period, as the material collected on Scotian Shelf. Frequency distributions of total caudal fin rays in <u>U</u>. <u>tenuis</u> pelagic-juveniles collected during the present study (Table 5) also indicate a similarity to Scotian Shelf material. The mean count (35.8) and range (33-39) correspond with values given for Scotian Shelf material (36.5 and 33-39) (Methven 1985).

Larval and pelagic-juvenile U. tenuis have also been collected in early June from an area seaward of the Scotian Shelf. Samples along a transect from the edge of Scotian Shelf to the center of a Gulf Stream warm core ring included U. tenuis ranging from 0(sic) to 48 mm SL with a mode between 12 and 18 mm SL (Wroblewsky and Cheney 1984). The largest individuals were collected on stations nearest the continental shelf break, while the smallest larvae were collected farther offshore. Seaward entrainment of continental shelf-spawned species by this warm core ring is not indicated since larvae of shelf species (i.e. Gadus morhua, Melanogrammus aeglefinus) were conspicuously absent, while larvae typifying slope and oceanic waters (i.e. Anthias sp., Bothus sp., Gonichthys cocco, Helicolenus dactylopterus) were abundant.

FIRST-DEMERSAL JUVENILES: Among all sources listed (Table 1), <u>Urophycis tenuis</u> in the first-demersal stage occurred only in Damariscotta River estuary and Nauset Marsh collections. Sampling by the NMFS bottom trawl survey does not detect <u>U</u>.

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tenuis less than about 20 cm and commercial landings (including discards) do not provide information on fishes less than about 25 cm (Burnett et al. 1984). Damariscotta River collections were taken during July 1972 and May-July 1973. Mean lengths were 57 mm TL on May 29, 1973 (n=6) and 94 mm TL on July 11, 1973 and July 14, 1972 (n=19).

The collections made as part of the habitat-specific ecological study of Nauset Marsh (Heck et al. in review) provide the best time series available for first-demersal juvenile U. tenuis. Otter-trawl collections provided 77 young-of-the-year U. tenuis from August to October 1985 and from June to October 1986, primarily from eelgrass beds (Fig. 4) or in a few cases from a station selected for its greater relative depth and characterized by the seasonal occurrence of drift algae (Gracilaria verrucosa). Among the 22 species of fishes collected from eelgrass beds during the three-year study, Urophycis tenuis ranked seventh in abundance and was the most abundant species among non-residents. Lengths of U. tenuis collected ranged from 56-107 mm TL in June to 191-295 mm TL in October (Figure 5). Otoliths were removed from representative fish through the summer of 1986. These were sectioned and analyzed, found to lack a first annulus, and thus represent young-of-the-year (J. Burnett, NMFS, NEFC, pers. commun.).

There are consistent patterns in size with time of year and depth of capture between Nauset Marsh collections and those from Bay of Fundy (Markle <u>et al</u>. 1982) and the offing of Little Egg

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Inlet, NJ (Thomas and Milstein 1973) (Fig. 6). The Bay of Fundy data were collected in two depth strata: the smaller specimens from sampling in 2-18 m in Cumberland Basin; the larger from 28-73 m in Passamaquoddy Bay. In September and October, Markle <u>et</u> <u>al</u>. (1982) noted a trend for fish from the shallow water group to join the deeper water group, while larger members of the latter group emigrated from the area, thus the apparent rate of growth in both groups decreases during the fall. The upper Bay of Fundy data points, then, describe one-year-old fish initially, with an infusion of young-of-the-year in the fall. These data indicate that in the Bay of Fundy, where eelgrass beds are rare, young-ofthe-year are spatially segregated from older fish by occupying shallower areas (i.e. Cumberland Basin).

Comparison with samples collected off Little Egg Inlet, New Jersey was confounded by a blend of trawling locations in various depths. During May-August, <u>U. tenuis</u> collections were made in depths ranging from 1.5 to 12 m, with most between 6 and 12 m. During November and December, <u>U. tenuis</u> were collected from depths ranging from 6 to 15 m, with most between 12 and 15 m. By virtue of the depths selected for sampling during these periods therefore, these data indicate a situation similar to that of Bay of Fundy, with young-of-the-year occupying shallower water during the summer and joining older fish in deeper water during the fall. In both cases, young-of-the-year and one-year-old fish are spatially segregated from each other and from the adult population (i.e. fish >40 cm).

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The rate of growth in Nauset Marsh young-of-the-year, observed in serial collections made between June 3 (Julian Day 154) and October 14, 1986 (Julian Day 287) was 1.02 mm/day (n=60). The estimate based on two collection dates in 1985 was 1.21 mm/day (n=17). Estimates of the rate of growth in larval and pelagic-juvenile stages have been based on means or modes of serial collections (Markle et al. 1982) or on unspecified methods (Lambert and Ware 1984). In the former study, estimates ranged from 0.35 to 0.73 mm/day, in the latter, 0.70 mm/day. The rates of growth might be expected to differ between pelagic and demersal life history stages and while we do not include the latter estimates in our calculation, we estimate a pelagicjuvenile growth rate of 1.16 mm/day (Table 6). This estimate is a preliminary one and subject to reevaluation based on age/length studies and a study of the mechanisms controlling the distribution of various sized pelagic-juveniles. Lengths of pelagic-juveniles from oceanic collections are compared with those of young-of-the-year from Nauset Marsh in Fig. 7.

CIRCULATION PATTERN RELATIVE TO Urophycis tenuis DISTRIBUTION:

The relationship between Scotian Shelf and Gulf of Maine circulation is especially critical when considering the suggested role the Scotian Shelf <u>U</u>. <u>tenuis</u> population plays in recruitment to the Gulf of Maine population. A generalized model of circulation within the range of <u>U</u>. <u>tenuis</u> emerges from a variety of studies using several methods, together indicating that the

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area including the Gulf of St. Lawrence, Scotian Shelf, and Gulf of Maine operates as an oceanographic unit, influenced both by Labrador Current and St. Lawrence River discharge, and displays different characteristics depending on time of year. Included in the variety of methods employed are studies of geostrophic flow (Drinkwater <u>et al</u>. 1979; Houghton <u>et al</u>. 1978), temperature or salinity minima lag times (Sutcliffe <u>et al</u>. 1976), zooplankton distribution and drift (Redfield 1941), and drift bottle studies of surface circulation (i.e. Bumpus and Lauzier 1965).

A nearshore arm of the Labrador Current rounds the coast of Newfoundland and enters the Gulf of St. Lawrence via the deeper layers of the northern half of Cabot Strait. This current contributes to the cyclonic circulation within the gulf and is enhanced by seasonally variable discharge from the St. Lawrence This current and low saline discharge then flows through River. the Magdalen Shallows (southwest of Laurentian Channel in the southern part of the gulf) and leaves the gulf through the shallower layers of the southern part of Cabot Strait. After rounding Cape Breton Island, the flow is southwesterly along the coast of Nova Scotia. This Nova Scotia Current reaches maximum strength during winter, when it continues into the Gulf of Maine and contributes to the cyclonic gyre present there. During the summer, however, the Nova Scotia Current reaches a nadir, becomes confused by cross-shelf mixing, generally fails to reach the Gulf of Maine, and instead turns in a counter-clockwise direction in the vicinity of Northeast Channel, thus effectively creating a

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cyclonic gyre on Scotian Shelf, with only limited input to the Gulf of Maine from August to November (Trites and Banks 1958; Smith 1983), during the period when Scotian Shelf <u>U</u>. <u>tenuis</u> spawning occurs (Markle <u>et al</u>. 1982).

Further details in this basic circulation pattern are germane to analyses of dispersal patterns of pelagic-juvenile hakes. As the relatively low saline water leaves the Gulf of St. Lawrence and flows southwest along the Scotian Shelf, it gradually mixes with more saline slope water and thus the salinity increases with distance to the southwest. Most of this mixing occurs near the shelf break (McLellan 1954; Houghton <u>et</u> <u>al</u>. 1978). Furthermore, a major component of Gulf of Maine water is slope water (Hachey <u>et al</u>. 1954), and deeper water such as in Emerald Basin (Scotian Shelf) and Georges Basin (north of Georges Bank) consists of slope water which originates from subsurface penetration (Halliday <u>et al</u>. 1986).

Temperature lag times (Sutcliffe <u>et al</u>. 1976) or the drift of oil droplets following the grounding of a tanker (Forrester 1971) yield estimates of the time required for a particle of water to drift from Cabot Strait into the Gulf of Maine. The former study found current drift speeds varying from 7.4 to 9.7 km/day, while the latter study confirmed the southwesterly flow at ca. 8 km/day. This translates to lag times between Cabot Strait and Boston Lightship of five to seven months.

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DISCUSSION

Based on the present data from several life history stages and an appraisal of circulation patterns between Gulf of St. Lawrence and New England, we suggest that <u>Urophycis tenuis</u> recruiting to nearshore areas of the Gulf of Maine originate from early-spring spawning along the edge of the continental shelf from Nova Scotia to southern New England. These conclusions do not support earlier inferences regarding spawning seasonality or the relationships between Scotian Shelf and Gulf of Maine populations.

Late summer spawning by <u>U</u>. <u>tenuis</u> is well-documented in southern Gulf of St. Lawrence and on Scotian Shelf (Markle <u>et al</u>. 1982). During this period the Nova Scotia Current reaches a nadir, and rather than contributing to Gulf of Maine circulation, results in a cyclonic gyre over the Scotian Shelf. The potential for passive transport of eggs or larvae from Scotian Shelf spawning into the Gulf of Maine is therefore not supported by the prevailing currents. Summer circulation in our study area is typified by a well-marked cyclonic gyre in Gulf of Maine and an anti-cyclonic gyre over Georges Bank (Butman <u>et al</u>. 1982; Colton and Anderson 1983). The observed migration of pelagic-juveniles across Georges Bank and into the Gulf of Maine is counter to these current patterns and we suggest therefore that this migration is an active one, as Musick (1969) has also suggested.

It has been postulated that U. tenuis recruiting to the Gulf

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of Maine are spawned in late fall or winter and that the resulting larvae are then carried into New England waters by prevailing currents from Scotian Shelf (Musick 1969). This hypothesis ignores the absence of larvae (January through June) or pelagic-juveniles (January through April) in Gulf of Maine or Scotian Shelf waters and would also require that eggs and larvae (were they present) be retained on Scotian Shelf until they are released into the Gulf of Maine by some hydrographic feature in late spring. Lacking evidence of such a seasonally-limited hydrographic feature (i.e. Bumpus and Lauzier 1965), and considering the absence of larvae on Scotian Shelf before August-September (Markle et al. 1982), an alternate hypothesis must be proposed for the occurrence of pelagic-juvenile U. tenuis which regularly occur in Georges Bank and Gulf of Maine waters during May and June and recruit to nearshore areas beginning in June.

Although larvae are not detected on Scotian Shelf until August-September (Markle <u>et al</u>. 1982), pelagic-juveniles occur there at the same time (May-June) and in the same lengthfrequencies as the occurrences we report here for Georges Bank-Gulf of Maine. Based largely on size distributions of those early-occurring Scotian Shelf pelagic-juveniles, Markle <u>et al</u>. (1982) determined the upstream source as near Cape Breton Island and suggested northeast Gulf of St. Lawrence as a potential winter spawning site. Pelagic-juveniles co-occurring with larvae in August-September were attributed by these authors to local spawning on Scotian Shelf.

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During 1984-1986 we found no evidence that young-of-the-year U. tenuis recruiting to nearshore areas in the Gulf of Maine originate from spawning on Scotian Shelf, with the exception of a 49 mm SL individual collected in September near the mouth of Bay of Fundy. With this single exception, the pelagic-juveniles which we detect annually must originate from an earlier spawning event than that which occurs on Scotian Shelf in late summer and fall. Within the area of this study, furthermore, the smallest pelagic-juveniles are collected near the shelf/slope break while the largest are observed near the coastline in the Gulf of Maine or Southern New England. The limited evidence from sampling farther offshore than the shelf/slope break (Wroblewsky and Cheney 1984) suggests that the smallest larvae are found well offshore of the shelf (in the latter case associated with a warmcore ring), and that size increases with proximity to the shelf. Based on the foregoing evidence, we suggest that U. tenuis spawning occurs on the slope of Georges Bank (and probably also the slopes of Scotian Shelf, Southern New England and Middle Atlantic Bight) in early spring. A later, local spawning event on Scotian Shelf (during August-September) probably has limited impact on the Gulf of Maine population since it co-occurs with a period of limited or non-existent currents between the two areas and all available evidence suggests recruitment to nearshore areas in the Gulf of Maine occurs during June or July.

The results of the present study confirm earlier suppositions regarding the negligible spawning contribution made

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by the Gulf of Maine population and instead suggest that progeny recruiting to Gulf of Maine nearshore areas are produced by an offshore (slope) population. In the Gulf of Maine, it has not been determined whether those fish occupying deeper basins mingle with those occupying slope areas south of Georges Bank. Further studies defining the relationship between gulf-basin and slope populations would clarify the question of how the Gulf of Maine population is sustained.

The present data also suggest the existence of two stocks of <u>Urophycis tenuis</u> with separate spawning schedules: a deep-water, early spring-spawning population occurring in northeast Gulf of St. Lawrence (possibly) and extending along the slopes of Scotian Shelf, Georges Bank, Southern New England, and Middle Atlantic Bight; and a shallower-water, summer-spawning population occurring in southern Gulf of St. Lawrence and Scotian Shelf. The former group produces pelagic-juveniles which recruit to nearshore areas of the Gulf of Maine in early summer, while the latter may produce pelagic-juveniles which recruit to undescribed areas adjacent to Scotian Shelf in the fall.

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FIGURE CAPTIONS

- Figure 1. Capture locations of pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> (listed in Table 4).
- Figure 2. Size-depth distributions of pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> collected in 10m² multiple opening-closing net (MOCNESS) during 48-h vertical distribution study over eastern Georges Bank 18-19 June 1986. The integrated net sampled the entire water column while the remaining nets sampled discrete strata. Each circular symbol represents one fish.
- Figure 3. Capture locations of pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> reported by Marak and Colton 1961, Marak et al. 1962a, 1962b. Only those specimens <30.0 or >49.9 mm TL plotted. All collections made with 1-meter net towed at surface.
- Figure 4. Habitat distribution of young-of-the-year <u>Urophycis</u> <u>tenuis</u> collected in Nauset Marsh, MA. (Cape Cod National Seashore).
- Figure 5. Length-frequency histograms of young-of-the-year <u>Urophycis tenuis</u> collected in Nauset Marsh, MA. Numerals over columns indicate number of fish selected for otolith examination.

- Figure 6. Periodic mean lengths for 0+ and 1+ <u>Urophycis tenuis</u> collected from various localities. Bay of Fundy data from Markle et al. (1982). Little Egg Inlet data after Thomas and Milstein (1973). Vertical bars indicate ±1 standard deviation for Nauset Marsh values.
- Figure 7. Mean lengths of young-of-the-year <u>Urophycis</u> <u>tenuis</u> collected in Nauset Marsh, MA., 1985-1986, compared with collections of pelagic-juveniles during 1984-1987.

FIGURE 1







FIGURE 3



00 000



Number of U. tenuis

FIGURE 4



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FIGURE 6







Table 1. Dates pertinent to material examined for this study and numbers of <u>Urophycis tenuis</u> collected. Egg and larval collections described in Table 3. Dates for cruises pertain only to period within Georges Bank-Gulf of Maine. Not included are pelagicjuveniles retrieved from feeding seabirds or collections of firstdemersal juveniles made in Damariscotta River estuary during 1973-1974.

| CDUILER OD | | PELAGIC- | JUVENILES | JUVENILES |
|-------------------|---------------------|------------|-----------|-----------|
| CRUISE OR | | NEUSION | MIDWAILR | OTTER |
| LOCATION | SAMPLING DATES | <u>NET</u> | (MOCNESS) | TRAWL |
| Del 84-01 | Jan 10-24, 1984 | 0 | | |
| Alb 84-03 | May 23-Jun 2, 1984 | 4 | | |
| Alb 84-05 | Jun 17-19, 1984 | | 2 | |
| Del 84-09 | Nov 20-Dec 5, 1984 | 0 | | |
| Del 85-01 | Jan 8-26, 1985 | 0 | | |
| Del 85-03 | Apr 2-7, 1985 | 0 · | | |
| Alb 85-04 | May 9-14, 1985 | 14 | | |
| Nauset Marsh | Aug 12-16, 1985 | | | 8 |
| Del 85-07 | Sep 12-22, 1985 | 1 | | |
| "Gloria Michelle" | | | | |
| 8592, Sta. 54 | Sep 12, 1985 | | | 0 |
| Alb 85-07 | Aug 4-29, 1985 | | | 0* |
| Nauset Marsh | Oct 13-17, 1985 | | | 9 |
| Del/Alb 85-08 | Oct 19-Nov 15, 1985 | | | 0 |
| Del 85-10 | Nov 21-Dec 12, 1985 | 0 | | |
| Nauset Marsh | Dec 10-12, 1985 | | | 0 |
| Del 86-01 | Jan 25-Feb 12, 1986 | 0 | | |
| Nauset Marsh | Apr 1-4, 1986 | | | 0 |
| Alb 86-02 | Apr 8-27, 1986 | | | 0 |
| "Gloria Michelle" | May, 1986 | | | 0 |
| Nauset Marsh | Jun 1-5, 1986 | | | 15 |
| Alb 86-03 | Jun 18-19, 1986 | | 16 | |
| Del 86-03 | May 29-Jun 6, 1986 | 31 | | |
| Nauset Marsh | Jul 28-Aug 5, 1986 | | | 21 |
| Nauset Marsh | Sep 7-13, 1986 | | | 16 |
| Nauset Marsh | Oct 12-16, 1986 | | | 8 |
| Del 87-04 | May 17-Jun 7, 1987 | 254 | | |
| | | | | |

* Sampling with scallop dredge

Table 2. Summary of pertinent meristic characters useful for the identification of four species of western North Atlantic hake species. Modal counts in parentheses.

| SPECIES | EPIBRANCHIAL GILL RAKERS | TOTAL CAUDAL FIN RAYS | <u>VERTEB</u> | RAE CAUDAL |
|--------------------------------|-----------------------------|--|--------------------------------|--------------------------|
| <u>Phycis</u> <u>chesteri</u> | 4-5 | 28-35 | 14-15 | 34-36 |
| <u>Urophycis</u> <u>regia</u> | 3 | 30-32 | 13 - 15 (14+) | 31-35 33) |
| <u>Urophycis</u> <u>chuss</u> | 3 | 28-34 | 14 - 15 (15+ | 32-36 34) |
| <u>Urophycis</u> <u>tenuis</u> | 2 | 33-39 | 15 - 16 (16+ | 33-35 34) |
| SOURCE | Musick 1973 | Methven 198 Fahay and Markle 1984 Wenner 1983 | 5; Methve Fahay ; Musick | n 1985; 1983; 1973 |

Table 3. Summary of egg and larval (bongo net) collections in Gulf of Maine (GOM) and Georges Bank (GB), January, 1984-June, 1986. Middle- and latestage egg identifications to genus only. Asterisk (*) = <u>Urophycis</u> chuss or <u>U. regia</u> (not <u>U. tenuis</u>). Double asterisk (**) = material not yet analyzed.

| | | JAN | JARY TH | ROUGI | H JUNE | | |
|-------------|-------|----------------------|-----------------------------------|-------------------|---------------------|------------------------|--|
| <u>CRUI</u> | ISE | INCLUSIVE DATES | NUMI <u>STAT</u> <u>GOM</u> | BER IONS GB | NUM COLL EGGS | BER ECTED LARVAE | LARVAE I.D. and SIZES |
| DEL | 84-01 | JAN 10-24 | 46 | 28 | 0 | 0 | |
| ALB | 84-02 | MAR 26-APR 25 | 38 | 36 | 1 | 0 | |
| ALB | 84-03 | MAY 23-JUN 2 | 54 | 30 | 4 | 1 | <u>Urophycis</u> sp. |
| DEL | 85-01 | JAN 8-26 | 8 | 33 | 0 | 1 | <u>U. regia</u> 17.8 mm |
| ALB | 85-02 | MAR 24-APR 12 | 28 | 28 | 0 | 0 | |
| DEL | 85-03 | APR 2-7 | 6 | 32 | 0 | 0 | |
| ALB | 85-04 | MAY 9-14 | 8 | 32 | 0 | 0 | |
| DEL | 86-01 | JAN 24-FEB 12 | 45 | 43 | ** | 0 | |
| ALB | 86-02 | APR 8-27 | 36 | 36 | ** | 0 | |
| DEL | 86-03 | MAY 28-JUN 6 | 36 | 40 | ** | 0 | |
| DEL | 84-06 | JUL 23-30 | 2 | 23 | 2303 | 16 | <u>Urophycis</u> sp.* |
| ALB | 84-07 | AUG 9-25 | 12 | 36 | 4014 | 259 | 1.6-8.6 mm Urophycis sp.* |
| ALB | 84-08 | OCT 5-NOV 3 | 47 | 35 | 24 | 3 | <u>Urophycis</u> sp.* |
| DEL | 84-09 | NOV 19-DEC 5 | 20 | 31 | 0 | 2 | <u>U. chuss</u> 10.5-13.1 mm |
| GYR | 85-07 | JUL 17-22 | 22 | 0 | 20 | 0 | |
| ALB | 85-07 | AUG 4-29 | 0 | 44 | ** | 1325 | <u>Urophycis</u> sp.* 1.5-5.5 mm |
| | | | | | | 29 | <u>U. chuss</u> 3.5-19.0 mm |
| DEL | 85-07 | SEP 12-22 | 43 | 34 | ** | 1179 | <u>Urophycis</u> sp.* 1.7-7.9 mm |
| | | | | | | 174 | <u>U. chuss</u> 3.2-25.3 mm |
| ALB | 85-08 | 000 10 11 | 38 | 11 | 0 | 15 | Urophycis sp.* |
| JEL | 85-08 | OCT 19-Nov 15 | 1 | 17 | ** | 12 | 2.0-6.8 mm <u>U. chuss</u> 4.1-23.8 mm |
| DEL | 85-10 | NOV 21-DEC 12 | 54 | 31 | ** | 4 | <u>Urophycis</u> sp.* 2.8-4.8 mm |

Table 4. Pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> collected in neuston sampling 1984-1987. See Table 1 for annual distribution of sampling effort.

| | LENGTH |
|--|-------------------|
| NUMBER | (mm TL) |
| CRUISE STATION DATE LAT(N) LONG(W) COLLECTE | ED RANGE |
| | |
| ALB 84-03 94 23 V 84 40°55' 69°06' 1 | 44.1 |
| 96 23 V 84 41°20' 69°07' 1 | 48.6 |
| 127 27 V 84 42°09' 66°20' 1 | 51.8 |
| 176 2 VI 84 42°48' 70°32' 1 | 56.1 |
| ALB 85-04 16 11 V 85 41°30' 66°20' 1 | 51.5 |
| 21 11 V 85 40°40' 67°05' 1 | 28.0 |
| 22 12 V 85 40°37' 67°41' 11 | 39.1-56.1 |
| 43 14 V 85 40°23' 68°17' 2 | 52.7-58.3 |
| DEL 85-07 168 19 IX 85 44°20' 67°43' 1 | 54.9 |
| DEL 86-03 36 13 V 86 37°59' 73°58' 6 | 20.0-51.4 |
| 46 14 V 86 38°39' 73°09' 3 | 18.9-25.1 |
| 47 14 V 86 38°59' 73°08' 1 | 42.2 |
| 70 17 V 86 41°20' 71°21' 3 | 31.7-50.1 |
| 78 18 V 86 40°04' 71°30' 3 | 31.3-30.8 |
| 143 28 V 86 40°13' 70°25' 1 | 32.0 |
| 166 31 V 86 41°16' 67°41' 3 | 22.1-34.8 |
| | 17 7 |
| 171 31 V 86 40°46' 67°19' 2 | 23 7-30 1 |
| | 35 7-49 7 |
| 187 2 VI 86 42°28' 66°20' 1 | 31 7 |
| $\frac{107}{203} 4 \text{ VI } 86 41^{\circ}54! 69^{\circ}10! 4$ | JI.7 15 7-55 5 |
| 203 4 1 00 41 34 03 10 4 | 40.7-00.0 |
| | 26 0-41 2 |
| | 36.0-41.3 |
| | 30.1-43.8 |
| | 33.1-43.7 |
| | 43.9-48.1 |
| | 45.1-49.0 |
| 123 19 V 87 40°22' 67°40' 75 | 17.2-40.7 |
| 130 20 V 87 41°13' 66°56' 2 | 51.5-52.0 |
| 138 20 V 87 42°02' 66°50' 1 | 55.3 |
| 129 20 V 87 41°10' 66°19' 3 | 37.4-56.5 |
| 140 21 V 87 41°58' 67°25' 1 | 47.0 |
| 147 27 V 87 39°52' 71°49' 4 | 33.5-51.6 |
| 148 27 V 87 39°30' 72°09' 1 | 26.9 |
| 154 27 V 87 39°52' 73°05' 52 | 18.2-64.9 |
| 155 28 V 87 39°39' 73°23' 1 | 53.8 |
| 166 29 V 87 40°19' 72°43' 9 | 38.9-64.4 |
| 167 29 V 87 40°44' 72°40' 5 | 36.0-54.1 |
| 169 29 V 87 40°40' 72°07' 3 | 49.5-51.2 |
| 177 30 V 87 41°09' 71°15' 4 | 51.5-62.3 |
| 187 31 V 87 41°03' 70°33' 28 | 35.9-58.9 |
| 196 1 VI 87 40°39' 60°95' 6 | 37:8-46.0 |
| 204 1 VI 87 41°39' 69°09' 8 | 39.1-57.2 |
| | 43 0-53 0 |
Table 4 (cont.)

| CRUISE | STATION | DATE | LAT(N) | LONG (W) | NUMBER COLLECTED | LENGTH (mm TL) <u>RANGE</u> |
|----------------------|---|---|--|--|---|--|
| DEL 87-04 (cont.) | 222 230 231 232 238 239 240 247 249 | 4 VI 87 5 VI 87 5 VI 87 5 VI 87 6 VI 87 6 VI 87 6 VI 87 7 VI 87 7 VI 87 | 43°37' 44°16' 44°00' 43°32' 42°46' 42°43' 42°18' 43°08' 42°35' | 68°56' 66°36' 66°24' 66°20' 66°58' 67°28' 67°42' 69°01' 69°14' | 3 4 1 4 1 1 8 4 5 | 43.6-71.7 27.9-59.2 63.8 40.5-60.0 58.9 42.6 37.6-60.9 57.2-69.5 50.6-64.7 |
| | | | | | | |

| pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> (n=188; \overline{x} =35.8) and <u>U</u> . <u>chuss</u> (n=67; \overline{x} =31.2) collected in Gulf of Maine-Georges Bank waters during 1984-1987. | | | | | | | | | | | | | | | |
|---|---------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|--|
| | | <u>28</u> | <u>29</u> | <u>30</u> | <u>31</u> | <u>32</u> | <u>33</u> | <u>34</u> | <u>35</u> | <u>36</u> | <u>37</u> | <u>38</u> | <u>39</u> | <u>40</u> | |
| <u>U</u> . | <u>chuss</u> | 0 | 5 | 11 | 22 | 22 | 7 | 0 | | | | | | | |
| <u>U</u> . | <u>tenuis</u> | | | | | 0 | 6 | 18 | 53 | 57 | 39 | 12 | 3 | 0 | |

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Table 6. Pelagic-juvenile <u>Urophycis</u> <u>tenuis</u> collected over western Georges Bank during Parts I & II of cruise DEL 87-04. Specimens listed in Table 4. Lengths in mm TL. JD= Julian Day.

| | PAR | ΤI | | PART II | | | | | | | |
|--------|-------|-----------|-----------------------|---------|---------|-----------|----------------|--|--|--|--|
| STA. | DATE | <u>_N</u> | MEAN <u>LENGTH</u> | STA. | DATE | <u>_N</u> | MEAN LENGTH | | | | |
| 112 | 5-17 | 3 | 40.0 | 187 | 5-30 | 34 | 47.2 | | | | |
| 113 | 5-18 | 2 | 39.9 | 196 | 5-31 | 6 | 42.9 | | | | |
| 114 | 5-18 | 6 | 37.7 | 204 | 6-1 | 8 | 48.5 | | | | |
| 120 | 5-18 | 2 | 46.0 | 206 | 6-2 | 3 | 48.8 | | | | |
| 121 | 5-18 | 4 | 46.8 | | | | | | | | |
| 123 | 5-19 | 75 | 29.1 | | | | | | | | |
| X JD = | = 138 | Wt X | = 31.3 | X JD = | = 151.5 | wt X | = 46.9 | | | | |



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Fishes and Decapod Crustaceans of Cape Cod Eelgrass Meadows: Species Composition, Seasonal Abundance Patterns and Comparison with Unvegetated Substrates

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ABSTRACT: Bimonthly trawl samples from eelgrass and nearby unvegetated areas on Cape Cod, Massachusetts, showed greater species richness in eelgrass meadows relative to unvegetated areas, and greater summer abundance in vegetation for decapod crustaceans and fishes. The composition of eelgrass-associated decapods and fishes was dominated by cold-water taxa and was strikingly different from that of the better studied eelgrass meadows of the mid-Atlantic coast. Four of the eight decapod species collected, including the second and third most abundant taxa, do not even appear in collections reported from Chesapeake Bay eelgrass meadows. Similarly, 10 of the 22 fish species taken, including the first and sixth most abundant species, are not reported from Chesapeake Bay eelgrass samples. Cape Cod eelgrass beds seem to play a nursery role for several commercially important fish species, although the nursery function is less obvious than in previously studied mid-Atlantic eelgrass meadows.

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Introduction

Eelgrass meadows support characteristically high animal diversities and abundances, and increased recognition of the relationship between eelgrass abundance and fish and shellfish production has produced a growing record of published research on eelgrass habitabin North America (Briggs and O'Connor 1971; Thayer et al. 1975; Adams 1976a, 1976b; Heck and Orth 1980; Orth and Heck 1980; Weinstein and Brooks 1983; Onuf and Quammen 1983; Heck and Thoman 1984; Summerson and Peterson 1984; Tatham et al. 1984; Thayer et al. 1984; Wilson et al. 1987). Most of this work has been done on the Atlantic coast of the United States and, as Thayer et al. (1984) point out, the majority of these studies have been carried out in Chesapeake Bay and North Carolina waters.

In this paper we describe results from a multiyear study of the major habitats occurring in the Nauset Marsh complex, Cape Cod, Massachusetts. Eelgrass (Zostera marina) habitats were chosen for

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detailed study and here we report on initial efforts to characterize the natant macrofauna (decapod crustaceans and fishes) of the Nauset eelgrass meadows and nearby unvegetated sandy substrate. We consider seasonal and diurnal patterns in species abundance and composition within and between these habitats and compare our results with those of similar studies done in other eelgrass meadows along the east coast of North America. Our emphasis in these comparisons is directed toward those studies that have used similar sampling techniques and gear, although we also address in less detail the results of studies employing different sampling methods.

Methods

Sites were located in eelgrass meadows and in a nearby unvegetated sandy site within and adjacent to the Cape Cod National Seashore (Fig. 1). The eelgrass meadows occurred in waters of 1-2 m and were flanked by unvegetated substrates, as well as by salt marshes, mussel beds, and other habitats (Fig. 1). Although eelgrass was the dominant macrophyte present in the seagrass habitats, several species of macroalgae, including Ulva lactuca, Agardiella tenera, and Gracillaria tikvahiae, were seasonally present in the grass beds. These algal species, although not uncommon, never reached the abundances characteristic of "drift algae" in the Gulf of Mexico (Hooks et al. 1976) or along the Atlantic coast of Florida (Gore et al. 1981). The unvegetated site contained no rooted vegetation, and coarse sand dominated the sediments. Some small amounts of cobble were present in the shallowest portions of this site. Water depths ranged from 1 to 3 m.

Preliminary sampling in summer 1985 showed that most species collected by repetitive, 2-min trawl samples were taken in the first or second trawl. To ensure that all species susceptible to the gear were collected, we took five samples in August 1985 and subsequently set a regular sample size of four 2min trawls, or twice that determined as necessary by preliminary sampling.

Four (or five) 2-min tows of a 4.9-m otter trawl with 19-mm mesh wings and 6.3-mm mesh liner were made at high tide in eelgrass meadows at Fort Hill near the entrance of Town Cove. Tows over sandy substrate were made behind the barrier beach south of the inlet to the Nauset system (Fig. 1). Collections were made in August, October, and December 1985, and during April, June, and July 1986. Eelgrass meadows at Nauset Harbor were sampled similarly in December 1985, and in April, June, July, September, and October 1986. Night samples were also taken at the Fort Hill and Nauset Harbor eelgrass sites in October 1985, and at the Nauset Harbor site in September and October 1986. Trawling speed was estimated at two to three knots.

Decapod crustaceans and fishes retained by the trawl were sorted, identified, and counted. Some collections in August-October were so large that abundances were estimated by filling containers with known numbers of individuals and using calculated volumetric equivalents to estimate total numbers.

At the time of sampling a hand-held thermometer was used to measure surface water temperature, and a temperature-compensated refractometer was used to measure salinity. Vegetation density was estimated by removal of either 0.25 or 1.0 m² plots, and all aboveground biomass was then dried to constant weight at **B**^oC. Vegetation samples were taken during October and December 1985 and in August 1986 at Fort Hill and monthly from June to October 1986 at Nauset Harbor.

Results

Temperature, Salinity, and Plant Biomass

Physical characteristics of the waters overlying the study sites were similar. Salinities ranged from 26‰ in December to 32‰ in October and never varied more than 3% among stations on any sampling date. Temperatures ranged from 4°C in December to 16.5°C in July and were somewhat less consistent among sites, with a maximum betweenstation difference of 4°C recorded in April 1986. There is no doubt that lower temperatures occurred during the coldest winter months when no samples were taken.

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Plant biomass peaked in summer and dropped off rapidly as fall approached. Although we have little or no quantitative data from spring or winter during the sampling period, our unpublished data from winter and spring 1987 show low standing crops until growth begins in May. Maximum eelgrass biomass in Nauset Harbor occurred in July (672 g m⁻² dry weight) when flowering shoots were present, and declined to 50 g m⁻² by October. Biomass at the F() Hill eelgrass bed was lower, with dry weights ranging from 182 g m⁻² in August to 46 g m⁻² in December. Data gathered in Rhode Island by Harlin et al. (1982) and by Thorne-Miller et al. (1983) showed similar seasonal trends of Zostera marina standing stock.

COMMUNITY COMPOSITION

The species richness of the natant macrofauna at all study sites was low, especially at the unvegetated site. Only eight decapod species were taken in eelgrass daytime samples. Three species made



Fig. 1. Map of the study area. Eelgrass sampling stations are at Nauset Harbor (NH) and FL) Hill (FH). The unvegetated station is labeled Sand.

up nearly 98% of these: the sand shrimp, *Crangon* septemspinosa (55%); the green crab, *Carcinus mae*nas (38%); and the rock crab, *Cancer irroratus* (5%) (Table 1).

Fifteen fish species were collected in daytime sampling. Six species made up 98% of the total: the threespine stickleback, Gasterosteus aculeatus (56%) the fourspine stickleback, Apeltes quadracus (30%); the mumichog Fundulus heteroclitus (5%); winter flounder Pseudopleuronectes americanus (4%); the northern pipefish, Sygnathus fuscus (2%); and the grubby, Myoxocephalus aenaeus (1%) (Table 1).

On unvegetated substrate six decapod species were taken, with sand shymp making up 87% of the individuals collected, rock crabs 5%, green crabs 5%, and hermit crabs (*Pagurus acadianus*) 2% of the collection (Table 2). Only seven fish species were collected and two of these made up 95% of the total: the sand lance (*Ammodytes americanus*) 82% and winter flounder 13%.

Four of the 15 fish species caught in daytime sampling were not taken at night. Because these species were represented by only one or two individuals in day collections, their absence at night is most likely due to chance alone. Seven species were taken exclusively at night, including tautog, *Tautoga onitis*; Atlantic tomcod, *Microgadus tomcod*; Atlantic cod, *Gadus morhua*; and scup, *Stenotomus chrysops*; this probably was due to decreased net avoidance and increased activity at night (Table 3).

Among decapod crustaceans, seven of the eight species taken during day samples occurred in night samples. The exception was the caridean shrimp, *H. zostericola*, which was represented by only one individual in the daytime collections (Table 3).

Abundance and Species Richness Patterns

The greatest densities of decapod crustaceans and fishes in daytime eelgrass trawls occurred in early summer 1986 at $F(\underline{f})$ Hill, with subsequent decreases in late summer and into fail and winter (Fig. 2). At Nauset Harbor, greatest numbers of fishes and decapods occurred in fall 1986. Species numbers showed less seasonal variation, especially

| TABLE I. | Decapods and fish collected during daytime in eelgrass beds at FA Hill (FH) and Nauset Harbor (NH) with a 4.9-m otter |
|----------|---|
| trawl. | · · · · · · · · · · · · · · · · · · · |

| | | Octuber | Dece | December | | April | | ne | Jui | Juiv | | | |
|-------------------------------|-----|---------|------|----------|-----|----------|------|-----|-----|------|------------------|-------|-----------|
| Species | FH | FH | FH | NH | FH | ΝН | FH | NH | FH | ЯН | _September NH | NT | Total |
| Decapods | | | | | | | | | | | | | |
| Crangon septemspinosa | 15 | 81 | 2 | 30 | 106 | 6 | 506 | 30 | 245 | 4 | 4 | 145 | 1.174 |
| Carcinus maenas | 141 | 45 | 22 | 38 | 36 | 28 | 242 | 28 | 187 | 7 | 5 | 19 | 798 |
| Cancer irroratus | 4 | 11 | 0 | 12 | 1 | 4 | 4 | 1 | 7 | 1 | 9 | 54 | 108 |
| Libinia dubia | 15 | I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| Pagurus acadianus | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | Ō | 7 |
| Palamonetes vulgaris | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | Ō | 7 |
| Homarus americanus | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | ō | 6 |
| Hippolyte zostericola | 0 | 0 | 0 | Ι. | 0 | 0 | 0 | 0 | 0 | 0 | Ō | 0 | ĩ |
| Total | 178 | 139 | 25 | 82 | 144 | 39 | 754 | 65 | 443 | 12 | 18 | 218 | 2,117 |
| Fish | | | | | | | | | | | | | |
| Gasterosteus aculeatus | 4 | 0 | 0 | 9 | 1 | 6 | 156 | 164 | 92 | 20 | 878 | 1.241 | 2.571 |
| Apeiles quadracus | 161 | 16 | 0 | 35 | 7 | 33 | 55 | 127 | 548 | 56 | 89 | 222 | 1.349 |
| Fundulus heteroclitus | 109 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 105 | 0 | 0 | 11 | 225 |
| Pseudopleuronectes americanus | 23 | 5 | 12 | 4 | 24 | 8 | 55 | 13 | 15 | 9 | 9 | 6 | 183 |
| Syngnathus fuscus | 18 | 10 | 0 | 5 | 1 | 0 | 1 | 0 | 12 | Ō | 13 | 23 | 83 |
| Myoxocephalus aenaeus | 10 | 2 | 0 | 17 | 0 | 1 | 0 | 2 | 0 | 4 | 1 | 10 | 47 |
| Urophycis tenuis | 3 | 0 | 0 | 0 | 0 | 0 | 6 | 5 | 9 | 5 | 11 | 3 | 42 |
| Tautogolabrus adsperus | 4 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 10 | 24 |
| Pollachius virens | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 17 | 0 | 0 | 0 | 0 | 19 |
| Anguilla rostrata | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | Ō | ī | 2011 |
| Clupea harengus harengus | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | Ō | Ō | 0 | 2 |
| Ammodyles americanus | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Urophycis chuss | 0 | Ō | 0 | 0 | Ō | Õ | ĩ | Õ | Ō | Ō | 0 | Ő | ī |
| Cyclopterus lumpus | 0 | 0 | 0 | ī | 0 | 0 | Ō | 0 | 0 | 0 | 0 | Ő | ī |
| -timpines chass | 0 | 0 | 0 | | 0 | <u>_</u> | | | | | | | |
| Total | 334 | 36 | 15 | 7271 | 33 | 51 | 2734 | 328 | 793 | 95 | 1,203 | 1,527 | 4,507 4 5 |

for the few decapod species collected, although fish species richness was highest in late summer and fall (Fig. 2).

Night samples in vegetation produced much greater abundances of decapods than day samples (Table 1 and 3), primarily because of increased catches of the three dominant decapods. Increased activity and trawl vulnerability were presumably responsible for the large catches of these species at night. For fishes, nighttime catches were greater than daytime catches in October 1985 but lower in September and October 1986. The major difference between 1985 and 1986 results was the large nighttime catches of threespine sticklebacks in 1985, versus the greater daytime catches of both stickleback species in 1986.

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TABLE 2. Fishes and decapods collected during daytime over unvegetated substrate with a 4.9-m otter trawl.

| Species | August | October | December | April | June | Jய y | Total |
|-------------------------------|--------|---------|----------|-------|------|-----------------|-------|
| Decapods | | | | | | | |
| Crangon septemspinosa | 269 | 5 | 5 | 1 | 1 | 29 | 310 |
| Cancer irroratus | 12 | 3 | 1 | 1 | 1 | 1 | 19 |
| Carcinus maenas | 7 | 0 | 0 | 2 | 0 | 8 | 17 |
| Pagurus acadianus | 5 | 0 | 0 | 0 | 1 | 1 | 7 |
| Homarus americanus | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Ovalipes ocellatus | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Total | 294 | 9 | 6 | 4 | 3 | 39 | 355 |
| Fishes | | | | | | | |
| Ammodites americanus | 0 | 24 | 1 | 7 | 38 | 0 | 120 |
| Pseudopleuronectes americanus | 11 | 3 | 0 | 2 | 1 | 2 | 19 |
| Scophthalmus aquosus | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| Menidia menidia | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| Gasterosteus aculeatus | 0 | 0 | 0 | 0 | 0 | I | 1 |
| Selene vomer | 0 | I | 0 | 0 | 0 | 0 | I |
| Tautogolabrus adsperus | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total | 12 | 33 | 1 | 9 | 89 | 3 | 147 |

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TABLE 3. Decapods and fish collected during nighttime in eelgrass beds at Ft) Hill (FH) and Nauset Harbor (NH) with a 4.9-m otter trawl.

| | Octo | ober | £ | | |
|-------------------------------|-------|-------|-----|-------|-------|
| Species | FH | NH | NH | NH | Total |
| Decapods | | | | | |
| Crangon septemspinosa | 1,437 | 22 | 436 | 949 | 2.844 |
| Carcinus maenas | 307 | 8 | 27 | 102 | 444 |
| Cancer irroratus | 16 | 3 | 463 | 244 | 699 |
| Homarus americanus | 7 | 2 | 0 | 2 | 11 |
| Pagurus acadianus | 4 | 2 | 1 | 0 | 7 |
| Libinia dubia | 0 | 2 | 0 | 0 | 2 |
| Total | 1,771 | 39 | 927 | 1,297 | 4,007 |
| Fish | | | | | |
| Gasterosteus aculeatus | 0 | 761 | 161 | 167 | 1.089 |
| Apelles quadracus | 72 | 299 | 8 | 29 | 408 |
| Syngmathus fuscus | 3 | 152 | 47 | 161 | 363 |
| Pseudopleuronectes americanus | 75 | 44 | 11 | 15 | 145 |
| Fundulus heteroclitus | 1 | 9 | 0 | 5 | 15 |
| Myoxocephalus aenaeus | 21 | 12 | 9 | 23 | 65 |
| Urophycis tenuis | 0 | 8 | 4 | 5 | 17 |
| Tautogoiabrus adsperus | 0 | 23 | 0 | 3 | 26 |
| Menidia menidia | 3 | 13 | 12 | • 2 | 30 |
| Tautoga onitis | 0 | 11 | 1 | 0 | 12 |
| Pollachius virens | 0 | 0 | 5 | 4 | 9 |
| Microgadus tomcod | 0 | 1 | 1 | 2 | 4 |
| Anguilla rostrata | 0 | 0 | 1 | 1 | 2 |
| Stenotomus chrysops | 0 | 0 | 2 | 0 | 2 |
| Urophycis chuss | 2 | 0 | 0 | 0 | 2 |
| Cyclopierus lumpus | 0 | 0 | 0 | 1 | 1 |
| Centropristis striata | 0 | 0 | 0 | 1 | 1 |
| Stichaeus punctatus | 0 | 0 | 0 | 1 | 1 |
| Total | 177 | 1,334 | 262 | 420 | 2,194 |

Abundances of decapod crustaceans and fishes over the unvegetated areas showed smaller seasonal variation than in vegetated habitats (Figs. 2ab). Greatest total numbers of decapods occurred in August 1985 when the largest collection of sand shrimp was made. Fish abundances peaked in June 1986, although numbers were always relatively low.

Differences in abundance between vegetated and unvegetated areas were small during the winter and spring periods, but increased during summer and early fall (Figs. 2a-b) when water temperatures were warmest and eelgrass biomass greatest. Aff-test of mean abundances of decapods showed no significant differences (p < 0.05; n = 6) between vegetated (both eelgrass stations) and unvegetated stations, even though mean abundances were more than three times greater in vegetation ($\bar{x} = 185$) than in sand ($\bar{x} = 59$). Differences for fishes were significant (p < 0.01; n = 6), with eelgrass mean abundances nearly eight times greater in eelgrass ($\bar{x} = 200$) than in sand ($\bar{x} = 24.5$).

Discussion

The species composition of decapod crustaceans and fishes collected from Cape Cod eelgrass meadows is strikingly different from that reported in mid-Atlantic eelgrass meadows. The dominant taxa collected were cold temperate species whose ranges extend from the Arctic to the mid-Atlantic Coast of the United States (Bigelow and Schroeder 1953; Williams 1984). Among the decapods, the only warm temperate species collected was the single specimen of the caridean shrimp, *Hippolyte zostericola*. The fish species that also occur in warmer waters (e.g., *F. heteroclitus, Centropristis striata, S. fuscus*) are all species with very broad ranges.

The magnitude of these differences can be appreciated by comparing dominant taxa among studies. For example, using identical trawling techniques in Chesapeake Bay eelgrass beds over a 3-yr period, Heck and Orth (1980) and Heck and Thoman (1984) never collected four of the eight decapod species taken in this study, including the second and third most abundant species (green crabs and rock crabs). Similarly, 10 of the 22 fish species taken in this study did not appear in Chesapeake Bay collections (Orth and Heck 1980; Heck and Thoman 1984), including the first and sixth most abundant species (threespine sticklebacks and grubbies).

Decapods found in North Carolina eelgrass meadows by Stuart (1975), Summerson (1980), and



Fig. 2. Mean number of fishes (A) and decapod crustaceans (B) taken diurnally at each of the sampling stations during the study.

Thayer et al. (1984) show no overlap at all with the decapod species collected in Cape Cod eelgrass beds. Among fishes, only two of the 36 species listed by Thayer et al. (1984) from North Carolina eelgrass collections appear in the Cape Cod samples (northern pipefish and black seabass), and the most abundant species in North Carolina (pinfish, Lagodon rhomboides) does not appear in Cape Cod collections. Because collecting methods in North Carolina included drop nets (Adams 1976a, 1976b), seines, and gill nets (Thayer et al. 19840, but not trawls, caution must be applied in comparing Cape Cod and North Carolina results. Nevertheless, the differences are so large that dissimilarity in sampling gear cannot explain more than a small amount of the difference between data sets.

Abundance of both decapods and fishes was greater in eelgrass meadows than on bare substrate, although only mean fish abundance was significantly greater in eelgrass. This is the reverse of results from Chesapeake Bay, where decapod but not fish abundances were significantly greater in vegetated habitats (Heck and Thoman 1984). In addition, abundance of decapod crustaceans was usually less than that reported in Chesapeake Bay (Heck and Orth 1980; Heck and Thoman 1984), where peak abundances were often several times greater than in Cape Cod. The major factor influencing these differences in abundance was the large number of grass shrimp (*Palaemonetes vulgaris*) occurring in Chesapeake Bay but not Cape Cod collections. For fishes, abundances varied over the same orders of magnitude in both systems (cf. Orth and Heck 1980; Heck and Thoman 1984), although greatest abundances occurred in fall collections from Cape Cod eelgrass beds when large numbers of three spine sticklebacks were taken.

American lobster, the only commercially important decapod in the collections, was taken in low numbers (n = 17) by the trawl (Table 1 and 3). It is almost certain that more lobsters would have been taken if sampling had been carried out exclusively at night; however, nighttime abundances were less than one lobster per trawl, including adults as well as juveniles (Table 3). Thus, there is little evidence that eelgrass meadows are significant lobster nurseries in the study area. There are, however, lobster nursery areas in nearby salt marshes where densities of juvenile lobsters (6-30 mm CL) are on the order of 2-3 per m² (Able et al. 1988). 20

Among fishes there is evidence that Cape Cod eelgrass meadows do serve as nurseries for white hake (*U. tenuis*) and winter flounder (*P. americanus*), both of which are recreationally and commercially valuable species. Although white hake were found exclusively in eelgrass habitats, winter flounder appeared in collections from the unvegetated site (Table 2), and are commonly reported from unvegetated substrates in New England and Canada (Pearcy and Richards 1962; MacDonald et al. 1984).

In summary, Cape Cod eelgrass meadows support a decapod and fish fauna of low diversity that shows little overlap with the fauna of eelgrass beds in Chesapeake Bay or North Carolina waters. Decapods and fishes were more abundant in eelgrass than over nearby unvegetated substrates, significantly so for fishes, but not for decapods. Standing stock of decapods was much less than that of mid-Atlantic eelgrass meadows, while fish abundance was similar. Our data also indicate a less obvious nursery function for economically important species in Cape Cod eelgrass meadows than that reported for Chesapeake Bay and North Carolina meadows. We conclude by noting that the major differences in faunal composition between the Cape Cod and the better studied Atlantic coast eelgrass meadows suggest that future comparisons between New England and mid-Atlantic eelgrass faunas will likely reveal additional regional differences in functional relationships and interspecies interactions.

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Acknowledgments

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Life History and Food Habits of the Grubby, Myoxocephalus aeneus (Cottidae), in a Cape Cod Estuary

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The grubby, Myoxocephalus aeneus, is a year round resident of Nauset Marsh, Cape Cod, where it occurs primarily in eelgrass (Zostera marina) beds. Spawning occurs in winter. Some females may spawn during their first year. Larvae hatch in mid-winter and occur in plankton collections throughout the estuary in April, whereas juveniles first appear in summer collections. Based on lengths and age estimates from otoliths, juveniles grow to about 60–65 mm SL in the first year. Females grow to a larger maximum size than males. Myoxocephalus aeneus of all sizes feed primarily on crustaceans, particularly Crangon septemspinosa. Amphipods and isopods are more important in juveniles' diets whereas fishes are a minor component found only in adult stomachs.

THE grubby (Myoxocephalus aeneus) is a small sculpin found in the coastal waters of North America from New Jersey to the Strait of Belle Isle, Newfoundland (Bigelow and Schroeder, 1953: Liem and Scott, 1966). It occurs in eelgrass (Zostera marina) beds (Bigelow and Schroeder, 1953) and is common throughout the year in some southern New England areas (Sumner et al., 1913: Warfel and Merriman, 1944: Pearcy and Richards, 1962). In Newfoundland, M. aeneus is found in shallow (less than 1 m) protected areas on mud, sand and gravel bottoms, and in bedrock tide pools (Ennis. 1969). Although little life history information exists on this species, the majority deals with occurrence and seasonality of larvae (Richards, 1959: Khan, 1971) and/or adults (Dexter, 1944; Warfel and Merriman. 1944: Pearcy and Richards, 1962), descriptions of the eggs and larvae (Lund and Marcy, 1975) and a larval food study (Laroche, 1982). In this paper we present data on habitat utilization, reproduction, age, and food habits of *M. aeneus* in the Nauset Marsh estuary, Cape Cod, Massachusetts.

Methods

Nauset Marsh is a small (945 ha) estuary located on the outer coast of Cape Cod. Massachusetts at approx. 41°49'N. A relatively shallow (maximum depth—5 m) estuarine system, the marsh is characterized by *Spartina alterniflora* marshes, large intertidal sand and mud flats, eelgrass beds (*Z. marina*) and limited freshwater

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input. During this study, water temperatures and salinities recorded by thermometer and re-fractometer ranged from 2-19 C, and 24-35%. respectively.

We collected M. aeneus with otter trawl, seines, minnow traps and a suction sampler from Aug. 1985–Oct. 1986. Six trawl stations were located in the major habitat types within the system: eelgrass beds (2), sand-bottom channels (2), algal-mud flat (1) and a deep water basin characterized by drifting clumps of red algae, Gracilaria sp. (1). Trawl samples consisted of four 2-min tows with a 4.8 m otter trawl (19 mm mesh wings, 6.3 mm mesh liner) during the day at the six stations for a total of 171 samples. We made an additional 24 tows at night in eelgrass and drift algae habitats in Oct. 1985 and Sept.-Oct. 1986 to characterize diel differences in habitat utilization. Using a 7.7 m long (0.6 cm mesh) beach seine, we collected fish at several sampling locations in eelgrass beds, and over sand and mud bottoms. Collections also were made from submerged blocks of marsh peat (referred to herein as peat reefs) using a suction sampler (Able et al., 1988). In addition, we made diver observations on peat reefs in June, July, Sept. and Oct. 1986.

Larvae were sampled using a 0.5 m hoop, 20 cm bongo nets and a 0.5 m epibenthic sled, all with 0.505 mm mesh, from April-Oct. 1986. All cottid larvae collected were *M. aeneus*, identified by the presence of ventral rows of melanophores from the isthmus to the vent (Fahay, 1983). Preserved immediately in 10% formalin, all specimens were later washed in water and stored in 70% ethanol. Those used for aging were frozen as soon as possible after collection. Standard lengths (SL) of preserved juveniles and adults were measured to the nearest millimeter (mm) while larvae were measured to the nearest 0.1 mm using an ocular micrometer.

Prior to analysis of female reproductive seasonality, standard lengths were analyzed for seasonal variation by one way ANOVA using month of collection as the factor. Mean length of females did not show significant differences by month of collection (ANOVA, F = 2.0; 6,84 df; P > 0.05), suggesting calculation of a gonosomatic index (GSI) is appropriate. To prepare the gonosomatic index both ovaries were removed, blotted dry and weighed to the nearest 0.1 mg. After evisceration and air drying for 30 min, each female was weighed to the nearest 0.1 mg. The GSI was calculated as follows:

$$GS1 = \frac{\text{Weight of both ovaries (gm)}}{\text{Total gutted body weight (gm)}} \times 100$$

We quantified follicle diameters by slitting the ovarian tunic, removing all follicles and measuring the longest diameter of 50-70 randomly chosen follicles with an ocular micrometer. We distinguished mature ova based on follicular diameters and the description of Lund and Marcy (1975). The mean of replicate counts of ova (difference <2%) is presented.

Age was determined from whole saccular otoliths (n = 68) collected in Dec. 1985, April, July, Sept., and Oct. 1986. Otoliths were immersed in water and examined under reflected light against a dark background at $30 \times$ with a dissecting microscope. Measurements of annuli used for back calculation of SL at time of annulus formation (Bagenel and Tesch, 1978) were made using a dissecting microscope and ocular micrometer at $70 \times$. Ages were estimated from otoliths and then compared to SL frequencies of males and females using the probability paper method (Harding, 1949).

The stomachs of all juveniles and adults were examined for analysis of food habits. We identified food items to the lowest taxonomic group possible and recorded the frequency of occurrence of each food item. The volume of each item was determined by water displacement to the nearest 0.1 ml in a 10 ml graduated cylinder. A Wilcoxon signed rank test compared the effect of size (\leq or >60 mm SL) on diet (volume and frequency of occurrence, separately) of amphipods, isopods and *Crangon septemspinosa* over the eight sampling periods (Aug., Oct. and Dec. 1985, April, June, July, Sept. and Oct. 1986).

Results

Abundance and habitat utilization.—We collected 168 juvenile and adult *M. aeneus* in Nauset Marsh between Aug. 1985 and Oct. 1986. This species was: 1) the only cottid collected: 2) the seventh most abundant of 46 species collected: and 3) ranked sixth in 22 species collected by trawl in eelgrass beds. Day trawl samples probably underestimated their abundance since greater numbers $(2.4-10 \times)$ were collected with night tows in Oct. 1985 and Sept. and Oct. 1986 at the same stations. We collected larvae (n = 20, 5.7-9.3 mm SL) only in April, and at that time they ranked third in abundance of seven species



Fig. 1. Mean GS1 of female Myoxocephalus aeneus collected in Nauset Marsh. Mean \pm one SD and sample size shown for each month.

collected. Surface water temperatures ranged from 6-9 C, and the salinity averaged 30‰.

We collected *M. aeneus* in four different habitats, but most occurred in otter trawl collections in eelgrass beds (89.2%). They ranged from 37-109 mm SL ($\bar{x} = 68 \text{ mm}$, SD = 15.2 mm). The remaining individuals were collected in peat reef (5.4%), sand (3.6%) and deep water drift algae (1.8%) habitats. Divers observed both juveniles and adults on peat reefs from June-Oct. of 1986.

Reproductive seasonality and periodicity.—Our data indicate that M. aeneus spawns during winter. The mean GSI for females in Nauset Marsh began to increase in Oct. of both years (Fig. 1) and reached a peak in Dec. There was a large decline in mean GSI by April with lowest values occurring during the summer.

Changes in follicle diameters followed a seasonal pattern. The smallest follicles were present in summer, increasing in size in fall with the largest occurring in Dec. (Fig. 2). Mature ova (1.4-2.0 mm) were present only at this time. Five females collected in Dec. (67-95 mm) were gravid. Counts of matue ova ranged from 672-1554 ($\bar{x} = 1275$, SD = 415) in four females with intact ovaries. There were strong positive correlations between female size and ova numbers (r = 0.89) and maximum ova diameter (r = 0.94). In April, the presence of larger ova (0.8-1.2 mm, Fig. 2) found in the ovaries of the single adult female may indicate an extended spawn-

TABLE 1. FOOD OF SMALL ($\leq 60 \text{ mm SL}, n = 63$) and Large (>60 mm SL, n = 105) Myoxocephalus aeneus in Nauset Marsh. V = percent volume. F = percent frequency.

| | Inve | nie | Ad | |
|-----------------------|------|------|------|------|
| Frederic | | | | |
| | V | | • | |
| Polychaeta | - | 1.6 | 0.9 | 1.0 |
| Mollusca | | | | |
| Aequipecten irradians | 1.9 | 1.6 | _ | _ |
| Littorina sp. | _ | _ | 0.5 | 1.0 |
| Arthropoda | | | | |
| Insecta | _ | 1.6 | | 1.0 |
| Crustacea | 94.2 | 78.0 | 77.6 | 61.9 |
| Mysidacea | _ | | 1.9 | 1.9 |
| Isopoda | 13.5 | 25.0 | 0.9 | 6.7 |
| Amphipoda | 17.3 | 37.5 | 3.7 | 12.5 |
| Decapoda | | | | |
| Crangon septem- | | | | |
| spinosa | 61.5 | 32.8 | 58.5 | 46.2 |
| Carcinus maenas | _ | — | 4.2 | 5.8 |
| Cancer sp. | 1.9 | 1.6 | 1.9 | 1.9 |
| Unidentified | | | | |
| crustaceans | _ | 1.6 | 6.5 | 4.8 |
| Pisces | _ | _ | 19.1 | 6.0 |
| Fundulus heteroclitus | _ | — | 8.4 | 2.9 |
| Apeltes quadracus | _ | — | 1.9 | 1.9 |
| Unidentified fishes | _ | — | 8.8 | 2.9 |
| Unidentified material | 3.8 | 10.9 | 1.9 | 13.5 |
| Empty | _ | 12.5 | — | 21.2 |

ing season or residual follicles. Additional evidence of winter spawning included the collection of a running ripe male and two egg masses in Dec. The eggs were spherical, rose colored and attatched to the red algae, *Gracilaria* sp.

Myoxocephalus aeneus exhibits apparent sexual dimorphism in breeding coloration and adult size. Females and juveniles are greenish gray to brown with pale gray shading or irregular barrings, whereas all males (n = 10) collected in Dec. and April exhibit very pronounced black and cream coloration on the body and fins, especially the pelvics. Females were significantly larger, (t-test, P < 0.05) than males. Females (n = 61) ranged from 64–109 mm SL ($\bar{x} = 83.5$, SD = 9.7) whereas males (n = 43) were from 61–104 mm SL ($\bar{x} = 74.1$, SD = 9.5).

Age.—Rings in saccular otoliths appear to be annular structures based on data from several





sources. First, otolith size increased with fish size (r = 0.89). Second, length-frequency analysis (Fig. 3) showed two modes in 1986 that agreed with the back-calculated length of juveniles at the time of annulus formation (range = 45-72 mm SL: $\bar{x} = 59.8$, SD = 5.9) and a larger adult mode. However, these two modes were not apparent in data from 1985. Third, the progressive increase in size of the smallest fish and the larger mode from summer through fall of 1986 (Fig. 3) suggests that these modes represent separate year classes (<60 mm SL = 0 + and >60 mm SL = 1+). Plots of male and female length frequency distributions with probability paper also suggest that assigned ages were valid. Based on presence/absence of annuli, the age 0+ fish (n = 29) ranged from 40-69 mm SL ($\bar{x} = 53.7$, SD = 5.8) whereas age 1+ *M. aeneus* (n = 39) ranged from 66-98 mm SL ($\bar{x} = 82.8$, SD = 8.8).

Food habits.—Food was present in 139 (82.7%) M. aeneus examined. Sand shrimp, Crangon septempinosa, amphipods, and isopods were the major food items (Table 1). Some changes in food habits were apparent with increased size. The major food sources of small M. aenaeus were amphipods, C. septemspinosa, and isopods. Dif-



Fig. 3. Length frequency distributions for male and female Myoxocephalus aeneus collected in Nauset Marsh.

ferences in amphipod and isopod volumes were not significant between sizes, but amphipods (Wilcoxon signed rank test: P < 0.05) and isopods (P < 0.05) occurred more frequently in smaller individuals. The major food source of larger fish was *C. septempinosa*. Fishes and green crabs, *Carcinus maenas*, were found only in their stomachs.

DISCUSSION

Based on our observations during 1985 and 1986, *M. aeneus* is a common resident of Nauset Marsh, most abundant in eelgrass (*Zostera marina*) but also occurring on peat reefs and sand bottoms. They may be more abundant in early summer than our collections indicate: however, divers observed that juveniles and adults were common on peat reefs, a habitat that could not be adequately sampled with otter trawl or seines (Able et al., 1988).

Spawning occurs during the winter, based on increased ova diameters, the presence of mature gonads, the occurrence of egg masses, and reproductive coloration of males at that time of the year. The occurrence of larvae in April also indicates spawning took place in winter since incubation times for *M. aeneus* are about 40–44 d at 4.6–6.0 C (Lund and Marcy, 1975). The length of the spawning season in Nauset Marsh could not be determined due to an absence of sampling in Nov. and between Jan. and March. However, an extended winter spawning season has been reported (Bigelow and Schroeder, 1953; Liem and Scott, 1966: Lund and Marcy, 1975). Larvae were collected only in April 1986. However, the reduced frequency of ichthyoplankton sampling in the winter and early spring makes it difficult to determine the duration of larval occurrence in Nauset Marsh. Larvae have been reported from Jan.-June in other areas (Richards, 1959; Kahn, 1971; Laroche, 1982).

Myoxocephalus aeneus feeds primarily on crustaceans, particularly C. septemspinosa, in eelgrass beds. Bigelow and Schroeder (1953) report they feed on a diversity of organisms including annelid worms, shrimps, crabs, copepods, snails, nudibranch molluscs, ascidians and small fishes. Both juveniles and adults appear to be feeding on an abundant food source in Nauset Marsh because C. septemspinosa densities in eelgrass beds $(7-98/m^2)$ were among the highest observed for macroinvertebrates in suction samples (unpub. data).

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Northern pipefish, <u>Syngnathus fuscus</u>, occurrences over the Mid-Atlantic Bight continental shelf: Evidence of seasonal migration

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Synopsis

Data from several areas in the northern Mid-Atlantic Bight indicate northern pipefish, <u>Svngnathus fuscus</u>, undergo seasonal, inshore-offshore migrations. They are resident in estuaries during spring through fall, then move into nearshore continental shelf waters off Cape Cod in late September-October and Long Island and New Jersey in November. They return to estuaries in March-April. Most (>90%) continental shelf collections in fall (September-November) were at water temperatures of 10-15°C. In spring (March-May), most (>80%) collections occurred at water temperatures between 3-6°C. The majority of offshore collections were within 20 km of the coast and over 90% were at depths between 10 and 20 m. Length frequency data show both young-of-year and older fish migrate, possibly to avoid colder inshore water temperatures in winter.

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Introduction

The northern pipefish, Syngnathus fuscus, (Syngnathidae) is distributed along the Atlantic coast of North America from Jupiter Inlet, Florida to the Gulf of St. Lawrence (Dawson 1982). Information on the distribution, ecology, reproductive habits, egg and larvae development, age and size at maturity has been summarized in Hardy (1978) and Dawson (1982). However, little is known of <u>S. fuscus</u> ecology during the winter. They are an abundant component of the estuarine ichthyofauna in the Mid-Atlantic Bight from late spring through early fall (Warfel & Merriman 1944, deSylva et al. 1962, Orth & Heck 1980, Vouglitois 1983), but winter distribution is not documented (Warfel & Merriman 1944, de Sylva et al. 1962, Pearcy & Richards 1962, Lux & Nichy 1971, Derickson & Price 1973, Orth & Heck 1980, Vouglitois 1983). This rarity during the winter within estuaries suggests migration into continental shelf waters, but collections there are rare (Bigelow & Schroeder 1953, Liem & Scott 1966, Clark et al. 1969), although they are sometimes associated with floating rockweed (Kendall 1896). They are known to migrate from shallow inshore areas to deeper channels within Chesapeake Bay (Hildebrand & Schroeder 1928) and the York River, Virginia (Mercer 1973). Williams (1960) suspected migration to account for population shifts near Woods Hole, but only Wicklund et al. (1968) discussed shallow continental shelf waters as a possible winter refuge. We were prompted to pursue the possibility of migration from estuaries by the disappearance of this species from Nauset Marsh. Cape Cod estuary during the winter (Able et al. In prep.). Here we present evidence from a variety of sources for a S. fuscus seasonal migration out of northern Mid-Atlantic Bight estuaries into shallow continental shelf waters during fall and back into estuaries in spring.

We analyzed data and specimens of <u>S</u>. <u>fuscus</u> from several sources in the Mid-Atlantic Bight (Table 1). These data included number of collections, number and total length (TL) of specimens, bottom temperature, depth and date of collection. We calculated catch per unit effort (CPUE) based on the number of individuals collected per trawl tow.

All National Marine Fisheries Service (NMFS) collections were identified as S. fuscus or simply pipefish and thus we were concerned that identifications were correct. Therefore, we examined all the readily available pipefishes in museum reference collections that occurred in the Atlantic ocean north of Cape Hatteras as reported by Dawson (1982). Review of these capture records suggests that other syngnathid species do not occur in the western Atlantic Ocean north of Cape Hatteras prior to June. In summer, single collections of several rare species (Amphelikturus dendriticus, Oostethus lineatus and Cosmocampus elucens) have occurred off New Jersey and one S. springeri was collected off Massachusetts. Capture records examined by Dawson (1982) also suggested Syngnathus pelagicus usually occurs far offshore of the continental shelf in the Mid-Atlantic region and then only in summer and early fall. Bigelow & Schroeder (1936) report the only known specimen of S. pelagicus from Georges Bank. We also examined specimens from the New York Bight, Nantucket Shoals and Georges Bank (n=22), south of Nantucket Island (n=203), off Little Egg Inlet (n=111) and off southern New Jersey collected by Bingham Oceanographic Institution (n=640) and housed in the Academy of Natural Sciences of Philadelphia (ANSP). These specimens were identified according to Dawson (1982). All were S. fuscus. These results suggest that all the spring and fall pipefish collected on NMFS trawl surveys were S. fuscus.

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Results

Southern New Jersey

Syngnathus fuscus were most abundant in shallow continental shelf water off southern New Jersey in March-April and November (Fig. 1). A consistent pattern of high catch per unit effort (CPUE) occurred during March and April for four consecutive years and in November 1972, 1973 and 1975 and December 1973 as well. A fall peak was not obvious in 1974. Most spring collections (March-May) occurred at bottom temperatures of 5 to 7 °C (85.6%) while most fall (September-November) collections were between 9 and 12 °C (79.3%). All collections were made between 2 and 19 m in depth and within 10 km of shore. Examination of specimens collected by Bingham Oceanographic Laboratory from 1929 to 1932 revealed collections off southern New Jersey occurred primarily in March-April (41.5%) and October-November (54.6%) and provides historical support for the spring and fall occurrences of <u>S</u>. fuscus over the continental shelf.

New York Bight

Collections of <u>S</u>. <u>fuscus</u> off northern New Jersey and Long Island in the New York Bight (Fig. 2a) followed the same seasonal pattern as southern New Jersey. Collections occurred from February through May and August through November, but CPUE greater than 0.1 occurred only in February and March and from September through November with pronounced peaks in March and November. In November, two large collections (n=7120 and 1248) resulted in a very large CPUE. Most spring collections occurred at bottom temperatures of 4 to 6 °C (87.3%) and fall collections were between 10 and 12 °C (99.2%). Most collections were in depths of 10-20 m (98.5%).

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Cape Cod, Massachusetts

Numerous <u>S</u>. <u>fuscus</u> have been collected in southern Massachusetts waters off Cape Cod,. Martha's Vineyard and Nantucket Island in fall (Table 1). We examined all the specimens (n=218) collected in September 1987. Most (93.1%) were collected on September 25, 1987 from south of Nantucket Island (70 10', 40 14') in 15 m of water at bottom temperatures between 16 and 17[°]C.

Mid-Atlantic Bight Continental Shelf

Trawl collections over the Mid-Atlantic Bight continental shelf by NMFS found peaks of <u>S</u>. fuscus abundance in the spring and fall as well (Fig. 2b). The percent of stations with captures peaked in March (12.3%) and April (13.8%) and October (4.3%) and November (4.1%). Collections occurred at or greater than 1% of the stations in January, February and September. Most deeper continental shelf collections also occurred in March-April (23.9%) and October (74.5%). CPUE for shallow continental shelf tows was greater than 0.1 only in March (0.27) and April (1.08) and 0.1 or less the rest of the year. CPUE for deeper continental shelf tows was much lower and only greater than 0.01 for April and October. Most spring collections in both regions occurred at bottom temperatures of 4 to 6⁵C (87.8%), while most fall collections were between 12 and 15[°]C (70.0%). Depths of collection were primarily between 10 and 25 m (74.1%).

In spring (March-May), both shallow and deeper continental shelf collections (n=204) were concentrated off Long Island, New Jersey, Delaware, Maryland and Virginia (Fig. 3). Most (92.2%) of the 796 specimens occurred in shallow collections. In fall (September-November), collections (n=78) were located primarily off Long Island, on Nantucket Shoals, and Georges Bank (Fig. 3). Most (77.6%) of the 246 specimens collected in fall occurred in deep collections. Very few <u>S</u>. fuscus were collected in the winter (December-February). Nine individuals were collected at nine

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stations off New Jersey and Delaware; seven in shallow and two in deeper continental shelf waters. Three individuals occurred in three shallow continental shelf collections off Long Island, New Jersey and Maryland in summer (June-August).

A wide range in length was observed in <u>S</u>. fuscus over the continental shelf. Spring total length ranged from 11 to 24 cm (mean=16.8, SD=3.2, n=68) in the New York Bight, 8 to 36 cm (mean=17.3, SD=3.5, n=718) in shallow and 8 to 33 cm (mean=16.9, SD=4.8, n=58) in deeper continental shelf regions. In fall, total length ranged from 7 to 23 cm (mean=15.4, SD=3.0, n=101) in the New York Bight, 8 to 20 cm (mean=12.0, SD=3.2, n=203) off Nantucket Island, 7 to 31 cm (mean=17.0, SD=5.1, n=55) in shallow and 6 to 30 cm (mean=10.9, SD=2.9, n=190) in deep continental shelf regions.

Discussion

This analysis suggests that <u>S</u>. <u>fuscus</u> in the northern Mid-Atlantic Bight undertake seasonal inshore-offshore migrations. They are found in estuaries during summer (Warfel & Merriman 1944, deSylva et al. 1962, Orth & Heck 1980, Vouglitois 1983) and their consistent high abundance here coincides with their rare appearance in continental shelf waters. In fall, they move out of estuaries and appear in shallow continetal shelf waters off Cape Cod in late September-October and off Long Island and New Jersey in November. Their appearance off Little Egg Inlet, New Jersey occurs immediately prior to their winter disappearance in adjacent estuaries (Thomas & Milstein 1973, Thomas et al.1974, 1975, Milstein et al. 1976). In two long-term studies in nearby Barnegat Bay between December 1966 and October 1970 (Marcellus 1972) and between September 1976 and April 1980 (Vouglitois 1983), abundance also was high from April through November, but they were rarely collected in winter (December-February). The same pattern of rare or no winter occurrences has been

found in Massachusetts (Smith 1898, Lux & Nichy 1971), Connecticut (Warfel & Merriman 1944, Pearcy & Richards 1962) and Delaware (de Sylva et al. 1962, Derickson & Price 1973).

In March-April, S. fuscus apparently move from shallow continental shelf waters back into shallow habitats in estuaries. Their reappearance in the continental shelf collections preceeds their occurrence within these habitats at several estuaries in the Mid-Atlantic Bight (Warfel & Merriman 1944, de Sylva et al. 1962, Pearcy & Richards 1962, Lux & Nichy 1971, Marcellus 1972, Derickson & Price 1973, Vouglitois 1983). Although a few individuals occur over the continental shelf throughout most of the year (Bigelow & Schroeder 1953, Clark et al 1969, Milstein & Thomas 1977), almost all collections examined in this study occurred in March-April and October-November. These peaks in abundance coincide with dates of presumed migration within the Chesapeake Bay (Hildebrand & Schroeder 1928) and New Haven harbor (Warfel & Merriman 1944). Hildebrand & Schroeder (1928) suggested that S. fuscus overwinters in deeper bay channels and spends the other seasons along the immediate shores, migrating to and from these areas in late March-early April and in November, while in New Haven harbor their departure and arrival from the shallow shore zone occurred in late-October and mid-April, respectively (Warfel & Merriman 1944). However, there is no evidence of movement by S. fuscus into continental shelf waters in either of these studies.

This offshore movement may be caused by potentially stressful low water temperatures in shallow bays in winter. Shallow continental shelf bottom water temperatures are 8-10°C warmer in the New York Bight during winter (Bowman 1977a) when Barnegat Bay temperatures drop below 5°C (Vouglitois 1983). In spring, this gradient is reversed as shallow bays warm more rapidly than deeper, nearshore shelf waters (Bowman 1977a). Wicklund et al. (1968) also thought they left shallow estuaries to avoid lethal temperatures. Temperature-dependent migration also is

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suggested by the appearance of <u>S</u>. <u>fuscus</u> in more northern areas of the Mid-Atlantic Bight (Nantucket Island and Georges Bank) at an earlier period and their collection year-round within estuaries at more southern latitudes in North Carolina (F. J. Schwartz pers. comm.) and Georgia (Dahlberg 1972) where winter temperatures are milder. A similar pattern of migration from estuaries to continental shelf-waters in the northern Mid-Atlantic Bight has been proposed for Atlantic silverside, <u>Menidia menidia</u> (Conover & Murawski 1982) and bay anchovy, <u>Anchoa mitchilli</u> (Vouglitois et al. 1987).

Conover & Murawski (1982) examined similar NMFS offshore survey data for <u>M</u>, <u>menidia</u> and reported catches at 5.2% of the shallow and 0.7% deep continental shelf stations. These values compare favorably with our <u>S</u>. <u>fuscus</u> collections of 5.5% and 0.5% for the two regions, respectively. The lower catch frequency in the fall relative to spring may be a function of timing since less than 1% of NMFS shallow continental shelf effort occurred in November.

The wide range in length of <u>S</u>. <u>fuscus</u> from our collections over the continental shelf suggests that both young-of-year and older fish migrate. Although growth data is limited (Tracy 1910, Warfel & Merriman 1944, Mercer 1973), the large size range represented in our collections certainly encompasses, at least, two year classes.

A description of the behavior and habitat of <u>S</u>. fuscus from continental shelf waters is given by Wicklund et al. (1968). They observed numerous individuals off Jones Inlet, Long Island, on November 21-22, 1966 at bottom temperatures averaging 10.6 C over a ridged coarse-sand substate in 14-17 m of water. <u>Syngnathus fuscus</u> appeared in a torpid state partially buried in the sand with only their head and caudal fin exposed, or curled around starfish, or just lying motionless on the bottom. They exhibited no noticeable respiratory movements and only showed signs of activity after they were handled for several seconds. The winter habitat of <u>S</u>. fuscus may include deeper channel

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areas of some coastal bays since they occurred in these habitats within Chesapeake Bay (Hildebrand & Schroeder 1928) and the York River (Mercer 1973).

The migatory behavior of <u>S</u>. <u>fuscus</u> may be similar to behavior of syngnathids observed in eelgrass beds in Western Port, Australia (Howard & Koehn 1985) where there are two main behavioral types: species which orient themselves horizontally and are relatively strong swimmers and those which are more sedentary and attach to benthic vegetation by means of a prehensile tail. They found a less specialized use of vegetation cover by those species possessing a well-developed caudal fin and increased mobility and these pipefishes appear to occupy a wider range of habitats. <u>Svngnathus fuscus</u> appears to resemble the latter behavioral type because they can travel swiftly when alarmed (Bigelow & Schroeder 1953) and are not limited to vegetated habitats (Dexter 1944, Warfel & Merriman 1944, Briggs & O'Connor 1971, Bleakney & McAllister 1973, Briggs 1975, Hardy 1978). Our personal observations of nocturnal behavior in Nauset Marsh (Cape Cod) also indicate they are active swimmers.

Considerable evidence exists that other syngnathids are migratory. Herald (1943) noted extensive movements of bay pipefish, <u>S. leptorhynchus</u> in Point Mugu Iagoon eelgrass beds in California and they may migrate seasonally within the Yakima estuary in Oregon (Bayer 1980). The gulf pipefish, <u>S. scovelli</u>, undergoes seasonal movements in Florida (Hamilton 1942, Brown 1972). Hildebrand & Schroeder (1928) report dusky pipefish, <u>S. floridae</u> in the Chesapeake Bay undergo autumn-winter migrations into deeper bay or ocean waters and Schwartz (1964) found they move to deeper areas within Isle of Wight and Assawoman Bays to overwinter.

The migration of <u>S</u>. <u>fuscus</u> in fall may result in the net movement of biomass and energy from estuaries to the ocean in a manner similar to spot, <u>Leiostomus xanthurus</u> and other species (Weinstein et al. 1980), <u>M. menidia</u> (Conover & Murawski 1982), and <u>A. mitchilli</u> (Vouglitois et al. 1987). Although <u>S. fuscus</u> are thought to have few predators (Bigelow & Schroeder 1953, Dawson 1982), Briggs & O'Connor (1971)

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state they are locally important as forage fish in Great South Bay, Long Island. They occur in the stomachs of bluefish, <u>Pomatomus saltatrix</u> (Metzger 1978), striped bass, <u>Morone saxatilis</u> (deSylva et al 1962), and summer flounder, <u>Paralichthys dentatus</u> (Poole 1964, Allen et al. 1978) within estuaries and spiny dogfish, <u>Squalus acanthias</u> (pers. obs.), red hake, <u>Urophycis chuss</u> (Allen et al. 1978), cod, <u>Gadus morhua</u> (Dawson 1982), longhorn sculpin, <u>Myoxocephalus octodecimspinosus</u> (Bowman 1977b), and <u>M. saxatilis</u> (Schaefer 1970) in the Atlantic ocean. They also have been observed entangled in the tentacles of <u>Physalia pelagica</u> (Gordon 1956).

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| | | eries Service | | | n of Marine | . 1984, | | | 973, | 1975; | | |
|-----------------------|-------------------|-----------------------|------------------|------------------|-----------------------|-----------------------|-------------------|--------------------|----------------------|---------------------|-----------------------|--|
| Source | | National Marine Fishe | Groundfish Suvey | (Azarovitz 1981) | Massachusetts Divisio | Fisheries (Howe et al | 1985, 1986, 1987) | (Wilk et al. 1977) | (Thomas & Milstein 1 | Thomas et al. 1974, | Milstein et al. 1976) | |
| Number of Stations | | 4069 | 14816 | | 466 | | | 515 | 602 | | | |
| Number Collected | | 799 | 255 | | 1258 | | | 8541 | 1690 | | | |
| Years | | 1972-1986 | 1963-1986 | | 1982-1983 | 1985-1987 | | 1974-1975 | 1972-1975 | | | |
| Depth (m) | | 5-27 | 28-366 | | 7-24 | | | 5-366 | iy 2-20 | | | |
| Study area | Continental Shelf | Shallow | Deep | | Massachusetts | | | New York Bight | Southern New Jerse | | | |

Table 1. Sources analyzed for seasonal movements of Syngnathus fuscus in the Mid-atlantic Bight.

List of Figures

- Fig. 1. Catch per unit effort (number individuals per trawl) for <u>Syngnathus fuscus</u> collected offshore of Little Egg Inlet, New Jersey during 1972-1975. See Table 1 for data source.
- Fig. 2. Catch per unit effort (number individuals per trawl) for <u>Syngnathus fuscus</u> collected a) in the New York Bight from June 1974-June 1975; b) by National Marine Fisheries Service in shallow (5-27 m) and deep continental shelf (27-366 m) regions from 1963-1986. See Table 1 for data source.
- Fig. 3. Location of <u>Syngnathus fuscus</u> in spring and fall trawl collections in the Mid-Atlantic Bight by the National Marine Fisheries Service from 1963 - 1986, (n = number collected and st = number of stations). See Table 1 for data source.

Catch Per Unit Effort



FIGURE 2





PRODUCTION ECOLOGY OF EELGRASS (*ZOSTERA MARINA* L.) IN A CAPE COD SALT MARSH–ESTUARINE SYSTEM, MASSACHUSETTS

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ABSTRACT

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Primary production and biomass loss of Zostera marina L. were estimated at two sites within the Nauset Marsh system, Cape Cod, Massachusetts. Maximum live leaf-blade biomass at the Nauset Harbor (305 g dry weight (DW) m⁻²) and Town Cove (199 g DW m⁻²) sites peaked in mid-August. Maximum leaf-blade productivities, estimated by a leaf-marking technique, were 10.8 g DW m⁻² day⁻¹ and 5.5 g DW m⁻² day⁻¹, respectively. Leaf-blade production occurred throughout winter, but at much reduced rates (<0.2 g DW m⁻² day⁻¹, both sites). Net annual aboveground (leaf blades, reproductive shoots, sheaths) primary production was estimated at 987 g DW m⁻² year⁻¹ and 444 g DW m⁻² year⁻¹, respectively. Peak rates of leaf-blade biomass loss occurred in early September (Nauset Harbor, 8.5 g DW m⁻² day⁻¹; Town Cove, 4.7 g DW m⁻² day⁻¹), corresponding to a period of high eelgrass-wrack accumulation on New England shorelines. Annual leaf-blade biomass loss was 577 g DW m⁻² year⁻¹ and 303 g DW m⁻² year⁻¹, respectively. These loss rates, coupled with leaf-crop turnover rates of 6 crops year⁻¹, stress the role of eelgrass meadows in the support of estuarine detritus-based food webs.

INTRODUCTION

Eelgrass (Zostera marina L.) meadows represent an ecologically important habitat along the Atlantic coast of North America (Thayer et al., 1984a,b; Orth et al. 1984); yet, for this region and elsewhere there is a paucity of information on the primary production and decomposition dynamics of this ecosystem. The purpose of this study was to estimate annual eelgrass aboveground productivity and to evaluate the fate of this production in a New England estuary.

Previous studies conducted along the New England coast, the northern portion of the eelgrass range, have generally been limited to estimates of biomass

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(New Hampshire – Riggs and Fralick, 1975; Massachusetts – Conover, 1958; Rhode Island – Short, 1980; Thorne-Miller et al., 1983), with only a few esti-

Rhode Island – Short, 1980; Thorne-Miller et al., 1983), with only a few estimates of primary productivity (Dennison and Alberte, 1982, 1985; Thorne-Miller and Harlin, 1984). Seasonal chemical composition dynamics are reported for a Nova Scotia eelgrass meadow, yet no estimates of productivity or seasonal biomass were presented (Harrison and Mann, 1975). In this study eelgrass primary production estimates were derived from a leaf-marking technique, a procedure successfully employed on the mid-Atlantic (Vaughan, 1982) and Pacific Northwest (Kentula and McIntire, 1986) coasts of the U.S.A., France (Jacobs, 1979), Denmark (Sand-Jensen, 1975) and Japan (Mukai et al., 1979; Aioi et al., 1981).

MATERIALS AND METHODS

Study Sites

The 950-ha Nauset Marsh estuarine system is dominated by Spartina alterniflora Loisel. marsh, along with other habitats including, eelgrass beds, intertidal mud and sand flats, mussel beds, shallow tidal channels (maximum 3-m deep), and open-water ponds. Eelgrass beds occupy 6-10% of the system. Two subtidal sites were selected for the study of eelgrass production dynamics (Fig. 1). One site was located in Nauset Harbor, where eelgrass occurs throughout. A band of eelgrass encompasses the entire periphery of Town Cove, the area of the second study site. Mean tidal range at Nauset Harbor is about 1.1 m, and slightly less at the Town Cove study site owing to frictional attenuation (Aubrey and Speer, 1985). For both sites, water depth at mean low water was about 1 m. Mean tide salinity was generally 25-30‰, with water temperature ranging from 0° to 22°C during the one-year study period.

Biomass

Beginning in June, 1986, and continuing for one year, five harvest samples were collected from each site on each sample date. Harvest samples consisted of sediment and intact eelgrass collected with clam tongs. A section, $25 \text{ cm} \times 25$ cm, was cut from the center of each harvest sample for further analysis. During periods of active growth (April-October), harvest intervals ranged from 15 to 24 days, and from 33 to 58 days during other periods. In the laboratory the shoots from each sample were separated according to leaf age, sheaths and reproductive shoots. Live plant material not attached to a complete shoot was grouped as unidentified live biomass. Dead biomass was discarded. Epiphytes were removed from all leaf blades, sheaths and reproductive shoots by carefully scraping with a glass slide. Epiphyte biomass was negligible, and so the scraped material was discarded. All of the separated plant material was washed over a



Fig. 1. The Nauset Harbor and Town Cove eelgrass sampling sites within the Nauset Marsh system, Cape Cod, MA.

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1-mm mesh sieve, dried to a constant weight at $60 \degree C$, and weighed. Subsamples were combusted at $550\degree C$ for 3 h. Biomass data in this paper are presented on a dry weight basis; however, eelgrass biomass is occasionally presented in the literature on an ash-free dry weight basis. To allow comparison with these data it is noted that ash contents of all the sampled plant components were similar and relatively consistent on a seasonal basis, averaging 21% (range 14-29%) of the dry weight.

Turnover

Eelgrass boxes, adapted from Sand-Jensen (1975), were employed to estimate turnover rate. At each site four boxes, $30 \text{ cm}(\log) \times 30 \text{ cm}(\text{wide}) \times 10 \text{ cm}(\text{deep})$, were established with blocks of eelgrass and sediment dug from the sample sites and placed in the boxes. At each sampling date (corresponding to harvest samples), the youngest leaf (leaf Number 1) of a selected shoot was marked by making a small notch near the tip with a paper punch (adapted from Zieman and Wetzel, 1980). Shoots were selected from central portions of the boxes to avoid plants damaged by cut rhizomes. Six to fifteen shoots were marked from each box. A wire grid was used to assist with location of individual shoots. The total number of leaves per marked shoot was also recorded. The boxes were placed in the eelgrass meadow.

On the next sampling date the boxes were retrieved from the meadow, and for all marked shoots the leaf number of the marked leaf was recorded. New leaf No. 1s that had emerged during the interval, or leaf No. 1s on newly selected plants, were then marked, the total number of leaves per shoot recorded, and the boxes returned to the meadow.

Production and Loss Estimates

Leaf-blade production and leaf-blade loss during the sample intervals were estimated by coupling the turnover and biomass data. For each sample interval the mean progression of each leaf age toward an older leaf, and eventually to defoliation or loss, could be determined. With knowledge of mean leaf-age biomass at the beginning of a sample interval and mean leaf-age biomass of that leaf age as it had progressed at the end of the sample interval, it was possible to estimate net leaf production and/or net biomass loss, expressed as g DW m^{-2} day⁻¹. Because leaf-age progression was determined from the mean of 25-60 marked shoots per interval per site, the progression was often expressed as a fraction (e.g., Leaf Age 1 progressed to Leaf Age 2.8, Leaf Age 2 to 3.8, Leaf Age 3 to 4.8, Leaf Age 4 was defoliated, etc.). Therefore, biomass of the leafage fractions was determined from third order polynomial regressions fitted to the leaf age vs. biomass data. Fits were excellent, with coefficients of determination (r^2) for the 30 regression equations ranging from 0.81 to 0.99 (mean $r^2 = 0.97$). Integrating the leaf-blade production and leaf-blade loss rates over time yielded net annual estimates.

RESULTS AND DISCUSSION

Seasonal Biomass Trends

Total leaf-blade biomass at the Nauset Harbor site peaked in early June (246 g DW m⁻²) and again in mid-August (305 g DW m⁻²; Fig. 2). At the Town Cove site there was a single mid-August peak (199 g DW m^{-2}), yet this maximum value was significantly lower (t-test, P < 0.01, n = 5) than the mid-August peak at Nauset Harbor. An allocation of resources toward reproductiveshoot production at Nauset Harbor in early July, with a corresponding decline in leaf biomass at the next harvest date, may be the principal factor contributing to the observed bimodal cycle. Sand-Jensen (1975), studying an eelgrass meadow in Denmark, found that maximum reproductive-shoot biomass corresponded to only 12% of the total aboveground biomass (leaves and reproductive shoots), compared with about 50% for the Nauset Harbor site, suggesting a substantially different allocation of resources at the Cape Cod site. This apparent synergistic effect between vegetative- and reproductiveshoot production has been noted elsewhere (Thayer et al., 1984b). Maximum reproductive-shoot biomass at the Town Cove site represented only 9% of total aboveground biomass during the mid-June harvest.

Maximum aboveground biomass (live leaf blades; sheaths; reproductive shoots) was 570 g DW m⁻² at Nauset Harbor and less than half at Town Cove (252 g DW m⁻²). These estimates appear to be within the range of maximum values reported for other sites along the northeast coast of the U.S.A. (Burkholder and Doheny, 1968; Riggs and Fralick, 1975; Short, 1980; Vaughan, 1982; Thorne-Miller et al., 1983). However, a detailed comparison among sites is not appropriate owing to differences in sorting and processing of samples, and thus, in data presentation.

Productivity and Loss

Maximum leaf-blade production at both the Nauset Harbor $(10.8 \text{ g DW m}^{-2} \text{ day}^{-1})$ and Town Cove $(5.5 \text{ g DW m}^{-2} \text{ day}^{-1})$ sites occurred in mid-August (Fig. 3). Leaf-blade production for the winter period (December-April) was less than 0.2 g DW m⁻² day⁻¹ with minimum estimates of 0.08 g DW m⁻² day⁻¹ (Nauset Harbor) and 0.06 g DW m⁻² day⁻¹ (Town Cove) recorded. Dennison and Alberte (1982, 1985), studying a nearby Cape Cod eelgrass system, found similar summertime values, reporting a range of 1.8-6.3 g DW m⁻² day⁻¹ for areas sampled in August. Vaughan (1982) reports maximum and minimum leaf blade production values of about 3.0 g DW m⁻² day⁻¹ and less



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Fig. 2. Biomass of live leaf blades, sheaths and reproductive shoots $(\bar{x}\pm SE, n=5)$ during the period from June 1986 to June 1987 at the (a) Nauset Harbor and (b) Town Cove sites.

than 0.5 g DW m⁻² day⁻¹ in winter for a New Jersey system. Maximum leafblade production values from these studies along the northeast Atlantic coast of the U.S.A. are within the range of values reported for other coastlines where





studies have utilized similar marking procedures (Table 1).

Net annual aboveground primary production at the two Nauset Marsh sites is shown in Table 2. Except for the annual leaf-blade production estimates,

TABLE 1

Maximum leaf blade production at the Nauset Marsh sites compared with estimates from other regions

| Study site | Maximum leaf blade productivity (g DW m ⁻² day ⁻¹) | Source |
|-----------------------|--|----------------------------------|
| Nauset Harbor, MA | 10.8 | This study |
| Town Cove, MA | 5.5 | This study |
| Woods Hole, MA | 1.8-6.3 | Dennison and Alberte, 1982; 1985 |
| Little Egg Harbor, NJ | 3.0 | Vaughan, 1982 |
| Netarts Bay, OR | 4.7-13.6 | Kentula and McIntire, 1986 |
| Vellerup Vig, Denmark | 7.9 | Sand-Jensen, 1975 |
| Roscoff, France | 3.0 | Jacobs, 1979 |
| Nabeta Bay, Japan | 2.3 | Mukai et al., 1979 |

TABLE 2

Estimate of net annual aboveground primary production at the two Nauset Marsh sites

| Plant component | Productivity (g DW m ⁻² | ² year ⁻¹) |
|----------------------------------|------------------------------------|-----------------------------------|
| | Nauset Harbor | Town Cove |
| Leaf blades ¹ | 626 | 385 |
| Reproductive shoots ² | 237 | 6 |
| Sheaths ² | 124 | 53 |
| Total aboveground | 987 | 444 |

¹Estimate based on leaf-marking procedure as described in detail in materials and methods. ²Estimate based on peak live standing crop.

production of the other components is expressed as the peak live standing crop, a production method generally considered to be an underestimate (Zieman and Wetzel, 1980).

The rate of leaf-blade biomass loss was closely coupled to leaf production, as expected (Fig. 3). At both sites, peaks in loss were generally 20 days after production peaks. Although leaf defoliation does not necessarily imply export from an eelgrass meadow, maximum loss rates occurred in early September (Nauset Harbor, 8.5 g DW m⁻² day⁻¹; Town Cove, 4.7 g DW m⁻² day⁻¹), corresponding to the time when maximum quantities of eelgrass wrack are reported to occur at other New England estuarine systems (Josselyn and Mathieson, 1980; Thorne-Miller et al., 1983). Annual leaf-blade biomass loss was 577 g DW m⁻² year⁻¹ and 303 g DW m⁻² year⁻¹ for the Nauset Harbor and Town Cove sites, respectively. Several factors, including observed grazing by American Black Duck (*Anas rubripes* Brewster) and other waterfowl, and

TABLE 3

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| Site | Plastochrone inte | erval (days) ¹ | Leaf life spa | in (days) ² | Leaf crop turnover ^a | Source |
|--|--|--|-----------------------------------|-------------------------|---------------------------------|----------------------------|
| | Range | Mean | Range | Mean | (times year ⁻¹) | |
| Nauset Harbor, MA | 8.2-27.3 | 14.8 | 36-101 | 59 | 6.2 | This study |
| Town Cove, MA | 8.2-36.0 | 16.7 | 38-124 | 61 | . 0.9 | This study |
| Little Egg Harbor, NJ | 10-130 | 15.5 | 50 - 400 | 59 | 6.2 | Vaughan, 1982 |
| Netarts Bay, OR | I | 16.5 | I | 48 | 7.6 | Kentula and McIntire, 1986 |
| | | 11.6 | | 36 | 10.1 | |
| Vellerup Vig, Denmark | ı | 1 | ı | 56 | 3.4 | Sand-Jensen, 1975 |
| Roscoff, France | 13.1-28.7 | 19.3 | 55-83 | 68 | 5.4 | Jacobs, 1979 |
| ¹ Plastochrone interval i ² Leaf life span is plastoc ³ Leaf crowtnerwor is 3 | s the time interval chrone interval mul 65 days divided by | between the emerge ltiplied by number o | nce of two suc f leaves per sl | cesive leaves. 100t. | | |
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leaching and autolysis of dissolved organic matter (see review, Zieman 1982), may account for the differences between these values and net annual leafproduction rates.

The significance of eelgrass production in terms of organic-matter contribution to estuarine systems can be appreciated by studying growth dynamics and turnover rates. At both sites, a rapid turnover of leaves is noted, with about 6 new leaf crops produced per year (Table 3). As a comparison, turnover rate for short-form *S. alterniflora*, the dominant marsh plant of the Nauset Marsh system, is significantly lower (2 crops year⁻¹). Turnover data from the Nauset Marsh eelgrass study sites and other areas, expressed as plastochrone interval, leaf lifespan and leaf-crop turnover, clearly indicate the role of eelgrass meadows in the support of estuarine detritus-based food webs.

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PRIMARY PRODUCTIVITY OF ANGIOSPERM AND MACROALGAE DOMINATED HABITATS IN A NEW ENGLAND SALT MARSH-ESTUARINE SYSTEM: A COMPARATIVE ANALYSIS

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Keywords: Spartina, Zostera, Macroalgae, Primary Productivity,

Massachusetts

Abstract

Net primary productivity estimates are made for the major macrophyte dominated habitats of the Nauset Marsh system, Cape Cod, Massachusetts. Aboveground primary productivity of short form Spartina alterniflora, the dominant habitat of the system was 664 g m⁻² y⁻¹. Productivity of the other dominant angiosperm (Zostera marina) was estimated to range from 444-987 g m⁻² y⁻¹. The marsh creekbank habitat was dominated by an intertidal zone of fucoid algae (Ascophyllum nodosum ecad. scorpioides, 1179 g m⁻² y⁻¹; Fucus vesiculosus, 426 g m⁻² y⁻¹), mixed intertidal filamentous algae (91 g m⁻² y⁻¹), and a subtidal zone of assorted macroalgae (68 g m⁻² y⁻¹). Intertidal mudflats were dominated by Cladophora gracilis, with net production ranging from 59-637 g m⁻² y⁻¹. These angiosperm and macrophyte dominated habitats produce over 3 x 10^{6} kg y^{-1} of biomass (1.2 x 10⁶ kg Carbon y^{-1}). A significant 28% of this carbon production is derived from the Zostera and macroalgae habitats. Although S. alterniflora is considered the major macrophyte primary producer in Nauset Marsh and other north temperate salt marshes, it is concluded that other habitats also contribute significantly to total system carbon production.

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Introduction

Salt marshes of New England are dominated by Spartina alterniflora, although other vegetated habitats such as, eelgrass (Zostera marina) meadows and macroalgae-dominated mudflats and creekbanks, may also be prominent. Spartina is reported to occupy less than 65% of the total ecosystem area for some typical New England systems (e.g., Barnstable Marsh, Massachusetts - Redfield, 1972; Bissel Cove, Rhode Island - Nixon & Oviatt, 1973a; Flax Pond, New York - Woodwell et al., 1979). In contrast, over 95% of the Sapelo Island-Duplin River marsh (Georgia), a typical southeastern U.S. salt marsh system, is dominated by *S. alterniflora* (Reimold et al., 1973).

The objective of this paper is to evaluate the relative contribution of several dominant habitats to total system macrophyte production in a New England salt marsh-estuarine system. This evaluation is part of a comprehensive.study investigating the ecological role of estuarine habitats in the Nauset Marsh ecosystem, Cape Cod, Massachusetts. Primary production and biomass estimates of the major macrophyte-dominated habitats in Nauset Marsh will provide a basis for our ongoing studies of habitat utilization by estuarine fauna, secondary production, and nutrient interactions. In addition to providing estimates of *S. alterniflora* and *Zostera* production, this paper presents seasonal biomass and net primary production estimates for the macroalgae dominated habitats in Nauset Marsh, including intertidal mudflats and intertidal/subtidal salt marsh creekbanks. Few studies of salt marsh-estuarine primary production and biomass dynamics have included macroalgae (Nixon & Oviatt, 1973; Brinkhuis, 1976; Welsh et al., 1982;

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Chock & Mathieson, 1983; Thorne-Miller & Harlin, 1984), a component that appears to be significant to total macrophyte production in north temperate estuaries.

The study site

The 945 ha Nauset Marsh (Eastham and Orleans, Massachusetts) is a back-barrier estuary, with direct exchange to the Atlantic Ocean through a tidal inlet (Figure 1). Tidal range is about 1.5 m on the estuarine side of the inlet and less in other parts of the system due to frictional attenuation (Aubrey & Speer, 1984). Mean tide salinity throughout is 25-30 ppt, with annual water temperature ranging from -2°C to 22°C.

True color vertical aerial photographs (scale 1:18,000; October 22, 1982) were used to map the major habitat types, with ground truthing performed in spring-summer 1986. Salt marsh occupies 330 ha, or 35%, of the system. This habitat is dominated by extensive areas of short form *S*. *alterniflora*, with the tall form occasionally found as narrow bands (<1 - 3m) along the network of tidal creeks. Patches of *S*. *patens* and *Distichlis spicata* are rarely encountered. Salt Pond Bay and Nauset Bay contain most of the system's 115 ha (12%) of intertidal mudflat habitat. Patches of the green alga, *Cladophora gracilis*, occur throughout this habitat. Intertidal sand flats (105 ha, 11%) are a dynamic component of the system and mostly associated with the Inlet's flood tidal delta. New Island is dominated by supratidal sand flat habitat. Eelgrass beds occupy 55 ha or 6% of the system; however, recent observations indicate that this habitat has expanded since the aerial flight and subsequent ground truthing. Open

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water accounts for 33% (315 ha) of the system and is associated with tidal kettle ponds (Town Cove, Mill Pond and Salt Pond) and major tidal channels throughout the system. These channels are typically shallow at low water (<1 - 3 m).

Aside from the intertidal mudflat habitat, macroalgae occur along the marsh creekbanks. A typical vertical creekbank profile at Nauset Marsh contains an intertidal zone of fucoid algae (Ascophyllum nodosum ecad. scorpioides, Fucus vesiculosus) usually associated with tall S. alterniflora, an intertidal zone of filamentous algae attached to the substrate of exposed creekbank peat, and a subtidal zone of assorted macroalgae growing on chunks of marsh peat that have fallen into the tidal creek. These irregular sized peat blocks settled along the margins of deeper tidal channels are referred to as peat reef habitat (Able et al., in press).

Materials and methods

Four habitats were sampled to include the major macrophytic contributions to total system production; salt marsh, eelgrass bed, macroalgal-dominated intertidal mudflat, and macroalgal-dominated intertidal/subtidal creekbanks.

Salt marsh habitat

Beginning in June 1986 and continuing for 1 yr, aboveground harvest collections were made at 4-6 wk intervals from a short *S. alterniflora* sampling area and a tall *S. alterniflora* area. At each interval, 10

quadrats (0.25 m^2) were randomly harvested from each sample area. All standing vegetation was clipped at the marsh surface and separated into live and dead components. The samples were washed of sediment, filamentous algae and visible animals, dried to a constant weight at 60°C, and weighed.

Belowground biomass was collected following the method described by Gallagher (1974). At 6-8 wk intervals, beginning in February 1986 and continuing for 1 yr, 10 cores (10 cm diameter, 30 cm length) were collected from the short *S. alterniflora* sampling area and 5 cores from the tall form area. Each core was sliced into 10 cm increments and then the roots and rhizomes were washed free of sediment over a 1 mm mesh screen. For two short form cores and one tall form core, live and dead roots and rhizomes were separated by visual inspection. All belowground plant material was then dried to a constant weight at 60°C, and weighed.

Eelgrass habitat

Two subtidal sites within the Nauset Marsh system (Nauset Harbor and Town Cove) were selected to estimate Zostera biomass and primary production during the period from June 1986 to June 1987. Roman and Able (in press) describe the methods in detail. Briefly, five samples were harvested from each site at 15-24 day intervals during periods of active growth (April-October), and from 33-58 days during other periods. Samples (0.0625 m^{-2}) were collected with modified clam tongs. In the laboratory the live shoots were separated according to leaf blade age, reproductive shoots, and sheaths. Epiphytes were scraped from all plant material. The plant material was dried to a constant weight at 60°C, and weighed.

Primary productivity of leaf blades during each sample interval was

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estimated by coupling the biomass data with leaf blade turnover rates. Turnover was estimated by *in situ* marking of leaf blades, modified from Zieman and Wetzel (1980) and Sand-Jensen (1975). Integrating the leaf blade production estimates over time yielded estimates of net annual leaf blade primary production. Net annual primary production of the reproductive shoots and sheaths was estimated by the peak live standing crop method.

Intertidal mudflat habitat

Salt Pond Bay and Nauset Bay are predominantly intertidal mudflat habitat with the green alga, *Cladophora gracilis*, occuring in a patchy distribution. Collections were made at 6-8 wk intervals from Salt Pond Bay beginning in October 1985, and continued for 15 months. Collections were made at low water. A stratified-random sampling scheme was employed at each sample interval, with five quadrats (0.051 m²) taken from a densely and a sparsely vegetated area.

Intertidal/subtidal creekbank habitat

Biomass determinations of the intertidal fucoids were initiated in October 1985, and collections continued at 6-8 wk intervals for 15 months. At each interval, ten 0.051 m² samples were harvested from five sample sites. (Only five quadrats per site were harvested during the initial three sample collection dates.) In the laboratory, the samples were sorted by species, washed free of sediment and visible animals, dried to a constant weight at 60°C, and weighed. ANOVA revealed no significant differences (p<0.05) in mean biomass for the five sample sites, thus, the

data were pooled.

Macroalgae of the intertidal filamentous algae zone and the subtidal peat reef algae were harvested by diving in early July, 1987. The algae were scraped into a fine mesh bag (1.6 mm²) that was fitted over a 0.0625 m² sample quadrat. At two sites, five quadrats were collected from the intertidal zone and ten from the subtidal zone. Laboratory procedures were as described above. Data from the two sites were pooled as a Student's t-test revealed no significant difference (p<0.05) in total mean biomass between the sites.

Results and discussion

Salt marsh biomass and production

Live aboveground biomass of both short and tall form *S. alterniflora* peaked in mid-summer with a rapid decline to December when live biomass was absent until mid-spring (Figure 2). This seasonal pattern is similar to that observed in other New England salt marshes (Valiela et al., 1975; Ruber et al., 1981). In more southern regions, seasonal patterns are similar, but live *S. alterniflora* biomass is present year-round (e.g., Georgia -- Gallagher et al., 1980; South Carolina -- Dame & Kenny, 1986).

Net annual aboveground primary productivity of short form S. alterniflora in Nauset Marsh ranged from 445 g m⁻² y⁻¹ to 664 g m⁻² y⁻¹ and from 511 g m⁻² y⁻¹ to 732 g m⁻² y⁻¹ for tall form, depending on the computation method used (Table 1). The peak live method assumes that the single highest value of standing live biomass harvested during an annual cycle represents net primary production. The Milner and Hughes (1968)

method is more refined as it accounts for changes in live biomass over time, while the Smalley (1958) method is still more refined by considering temporal changes in both live and dead biomass. Assessing variability among methods has been the subject of several studies (Kirby & Gosselink, 1976; Linthurst & Reimold, 1978; Shew et al., 1981), with the general conclusion that the peak live standing crop, Milner and Hughes, and Smalley methods all underestimate net primary production. Despite this underestimate, the widespread utility of these methods allows for comparisons with other New England systems, as presented in Table 1.

For both short and tall form S. alterniflora, two peaks in total belowground biomass occurred in April and October, with minimum total biomass in mid-summer (Figure 3). With only bimonthly collections it is difficult to evaluate real trends in the data from inherent sampling variability -- a problem reported elsewhere for belowground biomass studies (Gallagher & Plumley, 1979; Roman & Daiber, 1984). However, it is interesting to note that a similar seasonal pattern was reported for a north temperate salt marsh in New Jersey (Smith et al., 1979). Conversly, a mid-summer peak was reported for a nearby New England salt marsh (Valiela et al., 1976).

Net annual belowground S. alterniflora production was estimated by calculating the annual increment after Gallagher and Plumley (1979). Annual increment is here defined as the mean of the two maximum biomass values minus the mean of the two minimum biomass values. Belowground production estimates from Nauset Marsh are comparable to the few estimates for other New England salt marshes (Table 1). For short S. alterniflora, belowground production was concentrated near the surface, with an annual

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average of 78% of live biomass occurring in the upper 10 cm. The zone of most active production occurred within the top 20 cm for tall *S*. *alterniflora*, with 57% of live biomass occurring from 0-10 cm and 41% from 10-20 cm. This distribution of living biomass near the surface is typical of most salt marsh species (Good et al., 1982).

Eelgrass biomass and production

As discussed in detail by Roman and Able (in press), eelgrass aboveground live biomass (leaf blades, reproductive shoots, sheaths) peaked in July at the Nauset Harbor site, corresponding to the time of active reproductive shoot development (Figure 2). At Town Cove reproductive shoot growth was minimal. Live biomass at Town Cove peaked in August, corresponding to a second biomass peak at the Nauset Harbor site. Unlike *Spartina* live biomass and production occurred throughout the winter, albiet at reduced levels.

Net annual aboveground production at the Nauset Harbor site was 987 g $m^{-2} y^{-1}$ and 444 g $m^{-2} y^{-1}$ at the Town Cove site (Roman & Able, in press). These estimates are clearly at the lower end of the range of annual production values reported for a Rhode Island coastal lagoon system (841-2557 g $m^{-2} y^{-1}$; Thorne-Miller & Harlin, 1984); however, direct comparisions must be made with caution as different methods were employed.

Algal-dominated habitats: biomass and production

Peak biomass of the intertidal mudflat alga, *Cladophora gracilis*, was 638 g m⁻² in dense patches and 60 g m⁻² in sparse patches (Figure 2; sparse data not plotted). Due to a very distinct biomass peak and seasonal

cycle, the single maximum biomass and the single minimum biomass values are used in the annual increment method for estimating net annual primary production. Thus, the net production estimate for dense areas is 637 g m⁻² y^{-1} , and 59 g m⁻² y^{-1} for sparse areas. Biomass or production estimates for intertidal *Cladophora* habitat in other New England systems could not be found; however, for a similar intertidal mudflat habitat dominated by *Ulva lactuca*, Welsh (1980) reports a maximum biomass of 185 g m⁻². In the Bissel Cove (RI) tidal embayment, biomass of a mixed *Ulva/Enteromorpha* habitat peaked in summer at 260-600 g m⁻² (Nixon & Oviatt, 1973a). Udell *et al.* (1969), studying an *Ulva*-dominated subtidal estuarine habitat along the southern shore of Long Island (NY), estimated a net annual production of 785 g m⁻² y⁻¹, similar to our production estimate for the Nauset Marsh *Cladophora* habitat.

Seasonal biomass trends (Figure 2) of the creekbank fucoid zone show maximum biomass of Ascophyllum (1459 g m⁻²) occurring in June and an August Fucus biomass peak (352 g m⁻²). Minimum biomass of these fucoids occurred in winter. In the Flax Pond salt marsh (Long Island, NY), Brinkhuis (1976) reports a maximum Ascophyllum ecad. scorpioides biomass of 175-225 g m⁻², similarly occurring in late spring, but with minimum biomass in September. For Fucus vesiculosus v. spiralis, Brinkhuis (1977) recorded maximum biomass of up to 500 g m⁻² occurring between March and July, and minimum biomass in late fall. Unlike the Nauset and Flax Pond systems, maximum standing crops of 350-500 g m⁻² for the ecad. scorpioides were recorded from September to November in a salt marsh of the Great Bay Estuary, New Hampshire (Chock 4 Mathieson, 1983). In that system peak biomass of Fucus was 128 g m⁻², also occurring in the fall, as at Flax Pond.

Net annual productivity of Nauset Marsh Ascophyllum and Fucus, estimated by the biomass increment method as described for belowground S. alterniflora, was 655 g m⁻² y⁻¹ and 185 g m⁻² y⁻¹, respectively. Brinkhuis (1977), however, in a comparison of productivity estimates based on biomass data versus photosynthesis measurements, concluded that the former method provides a severe underestimate due to the fairly high annual turnover of biomass. By using average biomass turnover factors of 1.8 times y⁻¹ for Ascophyllum and 2.3 times y⁻¹ for Fucus (Brinkhuis, 1977), more reasonable estimates of net annual productivity for these salt marsh fucoids in Nauset Marsh would be 1179 g m⁻² y⁻¹ and 426 g m⁻² y⁻¹. These estimates are comparable to those reported by Brinkhuis (1977) for the Flax Pond fucoid zone (Ascophyllum, 413 g m⁻² y⁻¹; Fucus, 375 g m⁻² y⁻¹).

The July harvest of intertidal and subtidal creekbank algae exhibited a diverse species composition (Table 2). Six filamentous intertidal creekbank species and 15 subtidal peat reef macroalgal species were collected from the Nauset Marsh study sites. Aside from the previously discussed creekbank fucoid zone, few investigators have documented the creekbank macroalgal species composition of New England salt marshes. Chock and Mathieson (1983) report a similar composition of intertidal filamentous species for the period of May-August in a New Hampshire system, but with a total maximum biomass of <2 g m⁻², substantially less than that reported here. The Nauset Marsh subtidal peat reef habitat was dominated by *Codium fragile*, and to a lesser extent by *Ulva* and the red alga, *Polysiphonia fibrillosa*. To our knowledge, only Webber and Wilce (1971, 1972) have described the seasonal species composition of attached subtidal, as well as intertidal, creekbank macroalgae in New England. Other detailed

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accounts of macroalgal species composition (Mathieson & Penniman, 1986) and relative abundance (Conover, 1958; Thorne-Miller *et al.*, 1983; Thorne-Miller & Harlin, 1984) in New England estuarine habitats have been made; however, these studies do not specifically pertain to the salt marsh creekbank habitat.

Maximum annual macroalgal biomass for other New England estuarine systems is reported to occur in summer (Chock & Mathieson, 1983; Thorne-Miller et al., 1983). Therefore, it is assumed that our July harvest from Nauset Marsh similarly represents maximum biomass for intertidal and subtidal creekbank macroalgae, and thus, provides estimates of net annual primary production (intertidal, 91 g m⁻² y⁻¹; subtidal 68 g m⁻² y⁻¹). These estimates clearly underestimate productivity, but a more accurate estimate cannot be made without seasonal biomass changes and a knowledge of biomass turnover rates for individual species.

Total system productivity

Angiosperm and macroalgae-dominated habitats in Nauset Marsh annually produce over 3 x 10⁶ kg of biomass (Table 3). Assuming an average carbon content of 40% (for *Spartina* see Roman & Daiber, 1984; *Zostera*, Harrison & Mann, 1975; fucoids, Brinkhuis, 1977), this represents an annual contribution of 1.2 x 10⁶ kg C toward the support of estuarine consumers. On an annual basis, *Spartina* marsh is the dominant producer of carbon in Nauset Marsh, yet the other habitats collectively contribute about 28% to total system carbon production. This carbon contribution by *Zostera* and macroalgae habitats becomes significant when considering several factors. First, decomposition rates of *Zostera* and macroalgae are greater than

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Spartina and the resultant detrital material is more labile due to fewer structural components (Thayer et al., 1977; Josselyn & Mathieson, 1980; Rice & Tenore, 1981; Wilson et al., 1986). Thus, the detrital material may provide a significant energy source for detrital-based food webs. Second, these habitats produce carbon year-round (Figure 2), which may be especially important during winter when *Spartina* production is absent (Brinkhuis, 1977). Finally, a significant 30% of the carbon produced by Nauset Marsh macrophyte-dominated habitats is derived from regularly flushed intertidal and subtidal environments (*i.e.*, tall *S. alterniflora*, *Zostera*, and macroalgae habitats) where it becomes immediately available to estuarine consumers or for transport to nearshore coastal habitats. Although *S. alterniflora* is often considered the major macrophyte primary producer in north temperate salt marshes, this study.demonstrates that other habitats also contribute significantly to total ecosystem energetics.

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Figure captions

- Figure 1. Habitat map of the Nauset Marsh estuarine complex, Cape Cod, Massachusetts.
- Figure 2. Seasonal biomass (g dry wt m^{-2} , \pm SE) of the major macrophyte-dominated habitats in Nauset Marsh. (a) Salt marsh habitat dominated by aboveground Spartina alterniflora, short and tall form, (b) Aboveground Zostera marina habitat at two sites, (c) Mudflat habitat dominated by Cladophora gracilis (t=trace amounts of biomass harvested), and (d) Creekbank macroalgal habitat dominated by zones of intertidal fucoids, intertidal filamentous algae, and subtidal algae (one harvest date in July 1987).
- Figure 3. Seasonal belowground biomass (g dry wt m^{-2} , \pm SE) of Spartina alterniflora, short and tall form.

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| SITE (Source) | NET PRODUCT Tall Form | TIVITY (g m ⁻² y ⁻¹) Short Form |
|---|---|---|
| ABOVEGROUND ESTIMATES | | |
| NAUSET MARSH, MA (This study) | 665(1) ^a 732(2) 511(3) | 472(1) 664(2) 445(3) |
| BAR HARBOR, ME (Linthurst and Reimold, 1978) | 431(1) 758(2) 431(3) | 246(1) 763(2) 246(3) |
| ROWLEY MARSH, MA (Ruber et al., 1981) | 1350(1) ^b | 460(1) |
| GREAT SIPPEWISSETT, MA (Valiela et al., 1975) | 510(4) | |
| RHODE ISLAND MARSHES (Nixon and Oviatt, 1973b) | 433-1380(5) | |
| TUCKERTON MARSH, NJ (Squiers and Good, 1974) | 1592(1) | 592(1) |
| BELOWGROUND ESTIMATES | | |
| NAUSET MARSH, MA (This study) | 3900 | 3300 |
| HOG BAY, ME (Gallagher and Plumley, 1979) | 210 | |
| GREAT SIPPEWISSETT, MA (Valiela et al., 1976) | 3500 | |
| MANAHAWKIN MARSH, NJ (Smith et al., 1979) | | 2200 |

Table 1. Comparison of above and belowground <u>Spartina alterniflora</u> net primary productivity for north temperate salt marshes.

^aMethod used to estimate net annual aboveground productivity.

(1) Peak Live

(2) Smalley, 1958

(3) Milner and Hughes, 1968

(4) Valiela et al. 1975

(5) End-of-Season Biomass

Belowground estimates were by an annual increment technique, except for Valiela et al., 1976.

^bRuber et al. (1981) presented data on an ash-free dry weight basis. Their data were converted to a dry weight basis by assuming an ash percentage of 11.5% after Roman and Daiber (1984).

Table 2. Biomass of intertidal and subtidal creekbank macroalgae from Nauset Marsh collected in July 1987. Dominant species are shown.

| SPECIES | BIOM | ASS (g m ⁻² \pm SE) |
|---|--------------------------|--|
| INTERTIDAL | | |
| Chlorophyta Ulotrichales <u>Enteromorpha flexuosa paradoxa</u> <u>E. intestinalis</u> Cladophorales <u>Cladophora gracilis</u> | <u>a</u> | _ ^a |
| Rhizoclonium riparium Siphonales Derbesia marina | | |
| Phaeophyta Ectocarpales <u>Pylaiella</u> <u>littoralis</u> | Intertidal Total = | 91.2 ± 29.3 ^b |
| SUBTIDAL | | |
| Chlorophyta Ulotrichales <u>E. f. paradoxa/ E. intestinal:</u> <u>E. f. paradoxa/ Cladophora ser</u> <u>E. linza</u> <u>Monostroma oxyspermum</u> <u>Ulva lactuca</u> Cladophorales <u>Cladophora sericea</u> Siphonales <u>Bryopsis plumosa</u> <u>Codium fragile</u> | is ^c ricea | 5.0 ± 1.8 0.6 ± 0.4 <0.1 <0.1 7.5 ± 3.0 0.3 ± 0.2 0.2 ± 0.1 33.8 ± 14.8 |
| Phaeophyta Ectocarpales <u>Ectocarpus</u> <u>siliculosus</u> Punctariales <u>Desmotrichum</u> <u>undulatum</u> | | 1.4 ± 1.0 <0.1 |
| Rhodophyta Ceramiales <u>Antithamnion floccosum</u> <u>Ceramium rubrum</u> <u>Polysiphonia fibrillosa</u> <u>P. nigra/ C. rubrum</u> | Subtidal Total = | $\begin{array}{r} 0.3 \pm 0.3 \\ 4.7 \pm 1.3 \\ 9.8 \pm 4.3 \\ 4.6 \pm 2.4 \\ 68.1 \pm 8.0 \end{array}$ |

^aAll intertidal species collected were identified, but not separated by species. Only a total (combined species) intertidal biomass is presented. ^bIntertidal n=10; Subtidal n=20. Slash denotes that the biomass presented is represented by two species.

| HABITAT | AREA $(r^2 \times 10^3)$ | PRODUCTION (g m ⁻² y ⁻¹) | HABITAT PRODUCTION kg y x 10 ³ | Z TOTAL SYSTEM PRODUCTION |
|------------------------------------|--------------------------|--|---|------------------------------|
| SPARTINA MARSH | | | | 72% |
| Tall Form | 20 | 732 | 15 | |
| Short Form | 3279 | 664 | 2177 | |
| ZOSTERA BEDS | 567 | 716 | 406 | 13% |
| CLADOPHORA MUDFLAT | | | | 137 |
| Dense Areas | 587 | 637 | 374 | |
| Sparse Areas | 587 | 59 | 34 | |
| CREEKBANK MACROALGAE Intertidal | | | | 2% |
| - Ascophyllum | 29 | 1179 | 34 | |
| - Fucus | 10 | 426 | 4 | |
| - Filamentous | 39 | 91 | 4 | |
| Subtidal | 24 | 68 | 2 | |

Table 3. Net annual primary productivity of the dominant angiosperm and macroalgae-dominated habitats in Nauset Marsh and the relative contribution of each habitat to total macrophyte production in the system.

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