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SPATIAL PATTERNS OF ESTUARINE HABITAT TYPE USE AND TEMPORAL PATTERNS IN ABUNDANCE OF JUVENILE PERMIT, *TRACHINOTUS FALCATUS*, IN CHARLOTTE HARBOR, FLORIDA

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ABSTRACT The life history of many marine fishes is a 2-phase cycle: juveniles and adults make up a demersal phase, whereas larvae are planktonic. Determining ontogenetic patterns of habitat type use of the demersal phase has important management and habitat conservation implications for species that use coastal habitat types as juveniles. Juvenile permit, *Trachinotus falcatus*, are presumed to be limited to beaches exposed to open ocean, but few studies have addressed juvenile permit use of estuarine habitat types. Ten years of fisheries-independent monitoring data from a subtropical estuary were analyzed to determine habitat type use patterns and seasonality of juvenile permit. Shallow (< 2 m) habitat types in Charlotte Harbor, Florida, were sampled with 21 m and 183 m seines from 1991 through 2000. Juvenile permit were most abundant along sandy beaches in the lower estuary and were in densities similar to or higher than along exposed coastal beaches reported in other studies. Size of captured permit ranged from 15 to 360 mm standard length. Small juveniles (< 100 mm) were present almost exclusively from June to December. Both small and large (∅ 100 mm) juveniles were most abundant over shallow bottom adjacent to unvegetated beach shorelines. These findings indicate that post-settlement permit recruit seasonally to specific estuarine habitat types. Then, as they grow, they shift to other habitat types, before migrating out of the estuary. Since identification of the suite of juvenile habitat types is prerequisite to determining their nursery value, and many estuarine habitat types are under anthropogenic stress, research on the relative importance of estuarine nurseries for juvenile permit is warranted.

INTRODUCTION

The life history of many marine fishes is a 2-phase cycle: juveniles and adults make up a demersal phase, whereas larvae are planktonic. During and after settlement of larvae, numerous processes act to influence the abundance and distribution of juvenile fishes. These processes include site selection at settlement (Kaufman et al. 1992, Sancho et al. 1997), priority effects (Shulman et al. 1983, Leis and Carson-Ewart 1999), competition (Frederick 1997), predation (Hixon and Beets 1989, 1993, Hixon and Carr 1997), food availability (Stoner 1980, Lenanton 1982), shelter (Hixon and Beets 1989, Tupper and Boutilier 1995, Beets 1997), and physiological requirements (Yamashita et al. 2001). For species that move into different habitat types as adults, the requirements (e.g., food and shelter) and risks (e.g., predation) will change as the fish proceeds through ontogenetic shifts (Vigliola and Harmelin-Vivien 2001). Given that the period of highest mortality for many fishes is during the early life stages (Booth and Brosnan 1995, Sogard 1997), and juveniles of many species use coastal and estuarine habitat types that are vulnerable to anthropogenic impacts (Montague and Ley 1993, Sargent et al. 1995, Tomasko et al. 1996, Rakocinski et al. 1997, Sklar and Browder 1998, Uhrin and Holmquist 2003), it is important to understand the patterns of habitat type use by juvenile fishes to better predict and assess impacts of anthropogenic stress.

Before these habitat-related processes can be examined, however, baseline information must be gathered on spatial and temporal distributions of the target species. In addition, identification of the suite of habitat types used by juveniles is essential to determining which habitat types act as nurseries and contribute to adult populations (Beck et al. 2001). This paper reports patterns of habitat type use by an economically important species and helps lay the foundation for further detailed research.

Permit, Trachinotus falcatus (family Carangidae), inhabit coastal areas of the North Atlantic as far north as Massachusetts and throughout the Gulf of Mexico (GOM) but are commonly found from southern Florida and the Caribbean Sea (Bohlke and Chaplin 1993). Permit are economically important and are an important component of the recreational fishery in Florida (Armstrong et al. 1996) and the Caribbean Sea. Unfortunately, comparative data on habitat type use by juvenile permit are limited, especially for estuarine habitats. Recent information on age and growth (Crabtree et al. 2002) and abundance (C.W. Harnden, Fish and Wildlife Conservation Commission, Melbourne, FL, pers. comm.) were largely based on data collected from the Florida Keys. Most previous research in Florida addressed only surf zones (Springer and Woodburn

1960, Naughton and Saloman 1978, Saloman and Naughton 1979, Peters and Nelson 1987) or did not address patterns of habitat type use (Carr and Adams 1973). Prior to our study, Finucane (1969) provided the only quantitative documentation of habitat type use patterns of permit associated with estuaries.

In this paper we summarize the available data on juvenile permit for Charlotte Harbor, a subtropical estuary of south Florida. Based on 10 years of data collected by the Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute's Fisheries-Independent Monitoring (FIM) program, we examined catch data of permit in Charlotte Harbor to determine 1) spatial distribution within the estuary, 2) patterns of habitat type use, 3) size distributions, and 4) seasonality of occurrence. Our study will contribute to the management of permit and provide a foundation for future research.

MATERIALS AND METHODS

Study system

Charlotte Harbor is a 700 km^2 coastal plain estuarine system located on the southwest coast of Florida and is one of the largest estuarine systems in the state (Hammett 1990, Figure 1). The Peace, Myakka, and Caloosahatchee rivers, as well as many small creeks throughout the drainage, transport large amounts of fresh water into the harbor. The harbor is connected to the GOM through Boca Grande Pass, San Carlos Bay, and 3 smaller inlets. The climate of Charlotte Harbor is subtropical, mean water temperatures range from 12º to 36 ºC, and freezes are infrequent (Poulakis et al. 2003). Anthropogenic development within the watershed has stressed the estuarine system; however, compared with other Florida estuaries (e.g., Tampa Bay), Charlotte Harbor has remained relatively unspoiled (> 80% of mainland shorelines under protection; R. Repenning, Punta Gorda, FL, Florida Department of Environmental Protection, pers. comm.; Hammett 1990; CHNEP 1999). Seagrass flats (262 km^2, Sargent et al. 1995) and mangrove shorelines (143 km^2, L. Kish, Florida Marine Research Institute, unpubl. data) continue to thrive as the dominant habitat types within the estuary.

Field Methods

Monthly daytime (between 9 AM and 5 PM) sampling was conducted in Charlotte Harbor using 2 different sampling strategies, Fixed-Station (FS) sampling (1991–1995) and Stratified-Random (SR) sampling (1996–2000). At each FS location 3 hauls were completed with a 21 m x 1.8 m center bag seine (3.2 mm stretch mesh, hereafter referred to as the 'small seine'). To collect each sample, the small seine was pulled parallel to the shoreline over a standardized area (330 m^2) and hauled up against the shore. Two FS locations, FS 3 and FS 13, accounted for all juvenile permit collected using this protocol. Fixed-Station 3 has a narrow sandy beach shoreline, with a sand/mud bottom and sparse Halodule wrightii (depth ~ 1.0 m) and is located in the upper harbor near the mouth of the Myakka River. Fixed-Station 13 has a broad, sandy, low-energy beach shoreline, with a sandy bottom and a few small dense patches of Halodule wrightii, Thalassia testudimum, and Syringodium filiforme (depth ~ 1.0 m). This station is located on the northeastern shore of Cayo Costa (barrier island immediately south of Boca Grande Pass) (Figure 1).

Stratified-Random sampling locations were selected based on a randomized design. Charlotte Harbor was subdivided into 1 x 1 nautical mile cartographic grids, and grids with appropriate water depths (< 1.5 m for the small seine, < 2.6 m for the large seine) for seine sampling were selected as the sampling universe. The sampling universe was then subdivided into 4 geographic zones. Monthly sampling grids were randomly selected from within each zone, and within each selected grid a microgrid (one tenth by one tenth of a nautical mile) was also randomly selected. All SR samples were collected inside the estuary using the small seine and a 183 m x 2.5 m center bag seine (37.5 mm stretch mesh, hereafter referred to as the 'large seine'). Twenty-four to 32 small seines and 17 large seines were completed each month, with effort distributed equally among zones. Half of the small seine samples were completed immediately adjacent to the shoreline (shoreline set), and half were completed > 5 m from shore (offshore set). The small seine was pulled over a standardized area (140 m^2) and then collapsed around a pivot pole to force the sample into the bag. The large seine was deployed by boat, set in a standardized rectangular shape (~ 40 m x 103 m) along the shoreline, and hauled up against the shoreline by hand. For all samples, T. falcatus were measured to standard length (SL) and released, and seagrass coverage (%), shoreline percent coverage by mangroves, water temperature (ºC), salinity (psu), and dissolved oxygen (DO, mg/L) concentration were recorded. Seagrass and mangrove coverage were visually estimated by samplers.

Data Analyses

Spatial patterns. We first examined whether juvenile permit abundance was similar throughout Charlotte Harbor. Following Poulakis et al. (2003), 5 zones that encompassed all of the shoreline and shallow water sampled in this study were defined based on hydrological characteristics (Alberts et al. 1969, 1970, Stoker 1992,

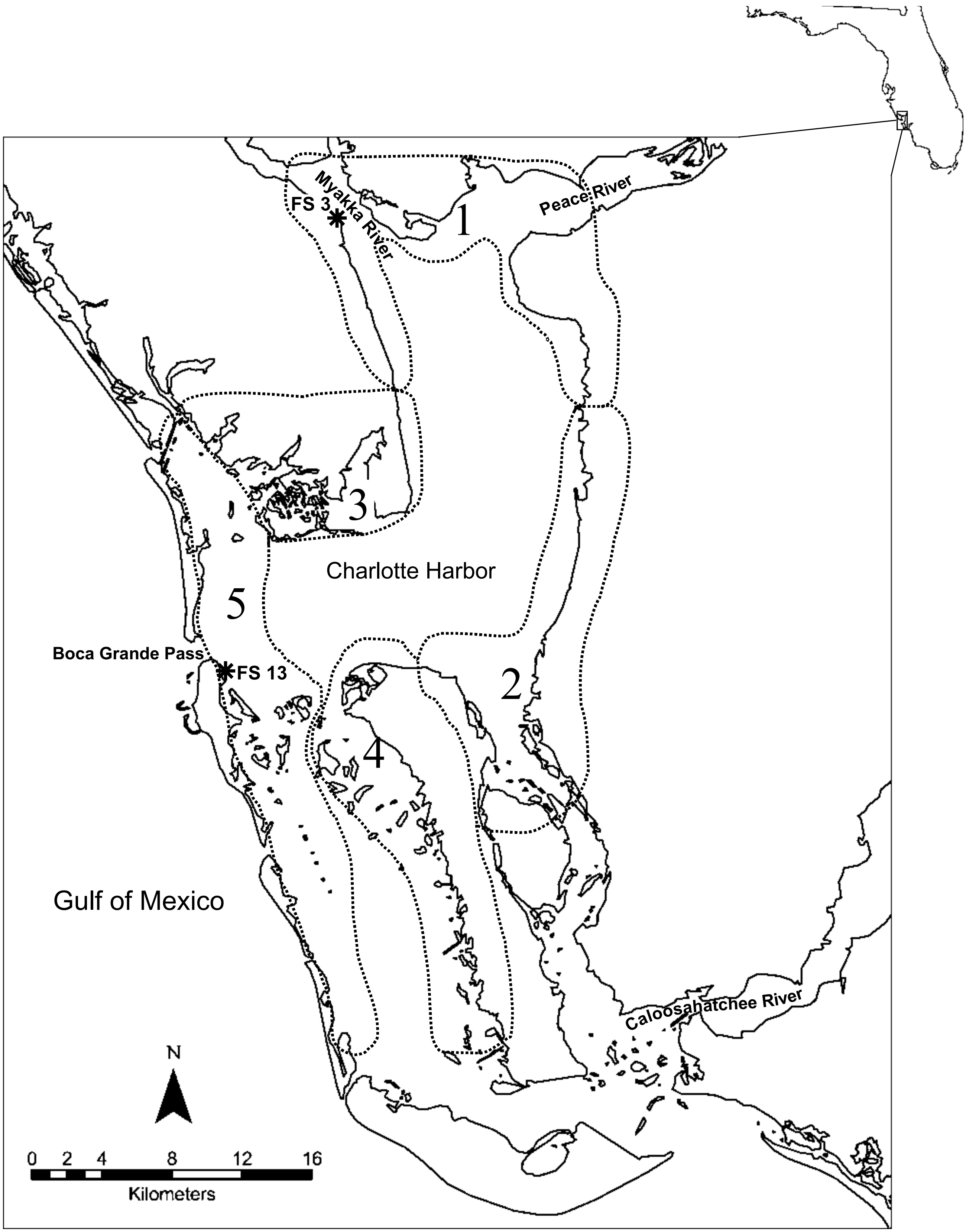

Figure 1. Locations of hydrological zones 1–5 (following Poulakis et al. 2003) and Fixed-Stations (FS) in Charlotte Harbor, Florida.

TABLE 1

Number of permit caught and number of samples by gear type. Fixed-Stations (FS) were sampled from 1991–1995 and Stratified-Random (SR) from 1996–2000. The 21 m seine was deployed immediately adjacent to the shoreline (Shoreline) or > 5 m from shore (Offshore). The 183 m seine was set only along the shoreline.

	21 m seine				183 m seine
	Shoreline (SR)	Offshore (SR)	Shoreline (FS 3)	Shoreline (FS 13)	Shoreline (SR)
Permit (n)	76	1	24	980	162
Samples (n)	787	785	189	165	948

Goodwin 1996) (Figure 1). Stratified-Random data were pooled within each zone, the number of fish per sample (large seine) or the number of fish/100 m^2 (small seine) were calculated, and results were examined graphically. Because only one permit was collected in offshore sets with the small seine (SR), only shoreline sets were used in the analysis. Fixed-Station data were not included in this analysis because only 2 of the 5 zones contained a fixed station that was sampled with a shoreline set. Data were pooled across years and months, because we sought to determine the overall distribution pattern of juvenile permit within the estuary, rather than temporal patterns of variation. We were able to eliminate all but zones 4 and 5 from further consideration with this analysis.

Habitat types were classified according to shoreline and benthic vegetation cover. A shoreline was considered "mangrove" if intertidal vegetation (red mangrove, *Rhizophora mangle*, or black mangrove, *Avicennia germinans*) covered ∅ 40% of the adjacent shoreline, otherwise, the shoreline was considered "beach." Benthic habitat types were classified as "high seagrass" if percent cover of seagrass (*Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*) was ∅ 40% and as "low seagrass" if < 40% cover. We chose a 40% cutoff based on regional classifications of seagrass coverage and recent Charlotte Harbor research (Adams et al. 2004, B. Robbins, Mote Marine Lab, unpublished summary of seagrass community classification systems in Florida).

To determine patterns of habitat type use by juvenile permit (H_o: abundance of juvenile permit is similar in all habitat types) within zones 4 and 5, SR seine data were analyzed with a Friedman non-parametric test (Zar 1984) with Shoreline (mangrove, beach) and Benthic (high seagrass, low seagrass) as factors. A non-parametric test was used because the data would not meet parametric statistics requirements, despite transformations, because of the high proportion of samples with no juvenile permit. If significant, habitat types were analyzed with a non-parametric post-hoc test similar to the Tukey procedure (Zar 1984).

Data from the small and large seines were analyzed separately. All permit from the small seine were < 100 mm SL. Permit captured in the large seine were divided into 2 size groups (< 100 mm SL = small and ∅ 100 mm SL = large). Within each gear type, data were pooled across years and months. The months of June through December were used for small juveniles (peak recruitment), and all months were used for large juveniles (year round occurrence). A significant result would indicate that numbers of juvenile permit differed among habitat types.

Temporal patterns. Monthly mean abundances of juvenile permit from FS 13 and from SR zones 4 and 5 were plotted to show seasonality of juvenile permit occurrence. Only these data were used because almost all juvenile permit were captured in these areas.

RESULTS

Totals of 1,081 and 162 juvenile permit were captured with the small and large seines, respectively (Table 1). The number of juvenile permit captured by FS sampling totaled 1004 (980 juveniles at FS 13), while 239 juvenile permit were captured in SR sampling. In the SR small seine samples, all but one permit were captured in shoreline sets (vs. offshore sets) (Table 1). Most juvenile permit were captured in zones 4 and 5 (Figure 2). Mean water temperature and DO varied little among the zones, in contrast to variable salinity (Table 2). Salinity differed among zones (ANOVA: $F_{4,1428} = 310.75$, $P < 0.001$), with salty zones 5 > 4 > 3 > 2 > 1 (Bonferroni, all $P < 0.05$).

Habitat type use patterns varied by gear and fish size, but indicate an overall higher use of habitats with lower complexity and habitat types adjacent to beach shoreline. Mean density of small (< 100 mm) juvenile permit caught in small seines was highest in low seagrass adjacent to beach shorelines (Friedman $\chi^2 = 11.74$, $P < 0.01$, df = 3) (Figure 3a). In contrast, abundance of small permit caught with the large seine was higher over high seagrass adjacent to beach shoreline (Friedman c2 = 11.86, *P* < 0.01, df = 3) (Figure 3b). Abundance of large (∅ 100 mm) juveniles

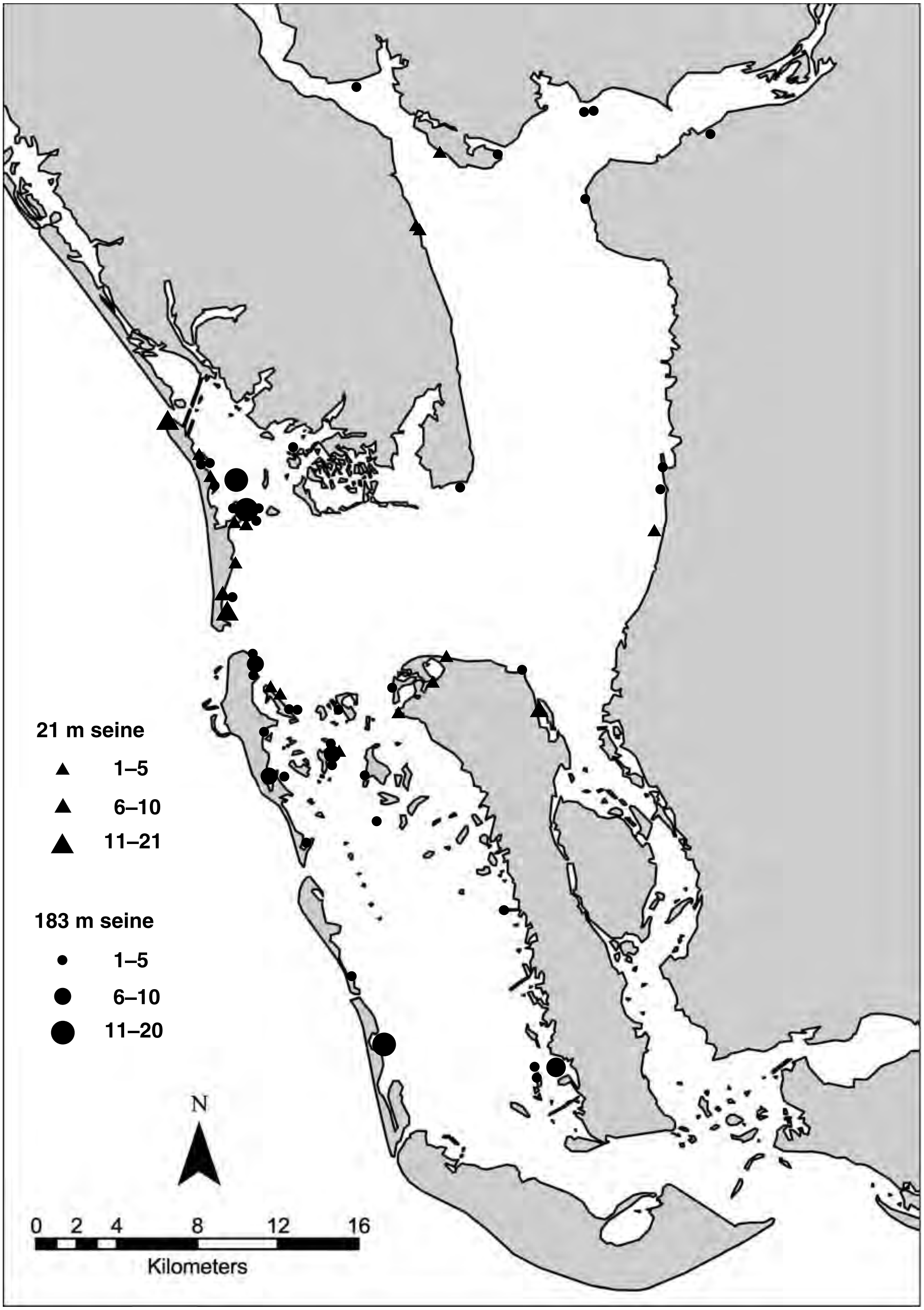

Figure 2. Locations and abundance of permit captured in Charlotte Harbor, Florida using 21 m (triangles) and 183 m (circles) seines.

TABLE 2

Summary statistics for abiotic variables from each zone during June–December, 1996–2000. $s_{\bar{x}}$ = standard error.

Zone	Temperature (ºC) Mean	$s_{\bar{x}}$	Range	Salinity (psu) Mean	$s_{\bar{x}}$	Range	Dissolved oxygen (ppm) Mean	$s_{\bar{x}}$	Range
1	27.0	0.25	14.8–34.5	18.6	0.39	0.6–33.2	6.5	0.13	0.9–16.2
2	27.7	0.23	14.3–34.4	23.6	0.29	5.2–37.4	6.5	0.12	0.2–12.0
3	27.4	0.29	14.5–36.2	26.5	0.40	6.4–37.9	7.0	0.16	1.0–17.0
4	27.3	0.30	15.8–34.1	31.1	0.24	13.2–39.0	7.0	0.16	0.5–14.1
5	26.7	0.29	15.8–35.0	32.4	0.20	11.7–37.7	7.9	0.13	1.5–16.7

was greater over low seagrass adjacent to beach shorelines, but this difference was not significant (Friedman χ^2 = 3.12, $P > 0.10$, df = 3) (Figure 3c).

Size of permit ranged from 15 to 360 mm SL, with each gear type biased toward different portions of the size range (Figure 4). The SR small and large seines captured juvenile permit from 15–72 mm and 42–360 mm, respectively.

Catches of juvenile permit at FS 13 were consistently higher than catches for estuary-wide SR samples, but temporal trends were similar: densities were greatest from June through December (Figure 5). Monthly length frequencies of small juvenile permit indicate 2 temporally distinct settlement events (May–June and September–October, Figure 6).

DISCUSSION

In contrast to most previously published studies of juvenile permit that report the use of only exposed beaches on outer coasts, our study demonstrates the use of estuarine habitat types in similar densities. Densities of small, juvenile permit in estuarine habitats in lower Charlotte Harbor (June–December) were similar to densities reported from the GOM along the beaches of central Florida (2.93 fish/100 m2, Saloman and Naughton 1979). They were also much higher than densities reported from the northern Florida GOM coast (0.13 fish/100 m2, Naughton and Saloman 1978), compared to overall mean densities of 1.42 fish/100 m2 from SR samples and 2.94 fish/100 m2 from FS samples in this study. Clearly, future studies that address the relative importance of nursery habitats for permit (Beck et al. 2001) should include both estuarine and coastal habitat types.

Within the Charlotte Harbor estuary, juvenile permit are present seasonally and appear to undergo habitat shifts as they grow before vacating shallow estuarine waters. However, the origin of new juveniles and the destination of emigrating juveniles are unknown. Our results suggest that both habitat processes and larval transport patterns play important roles in the distribution of juvenile permit within Charlotte Harbor. The occurrence of juvenile permit in estuarine headwaters indicates that larvae are able to reach well into Charlotte Harbor; however, the majority of juveniles were captured in the lower portions of the estuary. Finucane (1969) also found juvenile permit in an upper estuarine region in Tampa Bay, but only at a single beach location. In contrast, on the GOM coast of northern Florida, juvenile permit were only found at an outer beach location and not in the St. Andrew Bay estuary (Naughton and Saloman, 1978). In our study, juvenile permit were captured in similar habitat types in upper and lower Charlotte Harbor—low seagrass adjacent to sandy beaches. Possible explanations for our results are that fewer larvae reached the upper estuary which limited juvenile abundance, sufficient larvae did reach the upper harbor but quickly reached maximum densities in the few isolated areas with appropriate habitat types, sufficient larvae reached these areas but suffered high mortality, or differences in abiotic factors affected settlement site selection or post-settlement mortality.

The high association of small juvenile permit with low structural-complexity habitat types (low seagrass adjacent to beach shoreline) is counter to conventional wisdom. Small juvenile fishes use structurally complex habitat types as refuges from predation (e.g., Savino and Stein 1989, Sogard and Olla 1993, Jordan et al. 1996, Adams et al. 2004). Once fish reach a size where growth benefits afforded by access to more food outweigh predation risk, juveniles may move into less complex habitat types (e.g., Dahlgren and Eggleston 2000). In our study, small juvenile permit were most abundant in the least complex habitat types sampled and expanded their habitat type use to include more complex habitats as they grew. Whether this is due to low predation, availability of specific required food types, or foraging efficiency is unclear.

Juvenile permit undergo ontogenetic shifts in diet (Carr and Adams 1973). The diet of juveniles 15–20 mm

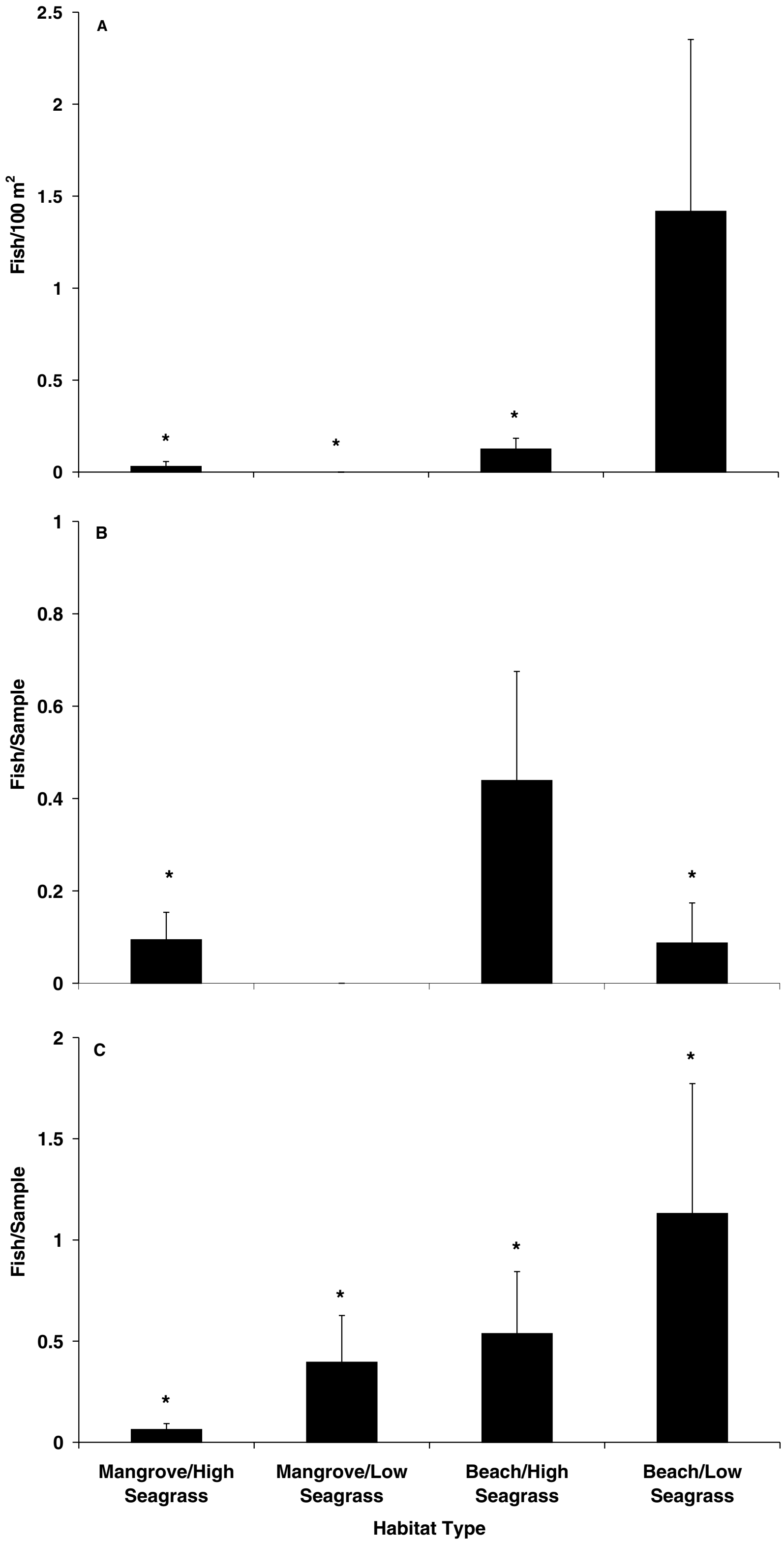

Figure 3. Habitat type use patterns of juvenile permit captured in 21 m and 183 m seines using the Stratified-Random (SR) sampling protocol. Only samples in June through December in zones 4 and 5 were used in this analysis for the 21 m seine; all months, only zones 4 and 5 for the 183 m seine. Values not significantly different among habitat types (Tukey, *P* < 0.05) share an*. (A) Density of juveniles < 100 mm SL caught with the 21 m seine (*n* = 197 hauls). (B) Number of juvenile permit ≤ 100 mm SL per sample caught with the 183 m seine (*n* = 339 hauls). (C) Number of juvenile permit > 100 mm SL per sample caught with the 183 m seine (*n* = 339 hauls). Mean ±1 Standard Error are plotted.

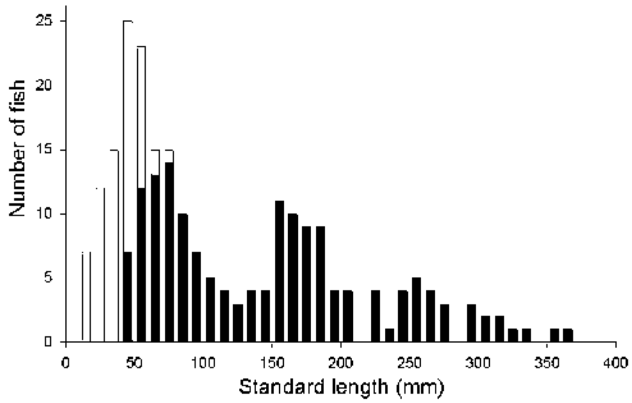

Figure 4. Length frequency distribution of 238 juvenile permit caught by the 21 m seine (open bars) and 183 m seine (black bars) using the Stratified-Random (SR) sampling protocol.

SL is dominated by small fish and mysids. Permit 61–70 mm eat mostly crabs and gastropods (Carr and Adams 1973). Larger crustaceans and mollusks dominate the diet of 50–100 mm permit, and mollusks are the predominant food of permit 100–138 mm (Finucane 1969). These data are insufficient to warrant a food-based explanation to the apparent habitat type shift observed in our study.

Permit catches from the small and large seines must be interpreted with regard to each gear's sampling bias. Large juvenile permit were likely able to avoid the small seine, and small permit passed through the mesh of the large seine (Figure 4). This results in size gaps in the comparisons of habitat types between juveniles (15–72 mm SL) collected in the small seine with juveniles (42–360 mm SL) collected in the large seine. In addition, the amount and areas of benthic habitat types sampled differed between the 2 seining operations. The small seine (shoreline set) only sampled the bottom to 15.5 m from shore, whereas the large seine sampled bottom out to 40 m and potentially sampled multiple habitat types per seine haul. Thus, the apparent use of high seagrass adjacent to beach by small juvenile permit caught with the large seine may have been confounded by the gear. The small permit may have been associated with low seagrass near the shoreline, but their habitat was characterized by assessment of habitat type farther offshore. Because small juvenile permit were collected primarily near the shoreline and the small seine sampled a single habitat type, we believe that the small seine data provided more precise information on habitat types where small permit reside (Finucane 1969, Naughton and Saloman 1978, AJA, unpubl. data). This supposition is supported by the near absence of small juvenile permit in offshore small seine samples. Moreover, habitat types adjacent to beaches had higher abundances of small and large juvenile permit than the same habitat types adjacent to mangrove shorelines (Figure 3).

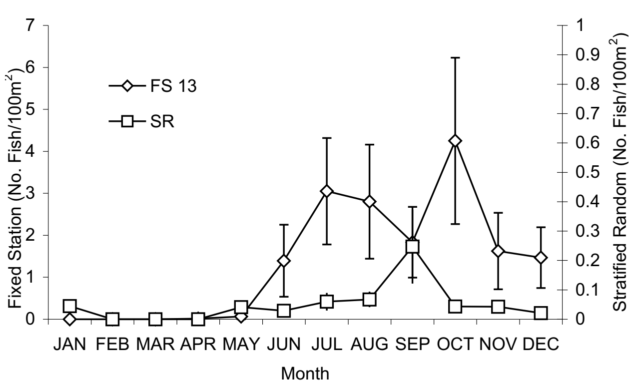

Figure 5. Density of juvenile permit caught in 21 m seines by month from 1991–1995 at Fixed-Station (FS) 13 and from 1996–2000 at Stratified-Random (SR) locations. Mean ±1 Standard Error are plotted.

The distinct seasonality of small juveniles in Charlotte Harbor is similar to findings from other locations in Florida, and support Crabtree et al.'s (2002) conclusion of a spring through summer spawning season. Peak abundance of juveniles in summer or fall also occurred along beaches of the GOM coasts of northern (Naughton and Saloman 1978) and central (Saloman and Naughton 1979) Florida, along the Atlantic coast of central Florida (Peters and Nelson 1987), and in Tampa Bay (Finucane 1969, Crabtree et al. 2002). However, these findings are in contrast to data from St. Croix, US Virgin Islands (I. Mateo, US Virgin Islands Division of Fish and Wildlife, Fredricksted, St. Croix, pers. comm.), Turneffe Atoll, Belize (AJA, unpub. data), and the Florida Keys (C.W. Harnden, Florida Marine Research Institute, Melbourne, FL, pers. comm.), where juvenile permit were captured throughout the year in similar sizes and habitat types as in our study. Numerous, non-exclusive explanations for these differences include 1) differences in spawning seasonality with Charlotte Harbor and other subtropical and warm-temperate locations receive post-settlement stage larvae during much of the year, but conditions become unsuitable for juvenile permit in winter, causing mortality or early emigration from estuarine nursery habitats, and 2) individuals experience highly variable growth rates.

Although seasonality of abundance was similar at FS 13 and for SR samples, the consistent differences in densities between FS 13 and SR samples highlights the tradeoffs of these sampling strategies. The SR strategy provides an overview of temporal and spatial use of Charlotte Harbor, but because all habitat types in all zones are sampled monthly, total catches relative to sampling effort are lower.

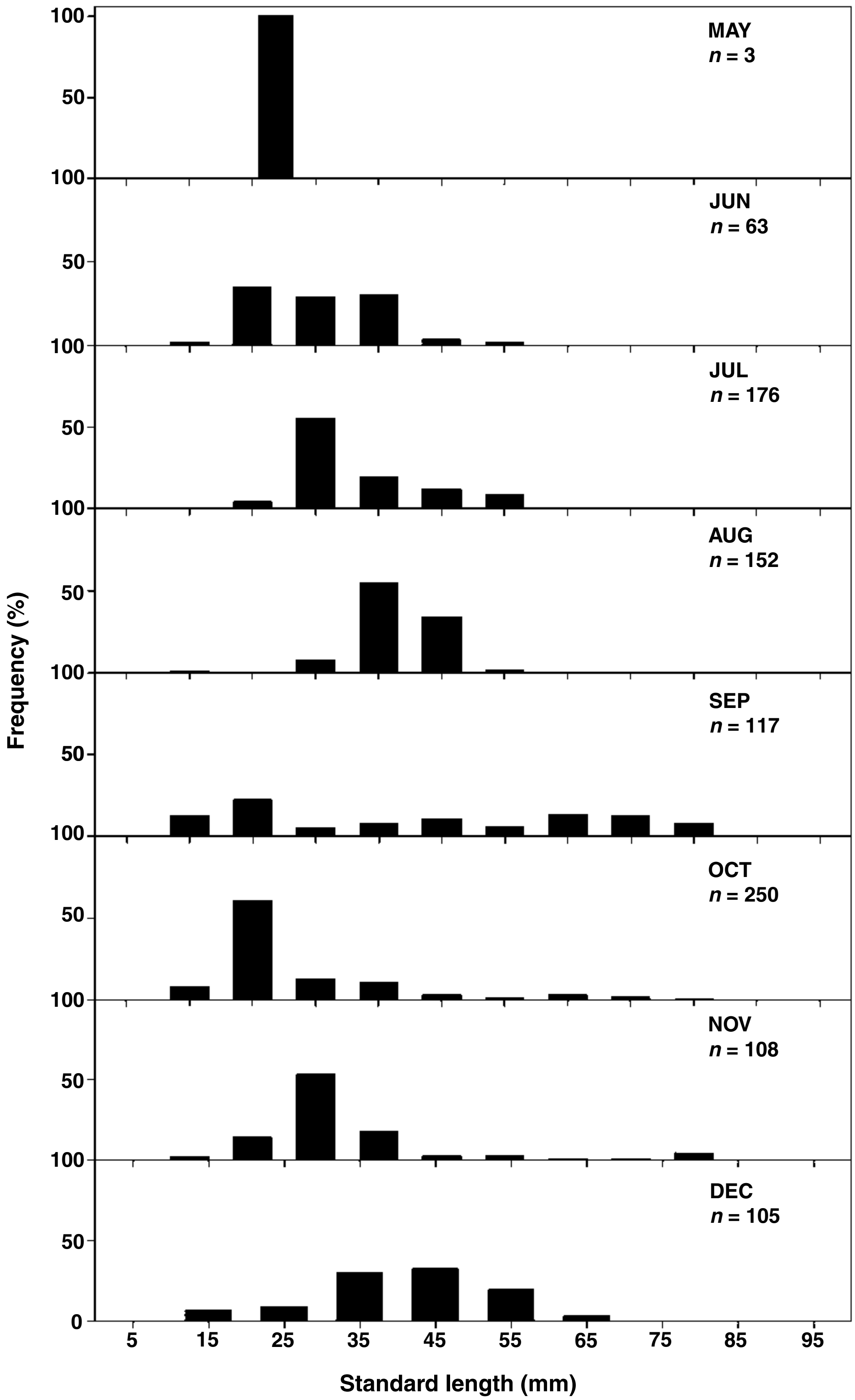

Figure 6. Monthly length frequency of permit caught with the 21 m seine at Fixed-Station (FS) 13. Data pooled over all years (1991–1995).

The SR sampling strategy is well suited for examining patterns of habitat type use within the estuary. The comparative sampling approach of the SR strategy allowed us to incorporate multiple habitat types (shoreline and subtidal benthic) into our examination of habitat type use by juvenile permit. While previous work showed use of habitat types adjacent to beach shorelines by juvenile permit, our study has further described the benthic habitat types adjacent to these shorelines. In contrast, the FS sampling strategy is not as well suited for determining patterns of habitat use, in part because not all habitat types are represented in all zones. When FS locations are found in habitats used by a target species, this is a good strategy for examining temporal trends, and appropriately chosen locations can be used as indexes of recruitment for that species.

The patterns of habitat type use, seasonality, and spatial distribution in Charlotte Harbor raise numerous questions. Are the estuary-wide distribution patterns caused by patterns of larval supply, habitat requirements, or a combination of factors? To what extent are the observed patterns of habitat type use in the lower estuary due to food limitation vs. predation? What are the sources of the juveniles in Charlotte Harbor? To what extent do juveniles found in Charlotte Harbor contribute to adult populations in the region, i.e., to what extent are estuarine juvenile habitat types sources or sinks? Since permit > 350 mm SL do not appear to use shallow shoreline habitat types in Charlotte Harbor, the potential function (i.e., the proportional contribution of permit from these nursery habitats to adult populations (Beck et al. 2001)) of Charlotte Harbor as a nursery should be investigated. Although each question addresses an important ecological and management concern, the last question pertains directly to potential impacts of coastal development, especially if the estuarine nursery habitats are determined to be a population source. Given rates of anthropogenic degradation of these nearshore habitat types, findings from studies that address these questions should have immediate management implications.

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