SEASONAL DISTRIBUTION AND ABUNDANCE OF FISHES AND DECAPOD CRUSTACEANS IN A CAPE COD ESTUARY

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ABSTRACT – Sampling in several habitat types (sand/mud, eelgrass, sand, gravel, macroalgae/mud) during all seasons with a variety of gears in Nauset Marsh, Massachusetts during 1985–1987 found a fauna consisting of 35 fish and 10 decapod crustacean species. Although most of the abundant species were found in several habitat types, species richness and habitat use appeared to be highest for vegetated habitats (eelgrass, macroalgae). The fishes and decapods were numerically dominated by cold-water taxa; however, numerous fish species, represented by rare individuals of predominantly southern forms, enriched the fauna. Species composition of Nauset Marsh could be distinguished from estuaries south of Cape Cod and even from the south shore of the cape. Both fishes and decapods were most abundant during the summer, apparently due to the contributions from spring and summer spawning in the estuary and the adjacent Atlantic Ocean. The location of Nauset Marsh and other estuaries on Cape Cod provide a unique opportunity to evaluate the importance of this region as a faunal boundary to estuarine species.

INTRODUCTION

For several decades it has been accepted that nearly two thirds of the coastal fishery resources in the U.S. are estuarine dependent (McHugh 1966; but see Able and Fahay 1998 for discussion of this term). Although often repeated, this generalization has seldom been critically reevaluated even though the extent, nature and focus of our fisheries have changed since the time of that estimate. A revised estimate, based on U.S. commercial fishery landings, indicated that 77% by weight (71% by economic value) of commercially important fishes were dependent on estuaries for reproduction, nurseries, food production, or migration (Chambers 1992). In this same analysis, a much lower percentage (32%) was considered estuarine dependent in the northeastern U.S. Our understanding of the extent and patterns of utilization of estuarine nurseries in the northeast extends beyond general faunal surveys for

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only a limited number of estuaries (Able and Fahay 1998, Conover and Ross 1982, Haedrich and Haedrich 1974, Lazzari and Tupper 2002, Nixon 1982, Oviatt and Nixon 1973, Pearcy and Richards 1962, Teal 1986, Werme 1981). Other studies have begun to examine habitat use by estuarine fishes in more detail including zoogeographic (Ayvazian et al. 1992) and temporal (Able and Fahay 1998; Jeffries and Johnson 1974; Rountree and Able 1992, 1993) comparisons. Despite this progress, we need more extensive and intensive observations of the patterns (see Underwood et al. 2000) of faunal use of estuaries over a broad latitudinal range to more fully understand the role they play in our fisheries.

To this end, we report on the seasonal distribution patterns for fish and decapod crustaceans by habitat type for a Cape Cod estuary, Nauset Marsh, Massachusetts. These observations are designed to complement prior faunal studies in Nauset Marsh that have focused on Zostera marina L. (eelgrass) communities (Heck et al. 1989), habitat use by Urophycis tenuis (Mitchill) (juvenile white hake) (Fahay and Able 1989), Homarus americanus H. Milne Edwards (juvenile American lobster) (Able et al. 1988), the life history of Myoxocephalus aenaeus (Mitchill) (grubby) (Lazzari et al. 1989), and estimates of secondary production (Heck et al. 1995).

STUDY SITE AND HABITATS

Nauset Marsh is a shallow (ranges to 5 m depth, most < 2 m), 950-hectare barrier island estuary on the outer edge of Cape Cod with direct exchange through an inlet to the Atlantic Ocean (Fig. 1). Tidal range was about 1.5 m just inside the inlet and less in other parts of the system due to frictional attenuation (Aubrey and Speer 1985). During 1985–1987 salinity ranged from 24 to 34‰ and temperature from -2 to 27°C. Freshwater input is predominantly by groundwater seepage (Portnoy et al. 1998).

The major habitat types were mapped with true color vertical aerial photographs (scale 1:18,000; date October 22, 1982) (Roman et al. 1990). Short-form Spartina alterniflora Loiseleur (smooth cordgrass) marsh (35% of the area), tidal kettle ponds, and shallow (< 3 m) tidal channels (33%) make up most of the system. Other habitats include intertidal mudflats (12%) often dominated by patches of the green alga Cladophora sericea (Huds.) Kutz, intertidal sandflats (11%) and eelgrass beds (6%). Additional habitats of minor areal extent but with potential ecological importance include peat reefs (Able et al. 1988, Roman 1988) and drift algae. Primary production by eelgrass (Roman and Able 1988) and total macrophytes (Roman et al. 1990) has been studied extensively. A list of fish species encountered in this system were included in the tabulations of Middle Atlantic Bight estuaries by Able and Fahay (1998).
MATERIALS AND METHODS

Extensive sampling throughout the Nauset Marsh complex began in August 1985 and continued through June 1987. Qualitative ichthyoplankton sampling, to determine the reproductive seasonality of the species spawning and utilizing Nauset Marsh, occurred from December 1985 through June 1987. Preliminary sampling was conducted with an epibenthic sled, a 0.5-m hoop net, and 20-cm bongo nets, all with 0.505-mm mesh. The tows were variable in duration until standardized tows of 5
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min with the 20-cm bongo nets were conducted between September 1986 and June 1987. Six locations were sampled in September and October 1986 and March, April, May, and June 1987 (Fig. 1). Additional samples were collected near Nauset Inlet on flood and ebb tides and during the day and night at Nauset Harbor and Town Cove stations. These collections were made in all the above months except March. In addition, 17 nightlight samples were collected during each sampling period from June—September 1986 and seven samples from May—August 1987 from Mill Pond, Town Cove, Hemenway Landing, and Salt Pond (Fig. 1). For these samples, we illuminated the water surface after dark for 30 to 60 minutes with a battery-powered 50-watt light bulb and collected larval and juvenile fishes attracted by the light with a dip net.

Sampling in benthic habitats was conducted with trawls and seines and in a variety of habitats characteristic of the Nauset Marsh system during August, October, and December 1985 and April, June, July, September, and October 1986 (Fig. 1, Table 1) to characterize the fish and decapod fauna as completely as possible. At most habitats several types of gear were used to more fully characterize the fauna. In deeper habitats an otter trawl (4.9 m with 0.6-cm cod end mesh) was towed for two minutes. Based on sampling in August 1985 we determined that four two-minute replicate tows at each habitat type were appropriate to characterize the fauna, based on species accumulation curves (Heck et al. 1989). Replicate samples were kept separate, sorted live, and returned to the system, except for species of interest, which were preserved in 10% formalin. All decapod crustaceans and fishes were identified, counted, and measured. The information for deep eelgrass habitat (e.g., Heck et al. 1989) is also included here to provide complete data for all habitats. At intertidal and subtidal habitats three replicate seine (7.5 m with 0.6-cm mesh) collections were made by sweeping over the study site while one end of the seine remained stationary at the water’s edge. All decapod crustaceans and fishes were identified and enumerated, a representative subsample was measured and then all animals were returned to the system.

Table 1. Sampling effort and physical characteristics for the major habitats sampled in the Nauset Marsh system.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Sampling Gear</th>
<th>Number of Samples</th>
<th>Mean Water Depth (m)</th>
<th>Dominant Vegetation</th>
<th>Temperature Range (°C)</th>
<th>Salinity Range (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eelgrass trawl</td>
<td>41</td>
<td>2.0</td>
<td>Zostera marina</td>
<td>4.0–16.5</td>
<td>26–30</td>
<td></td>
</tr>
<tr>
<td>Seine</td>
<td>18</td>
<td>&lt;1.0</td>
<td>Zostera marina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand/mud trawl</td>
<td>25</td>
<td>2.0</td>
<td>none</td>
<td>4.5–19.0</td>
<td>26–31</td>
<td></td>
</tr>
<tr>
<td>Seine</td>
<td>18</td>
<td>&lt;1.0</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand trawl</td>
<td>25</td>
<td>3.0</td>
<td>none</td>
<td>5.0–18.0</td>
<td>26–34</td>
<td></td>
</tr>
<tr>
<td>Gravel seine</td>
<td>18</td>
<td>&lt;1.0</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macroalgal/mud</td>
<td>25</td>
<td>1.0</td>
<td>Cladophora sericea</td>
<td>4.0–19.0</td>
<td>27–31</td>
<td></td>
</tr>
<tr>
<td>Drift algae trawl</td>
<td>25</td>
<td>5.0</td>
<td>Gracilaria tikvahiae</td>
<td>2.0–20.0</td>
<td>24–30</td>
<td></td>
</tr>
<tr>
<td>Water column plankton net</td>
<td>87</td>
<td>&lt;1.0</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Nightlight</td>
<td>24</td>
<td>surface</td>
<td>none</td>
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<td></td>
</tr>
</tbody>
</table>

Table 1. Sampling effort and physical characteristics for the major habitats sampled in the Nauset Marsh system.
Several types of gear were used at irregular intervals to augment our regular sampling to obtain a more complete inventory of fishes and decapods. During October 1985 and September 1986 experimental gill nets were deployed overnight in Salt Pond. The dominant fishes were collected, enumerated, measured, and returned to the system. Conical fish traps were deployed occasionally to collect fish at peat reef habitats and from marsh pools. To facilitate comparisons among life history groups and mode of utilization in other northeastern U.S.A. estuaries, we have classified species as either residents (species that spend their entire life span in estuaries), transients (species that spend only a portion of their lives there, typically young-of-the-year), and strays (only occasionally found in estuaries). These designations were based on larger faunal works (Bigelow and Schroeder 1953, Scott and Scott 1988) and our own experience in this (Heck et al. 1989) and other estuarine systems (Able and Fahay 1998).

RESULTS AND DISCUSSION

Physical characteristics

All the locations and habitats sampled were similar in temperature and salinity during the sampling period (Table 1). Salinity was consistently high in this polyhaline system. Depth was more variable but almost always 3 m or less for all habitats with the exception of that for drift algae. Submerged vegetation consisted of dense beds of eelgrass or green algae which occurred on intertidal mudflat habitat. The red alga *Gracilaria tikvahiae* McLachlan, which was the dominant component of the drift algae habitat, was variable in abundance with extensive accumulations during summer months.

Fish larval supply

The ichthyoplankton collections occurred at a variety of locations (Fig. 1) and over all seasons during the years sampled. In these collections, 23 species and > 1,300 individuals were encountered (Table 2). Of these, 16 species were transient forms that either spawned in adjacent oceanic waters (e.g., *Clupea harengus* L. (Atlantic herring)) or, occasionally spawned in distant areas and were transported to Cape Cod [(e.g., *Anguilla rostrata* [Lesueur] (American eel)]. The most abundant residents represented by larvae were *Apeltes quadracus* (Mitchill) (fourspine stickleback), and *Myoxocephalus aenaeus*. All of the dominant forms subsequently collected as juveniles were represented. Those not collected, or only rarely so, were resident forms whose larvae occur in very shallow waters [(e.g., *Fundulus heteroclitus* [L.] (mummichog)]; *Fundulus majalis* (Walbaum) (striped killifish), or were rarely collected in any life history stage. The species with the most abundant larvae were *Ammodytes americanus* DeKay (American sand lance),
Table 2. Total abundance of fishes collected in Nauset Marsh by trawl (deep), seine (shallow), plankton net, and nightlighting. The latter two are combined as Total Fish Larvae. Life history stage represented by L = larvae, J = juvenile, A = adult.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total fish larvae</th>
<th>Eelgrass deep</th>
<th>Eelgrass shallow</th>
<th>Sand/mud deep</th>
<th>Sand/mud shallow</th>
<th>Sand</th>
<th>Gravel</th>
<th>Macro-algae/mud</th>
<th>Drift algae</th>
<th>Total juveniles and adults</th>
<th>Life history stage</th>
<th>Mode of utilization</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apeltes quadracus</em> (Mitchill)</td>
<td>34</td>
<td>1,038</td>
<td>150</td>
<td>1</td>
<td>53</td>
<td>34</td>
<td>4</td>
<td>90</td>
<td>1,404</td>
<td>All</td>
<td>Resident</td>
<td></td>
</tr>
<tr>
<td><em>Clupea harengus</em> Linnaeus</td>
<td>66</td>
<td>2</td>
<td>14</td>
<td>65</td>
<td>1,195</td>
<td>1,342</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>L, J</td>
<td>Transient</td>
</tr>
<tr>
<td><em>Anmodyes americanus</em> DeKay</td>
<td>542</td>
<td>2</td>
<td>356</td>
<td>121</td>
<td>10</td>
<td>4</td>
<td>1,035</td>
<td>L, J, A</td>
<td></td>
<td>All</td>
<td>Transient?</td>
<td></td>
</tr>
<tr>
<td><em>Fundulus heteroclitus</em> (Linnaeus)</td>
<td>3</td>
<td>214</td>
<td>66</td>
<td>439</td>
<td>125</td>
<td>7</td>
<td>854</td>
<td>All</td>
<td></td>
<td>All</td>
<td>Resident</td>
<td></td>
</tr>
<tr>
<td><em>Menidia menidia</em> (Linnaeus)</td>
<td>29</td>
<td>6</td>
<td>293</td>
<td>2</td>
<td>191</td>
<td>19</td>
<td>5</td>
<td>545</td>
<td>L, J, A</td>
<td>All</td>
<td>Transient</td>
<td></td>
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<tr>
<td><em>Pseudopleuronectes americanus</em> Walbaum</td>
<td>43</td>
<td>168</td>
<td>2</td>
<td>36</td>
<td>17</td>
<td>19</td>
<td>86</td>
<td>149</td>
<td>520</td>
<td>L, J, A</td>
<td>Resident</td>
<td></td>
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<tr>
<td><em>Gasterosteus aculeatus</em> Linnaeus</td>
<td>33</td>
<td>452</td>
<td>1</td>
<td>3</td>
<td>8</td>
<td>39</td>
<td>8</td>
<td>59</td>
<td>188</td>
<td>L, J, A</td>
<td>Transient</td>
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<tr>
<td><em>Fundulus majalis</em> (Walbaum)</td>
<td>475</td>
<td>12</td>
<td>2</td>
<td>39</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>All</td>
<td>Resident</td>
</tr>
<tr>
<td><em>Myoxocephalus aeneus</em> (Mitchill)</td>
<td>20</td>
<td>36</td>
<td></td>
<td></td>
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<td></td>
<td>3</td>
<td>59</td>
<td>All</td>
<td>All</td>
<td>Resident</td>
<td></td>
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<tr>
<td><em>Brevortia tyrannus</em> (Latrobe)</td>
<td>35</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>37</td>
<td>L, J, A</td>
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<td></td>
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<tr>
<td><em>Urophycis temnis</em> (Mitchill)</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13</td>
<td>37</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
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</tr>
<tr>
<td><em>Tautogolabus adspersus</em> (Walbaum)</td>
<td>1</td>
<td>12</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>23</td>
<td>L, J, A</td>
<td>All</td>
<td>Transient</td>
<td></td>
</tr>
<tr>
<td><em>Pollachiuss vires</em> (Linnaeus)</td>
<td>1</td>
<td>19</td>
<td>1</td>
<td></td>
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<td></td>
<td>9</td>
<td>20</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
<td></td>
</tr>
<tr>
<td><em>Gasterosteus wheatlandi</em> Putnam</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13</td>
<td>14</td>
<td>L, J, A</td>
<td>Resident?</td>
<td>All</td>
<td></td>
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<tr>
<td><em>Ulvaria subbifurcata</em></td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>J</td>
<td>Stray</td>
<td></td>
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<tr>
<td><em>Tautoga onitis</em> (Linnaeus)</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
<td>8</td>
<td>J</td>
<td>Transient</td>
<td></td>
<td></td>
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<tr>
<td><em>Scophthalmus aquosus</em> (Mitchill)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>6</td>
<td>JA</td>
<td>All</td>
<td>Transient</td>
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<tr>
<td><em>Alosa sp.</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>5</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
<td></td>
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<tr>
<td><em>Anchoa mitelli</em> (Valenciennes)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>3</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
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<td><em>Menidia beryllina</em> (Cope)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
<td>JA</td>
<td>All</td>
<td>Transient</td>
<td></td>
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<tr>
<td><em>Pholis gunnellus</em> (Linnaeus)</td>
<td>3</td>
<td></td>
<td></td>
<td>2</td>
<td>1</td>
<td></td>
<td>3</td>
<td>J</td>
<td>Stray</td>
<td>J</td>
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</tr>
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<td><em>Conger oceanicus</em> (Mitchill)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>2</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
<td></td>
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<tr>
<td><em>Peprilus triacanthus</em> (Peck)</td>
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<td></td>
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<td></td>
<td>2</td>
<td>2</td>
<td>J</td>
<td>Stray</td>
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<td></td>
</tr>
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<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>1</td>
<td>J</td>
<td>J</td>
<td>Transient</td>
<td></td>
</tr>
<tr>
<td><em>Alosa pseudoharengus</em> (Wilson)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>J</td>
<td>Transient</td>
<td></td>
<td></td>
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<tr>
<td><em>Anchoa hepsetus</em> (Linnaeus)</td>
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<td></td>
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<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>J</td>
<td>Stray</td>
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</table>
**Table 3.** Total abundance of decapod crustaceans collected in Nauset Marsh by trawl (deep), seine (shallow), plankton net, and nightlighting. Life history stage represented by L = larvae, J = juvenile, A = adult.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total fish larvae</th>
<th>Eelgrass deep</th>
<th>Eelgrass shallow</th>
<th>Sand/mud deep</th>
<th>Sand/mud shallow</th>
<th>Sand</th>
<th>Gravel</th>
<th>Macro-algae/mud</th>
<th>Drift algae</th>
<th>Total juveniles and adults</th>
<th>Life history stage</th>
<th>Mode of utilization</th>
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<tbody>
<tr>
<td><em>Crangon septemspinosa</em> Say</td>
<td>1</td>
<td></td>
<td>1,025</td>
<td>1</td>
<td>5,748</td>
<td>136</td>
<td>310</td>
<td>2</td>
<td>23,768</td>
<td>104</td>
<td>All</td>
<td>Resident</td>
</tr>
<tr>
<td><em>Carcinus maenas</em> (Linnaeus)</td>
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<td>65</td>
<td>26</td>
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<td>8</td>
<td>1,321</td>
<td>74</td>
<td>2,232</td>
<td>All</td>
<td>Resident</td>
<td>Stray</td>
</tr>
<tr>
<td><em>Cancer irroratus</em> Say</td>
<td>45</td>
<td>2</td>
<td>19</td>
<td>1</td>
<td>1</td>
<td>105</td>
<td>313</td>
<td>173</td>
<td>117</td>
<td>All</td>
<td>Resident</td>
<td>Stray</td>
</tr>
<tr>
<td><em>Palaemonetes vulgaris</em> Say</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>15</td>
<td>28</td>
<td>17</td>
<td>1</td>
<td>All</td>
<td>Resident</td>
<td>Stray</td>
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<td>5</td>
<td>8</td>
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<td>7</td>
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**Table 2.** Continued.

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<tr>
<th>Species</th>
<th>Total fish larvae</th>
<th>Eelgrass deep</th>
<th>Eelgrass shallow</th>
<th>Sand/mud deep</th>
<th>Sand/mud shallow</th>
<th>Sand</th>
<th>Gravel</th>
<th>Macro-algae/mud</th>
<th>Drift algae</th>
<th>Total juveniles and adults</th>
<th>Life history stage</th>
<th>Mode of utilization</th>
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<td>1</td>
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<td>136</td>
<td>310</td>
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<td>23,768</td>
<td>104</td>
<td>31,094</td>
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<tr>
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<td></td>
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</tr>
</tbody>
</table>

**Table 3.** Total abundance of decapod crustaceans collected in Nauset Marsh by trawl (deep), seine (shallow), plankton net, and nightlighting. Life history stage represented by L = larvae, J = juvenile, A = adult.

**Table 2.** Continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total fish larvae</th>
<th>Eelgrass deep</th>
<th>Eelgrass shallow</th>
<th>Sand/mud deep</th>
<th>Sand/mud shallow</th>
<th>Sand</th>
<th>Gravel</th>
<th>Macro-algae/mud</th>
<th>Drift algae</th>
<th>Total juveniles and adults</th>
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<td>23,768</td>
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<td>All</td>
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<td>Stray</td>
</tr>
<tr>
<td><em>Urophycis chuss</em> (Walbaum)</td>
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<tr>
<td><em>Selene vomer</em> (Linnaeus)</td>
<td>1</td>
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<td></td>
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<td></td>
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<td>Stray</td>
</tr>
<tr>
<td><em>Magellanae</em> Valenciennes</td>
<td>1</td>
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<td></td>
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</tr>
<tr>
<td><em>Eurypanopeus depressus</em> Smith</td>
<td>1</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td>Stray</td>
</tr>
</tbody>
</table>
presumably from local spawning, and *Anguilla rostrata*. The latter was the result of directed night lighting for this species.

**Habitat use**

During extensive sampling with a variety of gears in representative habitats we collected >5,800 individuals representing 35 species of fishes, and >33,000 individuals representing 10 species of decapod crustaceans, during the period from August 1985 through July 1986 when sampling was consistent across all habitats (Table 2, 3). Species richness of fishes varied with habitat (Table 2), and although this measure varied with sampling gear and effort, it provided an indication of habitat use for the composite fauna. Of those habitats sampled by trawl (eelgrass-deep, sand/mud-deep, sand, macroalgae/mud, drift algae), the drift algae (18 species) and eelgrass-deep (18 species) had the greatest species richness. Of those habitats sampled by seine (eelgrass-shallow, sand/mud-shallow, gravel) all were similar in richness (6—8 species). For decapod crustaceans, which were represented by a less-rich fauna relative to fishes, patterns were similar (Table 3), with species richness greatest in drift algae and deep eelgrass (8 species each).

The abundance of fishes and decapods among habitats varied, especially by season, but general habitat specific patterns, based on trawl collections in deeper waters, were evident (Figs. 2, 3). For fishes, the greatest abundance was encountered around June in the drift algae habitat. Abundance was high through the summer in eelgrass, and to a lesser extent in sand/mud, as previously reported (Heck et al. 1989). Abundance in sand and macroalgae/mud was uniformly low during all months. Decapods were generally more abundant in the summer. In sand/mud, abundance was highest in August and October while the macroalgal mudflat was highest in June. The abundance of decapods in eelgrass was highest during June. Sand habitat had the highest abundance in August while abundance in drift algae varied little over the sampling period.

Shallow water seine samples appeared even more strongly seasonal than deep water samples, with very few fish or decapods collected in any habitats during December, April, or June although it should be noted that not every habitat was sampled in every sampling event (Fig. 3). Abundance was highest in eelgrass in August and October but the eelgrass cover was much reduced after that because of seasonal decline which accounts for the lack of individuals in this habitat thereafter. Over sand/mud substrate fish were abundant in summer (July, August) and early fall (September, October) while decapods, which were largely limited to this habitat type, were most abundant in August and September.

Most species of fish and decapods could be found across a variety of habitats and those that showed fidelity to a single habitat were rare (Table 2, 3). Of the fishes, several pelagic species were found in many of the
habitats sampled. These included *Menidia menidia* (L.) (Atlantic silver-side) (6 habitats), *Ammodytes americanus* (5), *Clupea harengus* (4), and *Gasterosteus aculeatus* L. (threespine stickleback) (4). Three species [*A. quadracus*, *Pseudopleuronectes americanus* Walbaum (winter flounder), and *Syngnathus fuscus* Storer (northern pipefish)] were found in seven habitats and these were among the most abundant species. Thirteen species were only found in one habitat, primarily because very few individuals were collected. Of the decapods, two species *Crangon septemspinosa* Say (sevenspine bay shrimp) and *Carcinus maenas* (L.) (green crab), were found in all eight habitats while *Cancer irroratus* Say (Atlantic rock crab)

![Graph showing seasonal variation in fish and decapod crustacean abundance by habitat type based on trawl collections.](image)

Figure 2. Seasonal variation in fish and decapod crustacean abundance by habitat type based on trawl collections.
(six habitats), *Palaemonetes vulgaris* (Say) (marsh grass shrimp), and *Pagurus acadianus* Benedict (Acadian hermit crab) (five habitats each), were commonly encountered (Table 3).

However, some species clearly used certain habitats more than others. For fishes, several species were more abundant in eelgrass, including sticklebacks with 91% of the individuals of *Gasterosteus aculeatus* in deep eelgrass and 85% of the *Apeltes quadracus* in deep and shallow eelgrass collections. *Myoxocephalus aenaeus* (92%) and *Pollachius virens* (L.) (pollock) (95%) were also most abundant in eelgrass. Other

![Figure 3. Seasonal variation in fish and decapod crustacean abundance by habitat type based on seine collections. NS = no sample.](image-url)
species were found primarily in either eelgrass or drift algae, including *Urophycis tenuis* (65% in eelgrass, 35% in drift algae) and *Tautogolabrus adspersus* (Walbaum) (cunner) (52% in eelgrass, 39% in drift algae). Both of these species were also common around peat reefs, based on diver observations. The preponderance of *Clupea harengus* (89%) in the drift algae habitat (Table 2) most likely reflected the abundance of this pelagic species in the upper ends of the Nauset Marsh system (Town Cove and to some extent Nauset Bay) rather than a preference for vegetation. Other species were collected rather ubiquitously across a variety of habitat types, including *Fundulus heteroclitus*, *Pseudopleuronectes americanus*, and *Syngnathus fuscus*. Curiously, the latter is often assumed to prefer eelgrass or other vegetation (Bigelow and Schroeder 1953). None of the decapods displayed any obvious habitat fidelity (Table 3), however, *Crangon septemspinosa* (76%) and *Carcinus maenas* (59%) were collected most frequently on macroalgal mudflats, although there may have been reduced gear efficiency for these species in complex habitats such as eelgrass.

**Individual Species Accounts**

The following treatments are included for species for which this study provided some new insights into the life history or because they are poorly known from this portion of their range.

*Clupea harengus*. Young-of-the-year (YOY) individuals apparently use Nauset Marsh as juvenile habitat. A single length mode was apparent in any month. Small juveniles (20—45 mm TL) were collected as early as April but no individuals longer than 70—75 mm were encountered with any of our collecting techniques. These YOY presumably resulted from spawning along outer Cape Cod or on Georges Bank based on numerous collections of larvae in the fall and early winter (Morse et al. 1987).

*Pollachius virens*. This species represented less than 1% of the fishes collected but its abundance in Nauset Marsh was probably underestimated because of gear avoidance by this actively swimming pelagic species. Although the numbers are small (n = 30), during 1986 the progression in lengths of YOY from 20—30 mm TL in April to 200—260 mm by October clearly represented a single year class. This estimate of growth is in agreement with that presented by Haberman and Jensen (1962) but indicates a slightly larger size than observed by Steele (1963) and Clay et al. (1989). Nauset Marsh individuals may have originated from spawning in the nearby Gulf of Maine and Georges Bank (Able and Fahay 1998, Morse et al. 1987).

*Apeltes quadracus*. This stickleback was the most abundant species collected (Table 2) and a resident of Nauset Marsh based on the year-round abundance of both juveniles (< 30 mm) and adults (30—60 mm)
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(c.f. Hildebrand and Schroeder 1928). The smallest individuals (20—25 mm TL) available to our gear appeared in July and August, which is consistent with spring and early summer spawning in the Gulf of Maine (Bigelow and Schroeder 1953).

**Gasterosteus aculeatus.** This abundant stickleback made up 6.9% of all fish collected (Table 2). The majority of the adults apparently moved into Nauset Marsh from the continental shelf during spring to spawn as do other Atlantic coast populations (Scott and Scott 1988; Able and Fahay 1998). The young-of-the-year appeared in samples by July at approximately 15–30 mm TL. At this time, the adults were much fewer in number and both juveniles and adults were rare by August. We suspect that this decline in numbers is due to the mortality of adults after spawning and the migration of juveniles out of the marsh to the continental shelf as occurs in the Mid-Atlantic Bight (Able and Fahay 1998, Cowen et al. 1991) although a few individuals were present during every collecting period.

**Ammodytes americanus.** This abundant species was not always well represented in our collections, presumably due to gear avoidance. Observations of large pelagic schools by divers and from the surface were common and juveniles (approximately 100 mm TL) were occasionally taken in benthic suction samples (Heck et al. 1995) where densities ranged as high as 8 m⁻². Aspects of the life history of this species are not well known because of taxonomic confusion with the offshore form *Ammodytes dubius* Reinhardt, northern sand lance. The identity of our specimens was validated as part of a study by Nizinski et al. (1990). Spawning presumably occurs in late winter or early spring because recently hatched larvae (< 10 mm TL) were collected in April. Additional collections suggested that they reach approximately 40—120 mm by October of the first year, the same approximate size found in New Jersey waters (Able and Fahay 1998).

**Pseudopleuronectes americanus.** At least some life history stage of this species appeared to be resident in Nauset Marsh the entire year, in a manner similar to that for other populations in Massachusetts coastal waters (Howe and Coates 1975). Recently hatched larvae (< 10 mm TL) from a winter spawning were collected in April. This cohort was represented by 30—90 mm individuals in July and August and 30—100 mm in October, which is similar to the size range reported by Bigelow and Schroeder (1953). They apparently do not grow much over the winter based on a 50—100 mm cohort observed in April samples. These and other one-year-old fish appeared as well-defined modes in June (80—150 mm) and July (120—160 mm).

Several other fish species were well represented as juveniles and adults in our summer collections (Table 2). *Syngnathus fuscus* (20—250
mm TL) was abundant but apparently moved offshore during the colder months (Lazzari and Able 1990). *Tautogolabrus adspersus* was more abundant than our collections indicated because individuals were consistently observed by divers around peat reefs where they were unavailable to trawls and seines. Young-of-the-year (25—70 mm TL) were abundant in October presumably as a result of summer spawning, based on the timing of spawning in Connecticut (Dew 1976) and the summer occurrence of larvae in adjacent offshore areas (Morse et al. 1987). Adult *Brevoortia tyrannus* (Latrobe), adult menhaden, taken in September 1986 had maturing gonads, which would agree with the fall spawning period reported for more northern areas (Ahrenholz et al. 1987) based on the occurrence of larvae in New England waters at that time (Morse et al. 1987). Juveniles (80—100 mm TL) were collected in September and October with gill nets and were observed in large schools during the same period. *Menidia menidia* probably spawn in Nauset Marsh. Juveniles were collected in July and October and then presumably moved offshore with the adults for the winter as occurs for other Massachusetts populations (Conover and Murawski 1982). *Fundulus heteroclitus* is a resident of Nauset Marsh, with several age classes represented in the collections based on modal lengths (20—45, 60—85, 110—120 mm TL). Other species that are resident or use the area as juvenile habitat have been discussed elsewhere including *Myoxocephalus aenaeus* (Lazzari et al. 1989), *Homarus americanus* (Able et al. 1988), and *Urophycis tenuis* (Fahay and Able 1989).

The dominant decapod crustaceans appear to be resident. *Crangon septemspinosa* appeared to be a year-round resident with juveniles and adults of typical sizes (15—50 mm) (Haefner 1979) present in almost all collections. *Carcinus maenas* was also resident with the smallest individuals (5 mm CW) present in October and adults present in almost every collection.

**Faunal Composition of Nauset Marsh**

The fish and decapod fauna of Nauset Marsh owes its origins to a variety of sources. Of the fishes, five species (14%) are considered resident, and 18 (51%) are categorized as transient species. The remainder (strays) were all represented by fewer than 10 individuals. For the decapods, there were seven (70%) resident species and three (30%) stray species.

Transient and resident species numerically dominated the fish fauna, comprising approximately 65.6% and 33.6%, respectively, while residents made up 99.9% of the decapod fauna. The distinction between residents and transient species is not clear for all components of the fauna. For example, Teal (1986) considered *Menidia menidia* and *Gasterosteus aculeatus* in Great Sippewisset Marsh, MA, to “spend most of their lives within the marsh.” However, both species spawn in
the marsh and produce young-of-the-year that migrate offshore in the fall (Conover and Murawski 1982) or early in the summer (Cowen et al. 1991). For others, such as *Pseudopleuronectes americanus*, at least some portion of the population is resident year-round, but there is a migratory component as well, in this case the adults.

In general, however, it appears that all of the most abundant species of fishes and all of the decapod species collected in Nauset Marsh use it as habitat for young-of-the-year. Of these, 30% of the fish species are economically important in commercial or recreational fisheries. This estimate for commercial species is similar to the 32% (by weight) of estuarine-dependent species estimated for the northeastern United States (Chambers 1992). For decapod crustaceans, only *Homarus americanus* and *Cancer irroratus* are commercially important. These comprised 20% of the total species and 0.5% of the total number of individual decapods collected.

These results expand on some aspects of a previous faunal investigation in Nauset Marsh that focused on the eelgrass habitat (Heck et al. 1989). First, the significance of Nauset Marsh as a habitat for juveniles broadens considerably when other habitats, besides eelgrass, are considered. For example, Nauset Marsh can be considered juvenile habitat for *Homarus americanus*, *Clupea harengus*, *Brevoortia tyrannus*, *Ammodytes americanus*, *Anguilla rostrata*, *Tautogolabrus adspersus*, *Carcinus maenas*, and *Cancer irroratus* as a result of the inclusion of more habitats in our evaluation. Second, species richness for the estuary is enhanced by the addition of two decapods (Table 3) and 13 generally rare fishes from these additional habitats (Table 2).

The composition of the fish fauna generally reflects the location of Nauset Marsh on Cape Cod, which is at the junction of two zoogeographic provinces (Ayvazian et al. 1992, Grosslein and Azarovitz 1982, Parr 1933). A northern, or boreal fauna, was well represented in Nauset Marsh by numerous cold water forms (e.g., *Clupea harengus*, *Gadus morhua* L. (Atlantic cod), *Pollachius virens*, and *Pholis gunnellus* (L.) (rock gunnel), while southern components are represented by such forms as *Fundulus majalis*, *Menidia beryllina* (Cope) (inland silver-side), and numerous southern transients that occurred only rarely, *Anchoa mitchilli* (Valenciennes), bay anchovy, *Anchoa hepsetus* (L.), striped anchovy, *Peprilus triacanthus* (Peck), butterfish, *Mugil curema* Valenciennes, white mullet, *Paralichthys dentatus* (L.), summer flounder. The southern transients were collected during late summer when water temperatures peaked. The fish fauna of Nauset Marsh was similar to Waquoit Bay, Massachusetts, based on the recent study by Ayvazian et al. (1992). At Nauset Marsh, 79% of the species were shared with Waquoit Bay, compared with Wells Harbor, Maine (Ayvazian et al. 1992), where only 50% of the species were in common (see also Targett and McCleave 1974).
The broad zoogeographic influences of Cape Cod on faunal composition as frequently recognized (Ayvazian et al. 1992, Grosslein and Azarovitz 1982, Parr 1933) may be evident on a smaller, local scale in Cape Cod estuaries. Many species that did not occur, or occurred only rarely, in our sampling Pomatomus saltatrix (L.) (bluefish), Caranx hippos (L.) (crevalle jack), Centropristis striata (L.) (black sea bass), Prionotus carolinus (L.) (northern searobin), Lucania parva (Baird and Girard) (rainwater killifish), Stenotomus chrysops (L.) (scup), and Sphoeroides maculatus (Bloch and Schneider) (northern puffer), were more important components of the fauna of Cape Cod estuaries located to the south of Nauset Marsh (Curley et al. 1975a, Curley et al. 1975b, Hoff and Ibara 1977, Mulkana 1966). In addition, several southern fishes that have been collected from Pleasant Bay (Fiske et al. 1967; Fig. 1), immediately to the south, did not occur at Nauset Marsh, including Opsanus tau (L.) (oyster toadfish), Strongylura marina (Walbaum) (Atlantic needlefish), Cyprinodon variegatus Lacepède (sheepshead minnow) (although the latter was collected previously from Nauset Marsh; H. Linde, pers. comm.), and Trinectes maculatus (Bloch and Schneider) (hogchoker) (Fiske et al. 1967, Sargent 1981). Also, Callinectes sapidus Rathbun (blue crab), a southern decapod species that was observed at Nauset Marsh only as a result of an apparent “fish kill” in Salt Pond Bay, was known to occur commonly in Pleasant Bay and in some years was even abundant. These differences may be related to inlet location. Nauset Marsh opens directly to the Atlantic Ocean, and is probably influenced largely by the prevailing southerly flow of cold water from the Gulf of Maine (Bigelow and Schroeder 1953). The inlet to Pleasant Bay, however, opened on the southern side of the Cape Cod “elbow” at the times of prior surveys (Fiske et al. 1967, Sargent 1981), where an easterly flow of warmer water from Nantucket Sound (Limeburner and Beardsley 1982) may have provided for the dispersal of more southerly components of the fauna along the coast to the north and east. A test of the relationship between estuarine faunal composition and temperature effects on Cape Cod may now be possible due to a storm (1988) that shifted the major Pleasant Bay inlet eastward to a position facing the Atlantic Ocean. Among other effects, colder ocean water may now dominate at Pleasant Bay and, if our observations are correct, we predict that the fauna will have fewer southern forms and will appear more like that of Nauset Marsh in future surveys.

In summary, a variety of habitat types contribute as juvenile habitat for resident and transient fishes and decapods in Nauset Marsh, but vegetated habitats (eelgrass and macroalgae) had the highest values for species richness. The location of Nauset Marsh and other estuaries on the outer portion of Cape Cod provide a unique opportunity to evaluate the impacts of this region as a faunal boundary for estuarine species.
ACKNOWLEDGMENTS

Barbara Baker and Terry Westhead assisted in data gathering and analysis. Capt. H. Morgan of the R/V Ursula assisted in many aspects of this study. Henry Linde shared his notes on the fauna of the estuary. Richard McBride provided comments on an earlier draft. The National Park Service, through the Cooperative Research Unit, the Institute of Marine and Coastal Studies (IMCS) at Rutgers University, and the National Marine Fisheries Service, Sandy Hook Laboratory provided support for this study. This is Rutgers University IMCS Contribution Number 2002-17.

LITERATURE CITED


