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Nocturnal Fish Use of New Jersey Marsh Creek and Adjacent Bay Shoal Habitats

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Night-time sampling with gill nets in the Little Egg Harbor estuary revealed a component of the estuarine fish fauna, hitherto poorly documented, which is comprised of relatively large size classes of juvenile and adult life history stages. The fishes *Mustelus canis, Pomatomus saltatrix, Paralichthys dentatus, Brevoortia tyrannus, Prionotus evolans* and *Alosa mediocris* were the most abundant fishes captured. These observations suggest that Mid-Atlantic Bight estuaries are important nurseries for juvenile stages beyond the first year, as well as for the young of the year (YOY). Although many other studies emphasise the importance of estuaries as nurseries for YOY stages, the importance of estuaries to later juvenile life stages has been largely overlooked. This component of estuarine fish fauna has been poorly represented in previous North American studies because of probable gear avoidance, and because most studies are conducted primarily during the day. The authors hypothesise that these later juvenile stages are likely to be important estuarine faunal components in other geographic regions, as well as in the Mid-Atlantic Bight. A descriptive comparison of catches between ebb and flood tide stages, and between bay shoal and tidal marsh creek habitats, suggests that later juvenile and adult stages of several species make tidal migrations into shallow estuarine habitats, such as shoals and marsh creeks, during the night hours.

Keywords: faunal survey; estuarine habitat; juvenile nursery; saltmarsh creek; tidal migrations; gill net; nocturnal; fish; Mid-Atlantic Bight

Introduction

The Little Egg Harbor estuary in southern New Jersey, U.S.A., has been the subject of a number of fish faunal studies utilising various gears, including wire mesh traps (Smith & Able, 1994), throw traps (Sogard & Able, 1991), suction sampling (Able *et al.*, 1989), weirs and seines (Rountree & Able, 1992*a*, 1993), otter trawls (Szedlmayer & Able, 1996), and a combination of these (Able *et al.*, 1996). Gill net collections in the estuary were commenced to obtain food habits and length-frequency data on *Paralichthys dentatus* and *Mustelus canis* to supplement data obtained with other gears during autecological studies of those species (Rountree & Able, 1992*b*, 1997). However, gill net sampling was found to provide unique data on the seasonal occurrence and habitat use patterns of several other species that are often under-represented in North American estuarine sampling programs. The goals of this paper, therefore, are: (1) to present new data on the temporal occurrence in the estuary of adult and late juvenile stages of fishes not normally collected; and (2) to describe patterns of habitat use by these fishes based on a descriptive comparison of catches between habitats and tide stages.

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Materials and methods

Study area

The study was conducted in marsh creek and adjacent shallow bay shoal habitats in a polyhaline (salinity 22–33) section of the Little Egg Harbor estuary located in southern New Jersey (Figure 1). Foxboro Creek is a shallow subtidal marsh creek (maximum depth 0·5 m at low tide and 1·1 m at high tide), with a shallow sill (<30 cm deep at low tide) at its mouth (Figure 2). Story Island Creek is largely intertidal except for a shallow (0–0·3 m) subtidal cove formed at its mouth at low tide. Both creeks have a mud substrate and empty onto extensive shoal areas (<2·0 m at high tide) bordering the relatively deep Marshelder Channel (approximately 4–9 m at high tide; Figures 1 and 2). The creeks are blind cul-de-sacs, approximately 1 km long, that receive freshwater only through local runoff.

Six gill nets (23 m long × 1·8 m high; 38 mm square mesh) were set in the mouths of the two marsh creeks, and in the shallow bay shoals (<2 m) immediately adjacent to Foxboro Creek (Figure 2). Gill Net 1

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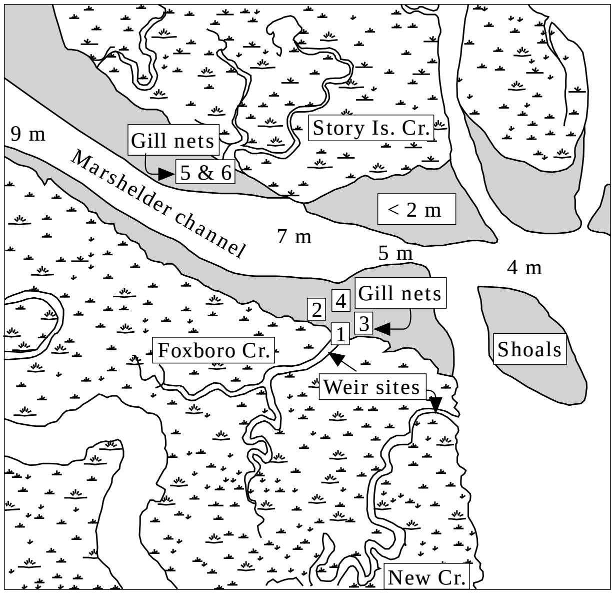

FIGURE 1. Sampling locations within a portion of the Little Egg Harbor estuary of southern New Jersey at 39°32′N, 74°18′W. Gill nets were placed in the mouths of Foxboro Creek (Net 1) and Story Island Creek (Nets 5 and 6), and in the shallow bay within 30 m of Foxboro Creek (Nets 2–4). Stippled areas indicate shoals of <2 m water depth at high tide.

(Figure 1) was located on the sill at the mouth of Foxboro Creek (Figure 2). It was stretched across the creek so as to completely block fish passage. Nets 2–4 were set in shallow bay shoal areas located 10–30 m from the mouth of Foxboro Creek (Figures 1 and 2).

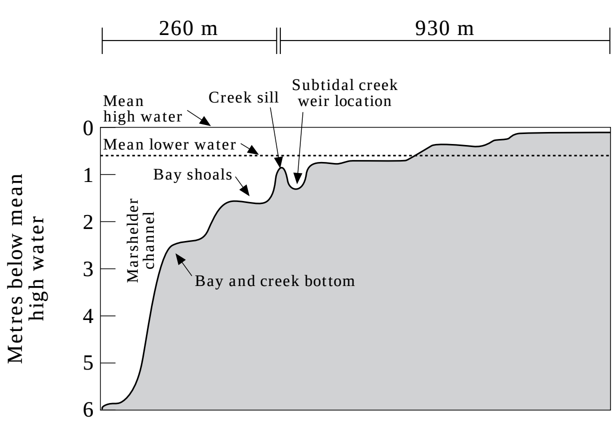

FIGURE 2. Depth profile along a transect from Marshelder Channel to the upper reaches of Foxboro Creek, redrawn from a fathometer tracing at high tide. Horizontal axis is not to scale. The mean-low-water level is estimated by subtracting the measured tidal range from the high tide water level. The location of weir sampling during a previous study (Rountree & Able, 1992*a*) is indicated for reference (see text).

Nets 5 and 6 were stretched across the mouth of Story Island Creek from either side, but together did not completely block fish passage (Figure 1).

The gill nets were set at night between 16.00 and 22.00h at either high or low tide, and were checked two to six times until 09.00–11.00h the next day. This sampling regime allowed sampling over one full ebb or flood tide, and part of the following flood or ebb tide. Catch per unit effort (CPUE) was defined as number of fish captured per net per hour (no. net^{-1} h^{-1}). A total of 550 net h^{-1} of sampling was conducted over 11 nights at approximately 2-week intervals during May and July-November 1990. Effort was approximately equally divided between ebb and flood tides (298 and 252 net h^{-1}, respectively). All captured fishes were identified and immediately measured to the nearest millimeter standard (SL) or total length (TL).

Descriptive statistics were used to compare CPUE between habitats and tide stages to determine if CPUE trends suggest differences in habitat use and tidal activity. Statistical hypothesis testing of time of day, tidal, seasonal, and habitat effects were not attempted for several reasons: (1) tide, time of day, seasonal and habitat effects are utterly confounded (i.e. it is impossible to sample during both ebb and flood tides at the same location and time); (2) there are tidal interactions with gear efficiency; and (3) sample sizes are too small to provide much statistical power to any test performed. Despite this inability to analyse the data in a completely rigorous fashion, the authors feel that the trends observed in this study provide an interesting insight into potential habitat use patterns by fishes, and are worth reporting on their own merits.

Results and discussion

A total of 933 individuals of 15 species were collected in 65 net sets during the spring–fall sampling period (Table 1). Eight species occurred in more than 10% of the net sets, and are considered common. The smooth dogfish, *Mustelus canis*, was the most abundant species collected, followed by the bluefish, *Pomatomus saltatrix*, summer flounder, *Paralichthys dentatus*, Atlantic menhaden, *Brevoortia tyrannus*, striped searobin, *Prionotus evolans*, and hickory shad, *Alosa mediocris*. Small numbers of spot, *Leiostomus xanthurus*, and weakfish, *Cynoscion regalis* were also collected frequently. Seven other species, *Menticirrhus saxatilis* ($n=7$), *Scophthalmus aquosus* ($n=5$), *Opsanus tau* ($n=2$), *Trinectes maculatus* ($n=2$), *Raja eglanteria* ($n=1$), *Carcharhinus plumbeus* ($n=1$), and *Pleuronectes americanus* ($n=1$) were collected in less than 10% of the net sets. An

TABLE 1. Summary statistics for fishes occurring in at least 10% of gill net samples collected from tidal marsh creeks (Nets 1, 5, 6) and adjacent bay habitats (Nets 2–4) located within the Little Egg Harbor estuary of southern New Jersey during May–November 1990 (see Figure 1)

Species	Total collected	Mean (SE) CPUE (no net $^{-1}$ h $^{-1}$)	Percent frequency of occurrence (% of net sets)	Length (mm)	
				Mean (SE)	Range
Mustelus canis	458	0·87 (0·12)	82	526 (3·6)	389–1025
Pomatomus saltatrix	140	0·24 (0·03)	63	298 (4·4)	111–521
Paralichthys dentatus	85	0·13 (0·03)	42	192 (3·3)	138–390
Brevoortia tyrannus	84	0·14 (0·04)	34	198 (6·4)	82–299
Prionotus evolans	84	0·14 (0·04)	26	183 (1·6)	145–225
Alosa mediocris	34	0·08 (0·04)	26	299 (4·1)	241–350
Leiostomus xanthurus	16	0·02 (0·01)	18	157 (6·6)	98–188
Cynoscion regalis	13	0·02 (0·01)	17	330 (26·6)	133–456
Total fish	933	1·69 (0·19)	95	N/A	N/A

CPUE, catch per unit effort.
All lengths were measured in standard length (SL), except for *Mustelus canis* which was measured in total length (TL).

average of 1·7 fish net h $^{-1}$ were collected (Table 1). The CPUE for total fish had a minor peak in mid July, and a major peak in late August (Figure 2). Thereafter, catches declined to near zero by November. Highest catches of total fishes occurred in the bay habitat and on flood tides (Table 2). Temporal, tidal and habitat patterns for total fish are strongly reflective of CPUE for the most abundant species; *Mustelus canis* (Figure 3). The relatively high number of fish captured (Table 2), despite the relatively small nets used (23 m long nets), strongly suggests that these fishes are, in fact, abundant in the bay shoal and marsh creek habitats during the night hours, and that these areas may be important habitats within the estuary for them.

Most of the fishes collected during this study were relatively large (>150 mm; Table 1), due to the size selectivity of the gill nets. Most species were represented by adults or large juveniles [not young of the year (YOY)], based on length (Table 1). However, *M. canis, P. dentatus*, and *Leiostomus xanthurus* were predominantly YOY. The single sandbar shark, *Carcharhinus plumbeus*, collected was a 619 mm TL pup with a fresh umbilical scar. The authors feel that individuals of most species over 200 mm SL were highly susceptible to the sampling gear, except for *P. evolans*, which was highly susceptible at smaller sizes because its head spines easily entangle in the nets. Thus, temporal patterns in length frequency data and CPUE are representative of the adult and

TABLE 2. Interaction among tide stage (ebb and flood) and habitat (tidal creek and adjacent bay) on catches of the six most frequently collected fishes (see Table 1) by gill net within the Little Egg Harbor estuary of southern New Jersey during May–November 1990 (see Figure 1 for sample locations)

Species	Tidal creek CPUE		Adjacent bay CPUE	
	Ebb tide	Flood tide	Ebb tide	Flood tide
Mustelus canis	0·29 (0·10)	0·77 (0·20)	0·65 (0·20)	1·51 (0·29)
Pomatomus saltatrix	0·19 (0·04)	0·16 (0·05)	0·24 (0·05)	0·38 (0·07)
Paralichthys dentatus	0·35 (0·08)	0·14 (0·05)	0·08 (0·03)	0·03 (0·02)
Brevoortia tyrannus	0·13 (0·09)	0·03 (0·02)	0·10 (0·04)	0·34 (0·09)
Prionotus evolans	0·03 (0·02)	0·24 (0·07)	0·04 (0·02)	0·20 (0·06)
Alosa mediocris	0·07 (0·04)	0·06 (0·03)	0·09 (0·04)	0·06 (0·03)
Total fishes	1·14 (0·19)	1·46 (0·26)	1·29 (0·20)	2·61 (0·40)
Sampling effort (net h $^{-1}$)	142	135	157	117

Catches are expressed as mean catch per unit effort (CPUE), where CPUE=no. net $^{-1}$ h $^{-1}$.
The standard error of each mean is given in parentheses.

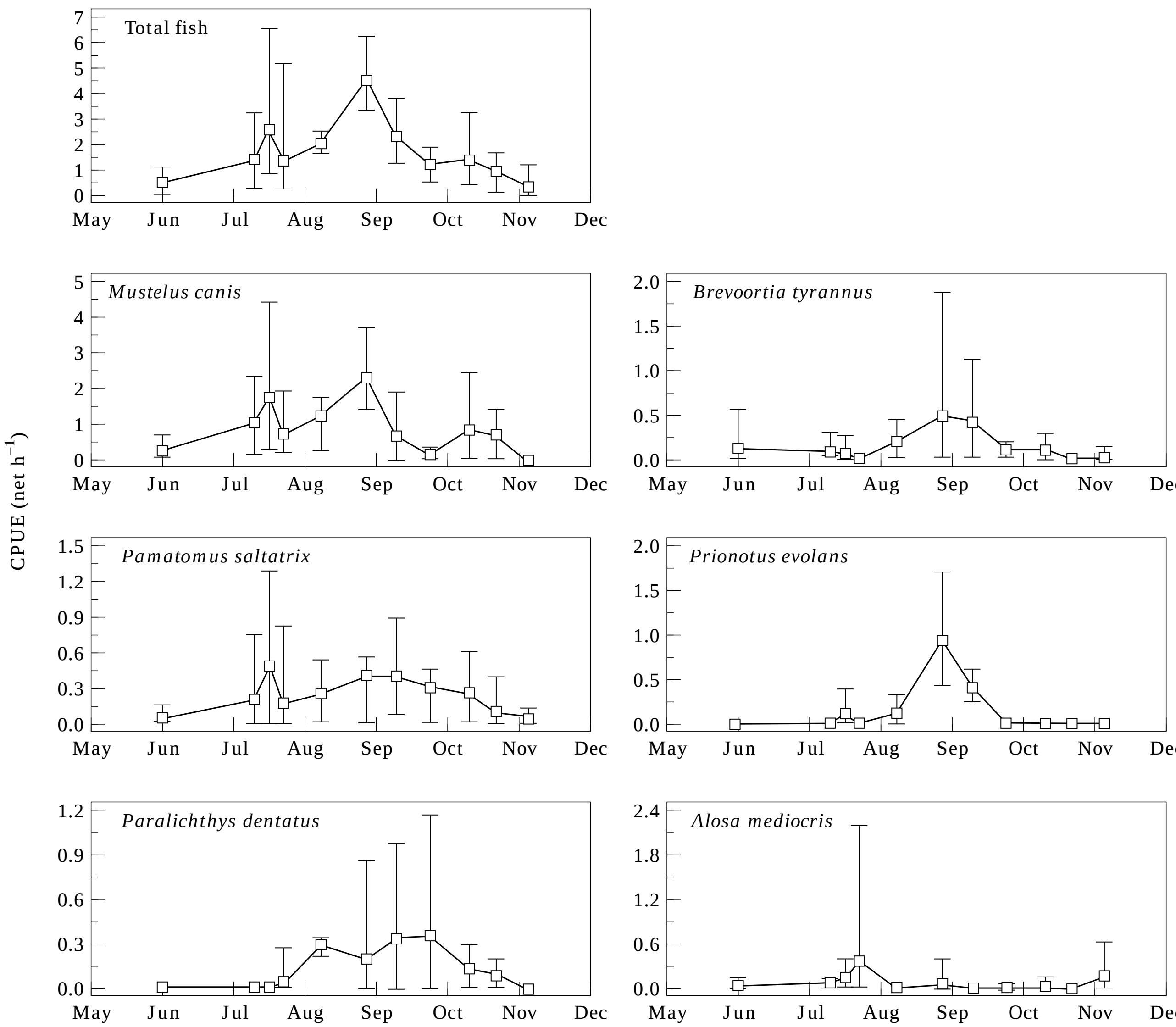

FIGURE 3. Temporal variation in catch per unit effort (CPUE) net^{-1} h^{-1} for total fish and each of the six most abundant fishes collected by gill net during 1990. Data are pooled from both marsh creek and adjacent shallow bay habitats samples in the Little Egg Harbor estuary of southern New Jersey (see Figure 1 for sample locations). Vertical bars are ranges.

large juveniles of most species collected. However, YOY of most species, except *M. canis* due to its large size, were only represented by the largest individuals.

Catches of *M. canis*, large (>200 mm SL) *P. saltatrix*, and *A. mediocris*, usually consisted of several individuals at a time in any given net check, while catches of large (>200 mm SL) *B. tyrannus* usually consisted of solitary individuals. This pattern suggests that these species tend to move into the shallow shoal and marsh creek habitats in loose, widely spaced aggregations, or even occasionally as solitary individuals, rather than in large densely packed shoals. Such behavior is not unexpected, since many otherwise strongly shoaling fishes are known to disperse at night (e.g. Helfman, 1993). Observations by the first author, in which solitary individuals of *M. canis* and *P. saltatrix* were observed at night in the shallow bay shoals on several occasions, further support this hypothesis. Alternatively, the catches may simply reflect poor gear efficiency for these species.

Catches were two to three times greater in the bay shoal habitats (Nets 2–4) than at the creek mouths (Nets 1, 5 and 6) for *M. canis*, *P. saltatrix*, and *B. tyrannus*, but were four times greater at the creek mouth for *P. dentatus* (Table 2). The relatively high catches in the bay shoal habitats, despite presumed higher gear efficiency in the creek mouth habitat, suggests that the bay shoals may be more important for some species. This is supported by a comparison with catches in previous studies in local marsh creeks using weirs placed a short distance up-creek of the creek mouths (as illustrated for Foxboro Creek in Figure 2; Rountree & Able, 1992*a*., 1993). The large juvenile and adult stages of *P. saltatrix, B. tyrannus, A. mediocris* and *P. evolans*, which were common in the bay shoal gill net sampling, were rare or absent in the weir samples, despite extensive collections during 1988–89 (Rountree & Able 1992*a*, 1993). However, these larger fishes were also common, though less abundant, in gill net sets at the mouths of marsh creeks. The lack of the larger fishes in the authors' earlier weir samples, despite their abundance in the marsh creek gill net samples, could result from several factors: (1) larger fishes avoid the weir; (2) annual variation (i.e. they did not occur in marsh creeks during 1988–89); or (3) larger fishes do not penetrate beyond the creek mouth. Since *M. canis, P. dentatus*, and *Cynoscion regalis* were common in weir sampling (Rountree & Able, 1992*a,b*, 1993), the authors do not believe that gear avoidance is a factor. The authors also feel that it is unlikely that annual variation in habitat use explains the observed patterns. It is suspected that the shallow sill formed at the creek mouth (Figure 2) forms a partial barrier to some of the larger fishes. In contrast, other species, such as *M. canis* and *P. dentatus*, move up the creeks well beyond the sill, and were abundant in both gill net and weir sampling. In fact, higher gill net CPUE at the creek mouths for *P. dentatus* result from their tidal foraging migrations into marsh creeks (Rountree & Able, 1992*b*; Szedlmayer & Able, 1993).

Species accounts

Mustelus canis was present in low numbers during the first sampling night in late May, peaked in late August, and had disappeared from the catches by November (Figure 3). Highest catches occurred in the bay during flood tides (Table 2). *Paralichthys dentatus* was present from late July through October, with a peak CPUE in late September. Most individuals were captured in the creek habitat, and on ebb tides (Table 2). Previously, the authors have examined patterns of habitat use by *M. canis* (Rountree & Able, 1996) and *P. dentatus* (Rountree & Able, 1992*b*), based in part on data presented herein; these patterns will not be discussed further here. Patterns of habitat use by the remaining species, however, are poorly known and are discussed below.

Pomatomus saltatrix

Pomatomus saltatrix occurred throughout the spring–fall sampling period, with peaks in July and late August–September (Figure 3). Catches were greater in the bay shoal habitat than in the marsh creeks (Table 2). Catches pooled over both habitats were not affected by tide stage, but catches in the bay were greater during flood tides (Table 2). Catches were dominated by age-1 and older juveniles (Table 1, Figure 4) based on length (Nyman & Conover, 1988; McBride *et al*., 1993). Large juveniles (<200 mm SL) were collected throughout the study period, while YOY (>200 mm SL) first appeared in low numbers during the late summer when they reached sizes large enough to be susceptible to the gill nets. The YOY were collected primarily in the marsh creek habitat (Figure 4).

Information on the use of estuarine habitats by older juveniles is largely anecdotal (Tracy, 1910; Schwartz, 1964; Tatham *et al*., 1984; except McBride *et al*., 1993), although several recent studies address aspects of estuarine habitat use by YOY (Friedland *et al*., 1988; Nyman & Conover, 1988; Juanes *et al*., 1993; Marks & Conover, 1993; McBride *et al*., 1993), including studies in this estuarine system (McBride & Conover, 1991; Rountree & Able, 1992*a*, 1993). The larger juveniles (approximately 25–35 cm TL) have been reported from July to September in Maryland bays (Schwartz, 1964), and June–November in Rhode Island waters (Tracy, 1910), in close agreement with the present findings. Similarly, data presented by McBride *et al*. (1993) suggest that they are present in North Carolina estuaries from May to November (although rare after September). The present data, together with anecdotal information from the literature, suggests that estuaries are important habitats for 1–2-year-old juveniles, as well as for YOY.

Lower catches in marsh creek habitat suggest that >200 mm juveniles use bay shoal habitats more extensively than marsh creeks. This interpretation is supported by the authors' earlier sampling with weirs and seines, in which YOY *P. saltatrix* were found to be among the most abundant fishes in marsh creek habitats, while larger juveniles (>200 mm SL) were absent (Rountree & Able, 1992*a*, 1993). It appears, therefore, that YOY and juvenile bluefish exhibit different habitat use strategies. The YOY migrate into both the shallow bay and marsh creek habitats at night, while the larger juveniles (>200 mm SL) enter the shallows only as far as the creek sill. Although the authors' earlier weir and seine sampling in the marsh creeks suggests that YOY also migrate into the creeks

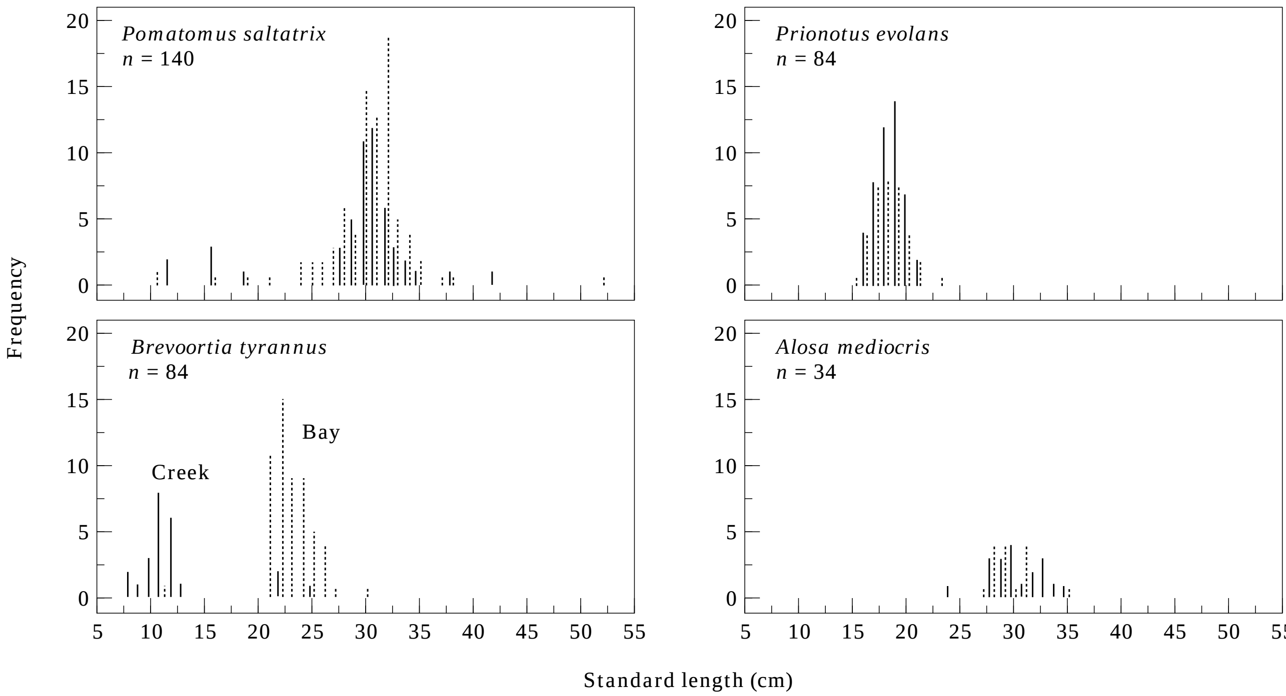

FIGURE 4. Comparison of length-frequency distributions of selected species between marsh creek (solid bars) and adjacent shallow bay habitats (stippled bars). Samples were collected with gill nets during May–November 1990 within the Little Egg Harbor estuary of southern New Jersey (see Figure 1 for locations).

during the day (in fact, they are more abundant during the day, Rountree & Able, 1993), whether the larger juveniles also use the bay shoals during the day is not known.

Brevoortia tyrannus

This species occurred through the spring and fall sampling period, with a peak in late August–September (Figure 3). A similar seasonal pattern was reported for Massachusetts Bay (Bigelow & Schroeder, 1953). Catches were generally greater in the bay habitat than in the marsh creeks (Table 2). Catches pooled over both habitats were not affected by tide stage, but an interaction between habitat and tide stage was suggested (Table 2). Although creek catches were relatively low, they were greatest during ebb tides, in contrast to bay catches which were greatest during flood tides (Table 2). This observed interaction between habitat and tide stage on CPUE may reflect different behavior patterns that affect catchability. Nets placed in the creek mouths were probably more efficient during ebb tide because fishes were attempting to leave the creeks, resulting in a higher ebb tide CPUE in marsh creeks. In contrast, nets placed in the bay did not block fish passage, and may more directly reflect tidal patterns in abundance or activity. The higher CPUE during flood tides in the bay habitat, therefore, suggests increased activity or tidal movements during flood.

Brevoortia tyrannus exhibited a pattern of segregation in habitat use by life stage similar to that exhibited by *P. saltatrix*. Catches were dominated by a 200–300 mm SL size class which was collected primarily in the bay and throughout the sampling period (Figure 4). According to published age-length keys, these larger individuals were age-2+ juveniles (McHugh *et al.*, 1959; Nicholson, 1972). Low numbers of YOY (<160 mm SL) were collected primarily in the creek habitat (Table 2, Figure 4), and these first appeared in August. The low incidence of juveniles in marsh creek habitats was also suggested by earlier studies in the area. Young of the year (33–155 mm SL) were collected exclusively in extensive sampling in intertidal (Rountree, Smith & Able, unpubl. data) and subtidal marsh creek habitats (Rountree & Able, 1992*a*). Additionally, marsh creek habitat was the only habitat in which YOY were abundant during a trawl survey of the Little Egg Harbor estuary (Szedlmayer & Able, 1996). As with *P. saltatrix, B. tyrannus* appears to use marsh creek habitat more extensively as YOY, and bay shoal habitats as older juveniles. Strong size stratification among estuarine habitats has also been reported for *B. tyrannus* in other estuaries (June & Chamberlin, 1959; McHugh *et al.*, 1959; Lewis *et al.*, 1971; Nicholson, 1972). Similarly, the closely related gulf menhaden (*Brevoortia patronus*) has been reported to undergo a sequential, size related, migration between marsh and open bay habitats (Deegan, 1990).

There is some evidence that juveniles continue to use estuaries as summer residences until maturity, after which they are restricted to marine waters (June & Chamberlin, 1959; McHugh *et al.*, 1959; Hildebrand, 1963). However, the relative importance of estuarine and coastal shelf habitats to these age classes are not known (June & Chamberlin, 1959).

Prionotus evolans

Prionotus evolans was collected during July–September, with a peak in late August. Similar seasonal abundance patterns have been observed in other estuaries (Jeffries & Johnson, 1974; Haedrich, 1983). The sudden appearance and rapid decline of this species suggests a rapid period of migration through the study area, perhaps at the end of the spawning season, which occurs from June to August (Richards *et al.*, 1979; McBride & Able, 1994). Recently, McBride and Able (1994) reported that adults occur in this estuary in low numbers during the summer and fall, and in much greater numbers in coastal marine waters during the fall, with a peak in October–November. This suggests that the present high August–September catches may have resulted from an aggregation of *P. evolans* in the lower estuary prior to offshore migration. Schwartz (1964) also reported abundant adult *P. evolans* (175–215 mm TL) in the Isle of Wight and Assawoman Bays of Maryland during August and September, which he suggested resulted from an inshore-offshore migration.

No difference in CPUE between habitats was noted, however, most fish were captured on flood tides (Table 2). This suggests tidal movement onto the shoals and into the mouths of marsh creeks. There was a single well defined size cohort (145–225 mm SL) in both habitats (Table 1, Figure 4). According to published length- at-age information (Richards *et al.*, 1979), the 15–23 cm individuals observed during this study were primarily age-1 to age-2. Previously, the present authors collected small numbers of early juveniles and adults (16–245 mm SL) in subtidal and intertidal marsh creeks using weirs (Rountree & Able, 1992*a*; Rountree, Smith & Able, unpubl. data).

Alosa mediocris

Alosa mediocris was the sixth most abundant species collected. It was present in low numbers in 26% of the net sets collected throughout the sampling period (Table 1, Figure 4), but was most abundant in July. Catches were also relatively high on the last sampling date in early November. No habitat or tidal differences in CPUE were observed. There was a single well-defined 241–350 mm SL size cohort, representing adults (Mansueti, 1962), in both habitats (Table 1, Figure 4).

Despite extensive sampling efforts in Little Egg Harbor, the present study is the first to suggest *A. mediocris* may be an important component of the estuarine fauna. In fact, *A. mediocris* was rare in extensive seine, weir and otter trawl collections over several years in the study area (Rountree & Able, 1992*a*, 1993; Szedlmayer & Able, 1996; Rountree, Smith, & Able, unpubl. data). In addition, Milstein (1981) reported on the occurrence of *Alosa* spp. juveniles just outside the inlet to Little Egg Harbor, but failed to collect this species.

To the authors' knowledge this study is the first report of seasonal abundance patterns and length-frequency data for this species other than anecdotal accounts (Smith, 1907; Tracy, 1910; Bigelow & Schroeder, 1953; Mansueti, 1962; Hildebrand, 1963; Schwartz, 1964). The species was described as occurring in Rhode Island (Tracy, 1910) and Massachusetts (Bigelow & Schroeder, 1953) waters from spring through fall. In contrast, adults have been reported to overwinter in North Carolina (Smith, 1907; Hildebrand, 1963) and South Carolina (Smith, 1907). More extensive gill net sampling, particularly during winter months, are necessary to clarify this species' seasonal estuarine use patterns.

Conclusions

The unique and useful insight gained with night-time gill net collections in the Little Egg Harbor estuary is that, even in this intensively studied estuary, an important component of the fish fauna has been previously underestimated and under appreciated due to daytime sampling bias and gear avoidance. This component consists of adult stages of some species, and juvenile stages beyond the first year of life for other species, which use shallow estuarine habitats. As a result of this study, understanding of the importance of estuaries to the entire life cycle of fishes has been enhanced. The authors strongly suspect that the importance of estuaries to later juvenile and adult life-history stages has also been overlooked in other regions, and hypothesise that future research will reveal that these stages constitute an important component of estuarine fauna around the world.

A second insight gained during this study is that a number of relatively large fishes appear to utilise shallow bay shoal and marsh creek habitats during the night hours. This observation weakens hypotheses that these habitats serve as predator refuges to YOY fishes (e.g. Boesch & Turner, 1984; Weinstein, 1984). The notion that shallow estuarine habitats serve as a predator refuge stems partly from the lack of collections of relatively large fishes in previous studies, which, as discussed above, is felt to be partly due to sampling biases. However, the relative magnitude of predation pressures between shallow estuarine and other habitats is unknown, and further research on the importance of shallow estuarine habitats as predator refuge for YOY fishes is needed.

An additional insight gained is that of an increased appreciation for the dynamic nature of habitat use by fishes in the estuary, where tidal, diel and ontogenetic movements among habitats are common.

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