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Patterns of juvenile habitat use and seasonality of settlement by permit, *Trachinotus falcatus*

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Synopsis

Permit, *Trachinotus falcatus* are economically and ecologically important throughout their range of the Caribbean, subtropical and tropical western Atlantic, and Gulf of Mexico. Despite their economic importance, little is known about the biology and ecology of permit, and most existing information is from Florida. While sufficient information is available to paint a general picture of permit life history, details are lacking for most life stages. For the juvenile life stage, nursery habitats and size and age at settlement have not yet been defined. Although six distinct habitat types (medium energy and low energy windward beaches, leeward beaches, and windward, leeward, and lagoon interior mangrove shorelines) were sampled to determine spatial patterns of habitat use by early juvenile permit at Turneffe Atoll, Belize, Central America, and the Florida Keys, USA, 99% of juvenile permit were found along medium energy windward beaches, indicating their role as nursery habitat for this species. A sub-sample of juvenile permit from Florida was examined to estimate spawning date and age at settlement from otoliths. Size-frequency distributions and otolith age analysis indicate that larval duration is approximately 15–20 days, and settlement occurs year-round. Since permit in Florida spawn March through July, from March through September in Cuba, and from February through October in Belize, year-round settlement indicates population connectivity via larval transport. These results lay the foundation for future research on larval supply, population connectivity, and juvenile ecology, and will aid in the ongoing formulation of a conservation plan toward a sustainable fishery for permit.

Introduction

Permit, *Trachinotus falcatus* are in the family Carangidae, and are common in coastal waters of the Caribbean, subtropical and tropical western Atlantic, and Gulf of Mexico (Bohlke & Chaplin 1993). Permit are economically and ecologically important throughout their range. In Belize, for example, the recreational fishery for permit and other flats species (bonefish, *Albula vulpes* and tarpon, *Megalops atlanticus*) is a major component of an ecotourism industry that is a centerpiece of the economy. Similar economically important recreational flats fisheries exist in South Florida, the Bahamas, and other locations in the Caribbean (Crabtree et al. 2002).

Like many marine fishes, permit pass through three distinct life stages (larval, juvenile, and adult), and while sufficient information on permit is available to paint a general picture of their life history, details are lacking for most life stages, especially larval and juvenile stages. Temporal and spatial patterns of settlement and juvenile abundance are unknown or only partly described. For example, use of ocean beach habitats (Springer & Woodburn 1960; Naughton & Saloman 1978; Saloman & Naughton 1979; Peters & Nelson 1987) by juvenile permit has predominantly been documented by studies that did not concurrently sample other habitat types. In contrast, when multiple habitats were concurrently sampled in a south Florida estuary, juvenile permit were found to use multiple habitat types (Adams & Blewett 2004). Such multi-habitat comparative sampling is an essential step toward defining nursery habitats (Beck et al. 2001; Gillanders et al. 2003).

Other aspects of early life history are also unclear. For example, Crabtree et al. (2002) reported that spawning in south Florida occurs May through July (Crabtree et al. 2002), but they also reported the presence of small juveniles throughout the year, which contradicts seasonal spawning. They suggested that spawning may occur year-round elsewhere. The presence of early juveniles in nursery habitats throughout the year could be explained by two mechanisms, or some combination thereof: (1) larval supply following the May to July spawning period reported by Crabtree et al. (2002), followed by differential growth of juveniles; or (2) spawning in Florida or in other 'source' locations outside the months reported by Crabtree et al. (2002). Although prolonged spawning periods occur in lower latitudes (from March to September in Cuba (Garcia-Cagide et al. 2001) and from February through October in Belize (Graham & Castellanos 2005)), differential juvenile growth vs. year-round settlement has not been examined because juvenile permit have not been aged. This study is the first to examine juvenile permit habitat use via multiple habitat comparative sampling in two locations in the western Atlantic and Caribbean (Florida and Belize), and to examine temporal patterns in settlement and juvenile distribution.

Materials and methods

Study locations

The purpose of this study was to document the use of coastal habitats by juvenile permit, and to determine seasonality of settlement, abundance and size. To this end, this study was conducted at two locations – Turneffe Atoll, Belize, Central America, and Florida Keys, Florida, USA (Figure 1).

Turneffe Atoll lies 48.2 km off the coast of Belize, and is the largest atoll in the Caribbean, measuring 48.2 km long by 16.1 km wide. The atoll is surrounded by a fringing reef, inside of which are mangrove-fringed islands with sandy and mangrove-lined shorelines. The interior lagoon of the atoll is seagrass (primarily *Thalassia testudinum*). Prevailing winds and seas are from the east.

The Florida Keys extend approximately 210 km SSW of the Florida Peninsula, and are a series of calcium carbonate islands with a mixture of beachrock, mangrove, sand, and anthropogenically altered shorelines. The Keys are bound by Florida Bay and the Gulf of Mexico to the west and north, and the Atlantic Ocean and Florida Straits to the east and south. The nearshore subtidal habitat types surrounding the islands are primarily sand, mud, marl, seagrass, and consolidated limestone. The side of the Keys facing the Atlantic Ocean is considered the windward side.

Spatial comparisons of habitat use

Shoreline habitats at Turneffe Atoll and the Florida Keys were sampled to determine spatial patterns of juvenile permit habitat use. At Turneffe Atoll, a seine (15×1.5 m, 3.1 mm mesh center bag) and visual transects (via snorkel: 100×2 m) were used to sample multiple habitat types at Turneffe Atoll, Belize (Figure 1). Sampling at Turneffe Atoll occurred in June 2003, when five habitat types were sampled: (1) lagoon interior mangrove shorelines (located on the shorelines of islands within the interior lagoon); (2) leeward sandy beaches and (3) leeward mangroves shorelines (located on the western side of the islands that ring the westernmost perimeter of the atoll, and are exposed to very low wave energy); (4) windward sandy beaches (on the eastern shoreline of the atoll, generally exposed to moderate wave

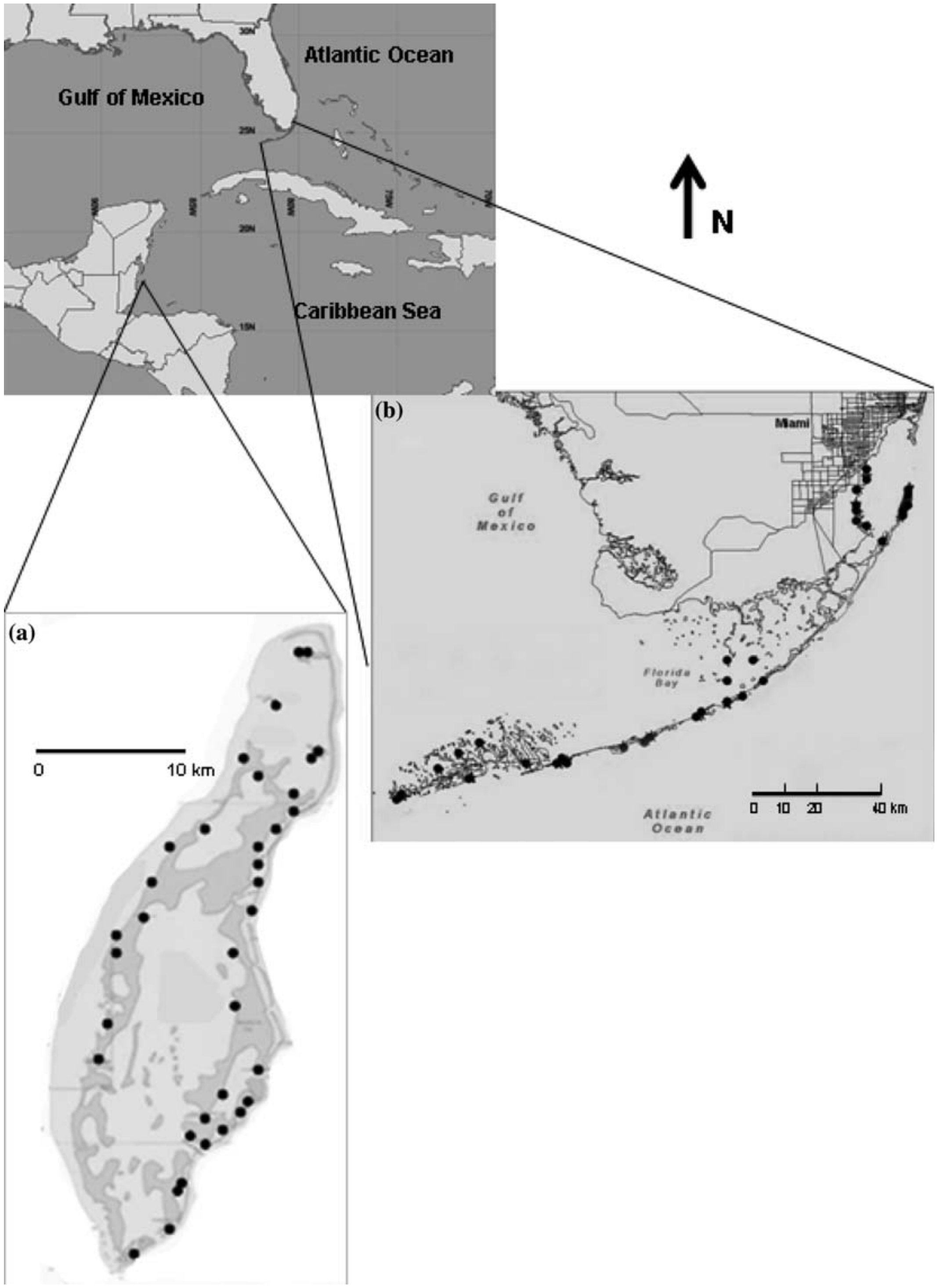

Figure 1. Map showing study locations Turneffe Atoll, Belize, Central America, and Florida Keys, Florida, USA.

energy, with a swath of sand bottom (6–9 m wide) between the high tide line and seagrass beds (primarily *Thalassia testudinum*, with some *Halodule wrightii*)) and (5) windward mangrove shorelines (located on the easternmost shorelines of the islands that make up the eastern perimeter of the atoll, and are protected from large waves by the barrier reef). Seine sampling methods are explained below. Interior mangrove shorelines were sampled by visual census using mask and snorkel because the permanently flooded prop root habitat was not accessible to seine sampling. Three visual transects were conducted at each interior mangrove location.

In the Florida Keys, six habitat types, (1) windward (2) leeward sandy beaches (3) windward (4) leeward beachrock shoreline (5) windward and (6) leeward mangroves, were sampled in October/November 2003 and January 2004 with seines (21 m×1.2 m, 3.1 mm mesh center bag seine (for small juveniles) and a 45.5 m×1.8 m, 9.5 mm mesh bag seine (for larger juveniles)) (Figure 1).

Temporal patterns of habitat use

To determine temporal patterns of settlement and juvenile habitat use, windward beach habitats in the Florida Keys were sampled with the 21 and 45.5 m seines every other month from November 2003 through January 2005. This sampling effort focused on windward sandy beach shorelines because of null catches in all other habitat types in the Florida Keys in November 2003 and January 2004, and in Belize (see results). A sub-sample of captured juveniles was retained for age analysis. Otoliths (lapilli) were removed and placed in immersion oil for >30 days to elucidate growth increments, and read with a compound microscope.

Sampling protocol

The 15 m (Turneffe Atoll) and 21 m (Florida Keys) seines were set perpendicular to shore with one end at or on shore, pulled parallel to shore for 15 m, and either hauled onto shore (sandy beaches) or pursed offshore (all other habitat types). For shore sets using the 45.5 m seine, the net was set perpendicular to shore, as above, the outer end pulled in an arc to shore, and the bag end hauled to shore, thus sampling a quarter-circle. For offshore sets where the net could not be pulled against shore, the net was pulled parallel to shore for 15 m and pursed. Sample locations were distributed along the length of the Florida Keys, and throughout Turneffe Atoll (Figure 1). A minimum of three seine sets were made at each location with each seine type. In the Florida Keys, where two seine sizes were used at each sample location, the seines were either pulled on non-consecutive days or at spatially separate sites at that location within a day to reduce the effect of net disturbance. Juvenile permit were measured (Standard Length) and released at the capture location, except for a subsample retained for age analysis.

Results

Spatial comparisons of habitat use

A total of 140 samples (101 seines and 39 snorkel surveys) at 34 locations covering six habitat types were completed at Turneffe Atoll in June 2003, and 159 seine samples covering six habitat types were completed in the Florida Keys in November 2003 and January 2004 (Table 1). Of the 281 juvenile permit captured at Turneffe Atoll, 280 were caught on windward beaches, and one was captured on a leeward beach. Juvenile permit captured in Belize ranged from 12 to 78 mm SL (mean = 33.7 mm, SE = 0.9) (Figure 2). In the Florida Keys, 580 juvenile permit were captured, all on windward beaches, and size ranged from 8 to 157 mm (mean = 44.4 mm, SE = 0.8). In each geographic location, juvenile permit were captured throughout the sample area (i.e. all windward beaches sampled contained juvenile permit).

Temporal patterns of habitat use

Settlement of permit occurs approximately 15–20 days after hatching, at 8–10 mm SL. Settlement-size individuals were captured in March, May, and November, and juveniles were captured in all months sampled (Figure 3). Permit <30 days of age (20 mm) were present in all months except July, indicating settlement throughout the year.

Table 1. Summary of sampling effort during multiple habitat sampling to determine habitat use, and captures of juvenile permit by habitat type in Turneffe Atoll, Belize (June 2003), and Florida Keys, Florida (November 2003, January 2004).

Habitat type	Number of locations		Number of samples[a]		Number of juvenile permit captured	
	Florida	Belize	Florida	Belize	Florida	Belize
Windward beach	16	15	79	56	580	280
Leeward beach	6	5	22	26	0	1
Windward mangrove	–	4	–	16	0	0
Leeward mangrove	13	4	41	18	0	0
Lagoon interior mangrove	–	6	–	18	–	0
Windward beachrock	1	–	4	–	0	–
Leeward beachrock	5	–	15	–	0	–
Total	41	34	161	134	580	281

[a]Number of samples for Belize are 15 m seine and visual transects, combined; for Florida, 23 and 45.5 m seines, combined.

Discussion

This research provides new information on permit early life history with direct implications for conservation and management. We sampled six distinct habitat types at two locations, and found settlement stage and juvenile permit almost exclusively on windward sandy beaches. Moreover, the capture of settlement stage and/or young juvenile permit in all sample months indicates that permit settlement occurs through much of the year. Since larval duration of permit is 15–20 days, this confirms prolonged spawning periods in some locations.

Comparative multi-habitat sampling is necessary for determining the full suite of habitats used by juveniles (since juveniles of many species use more than one habitat), and provides data essential to designating nursery habitat (Beck et al. 2001; Gillanders et al. 2003). Since juvenile permit were found almost exclusively on windward sandy beaches in two spatially disparate locations in this study, and this concurs with previous research in Florida (Naughton & Saloman 1978; Saloman & Naughton 1979; Peters & Nelson 1987), windward sandy beach habitats can be considered as important, though not exclusive, nursery habitat for this species (Beck et al. 2001). The use of

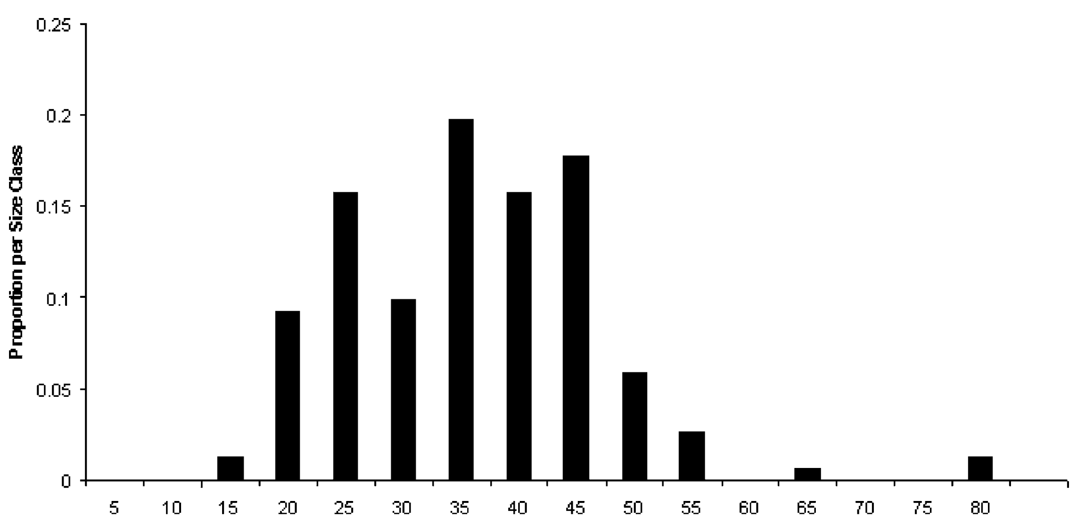

Figure 2. Length frequency of juvenile permit captured at Turneffe Atoll, Belize, in June 2003. n = 281.

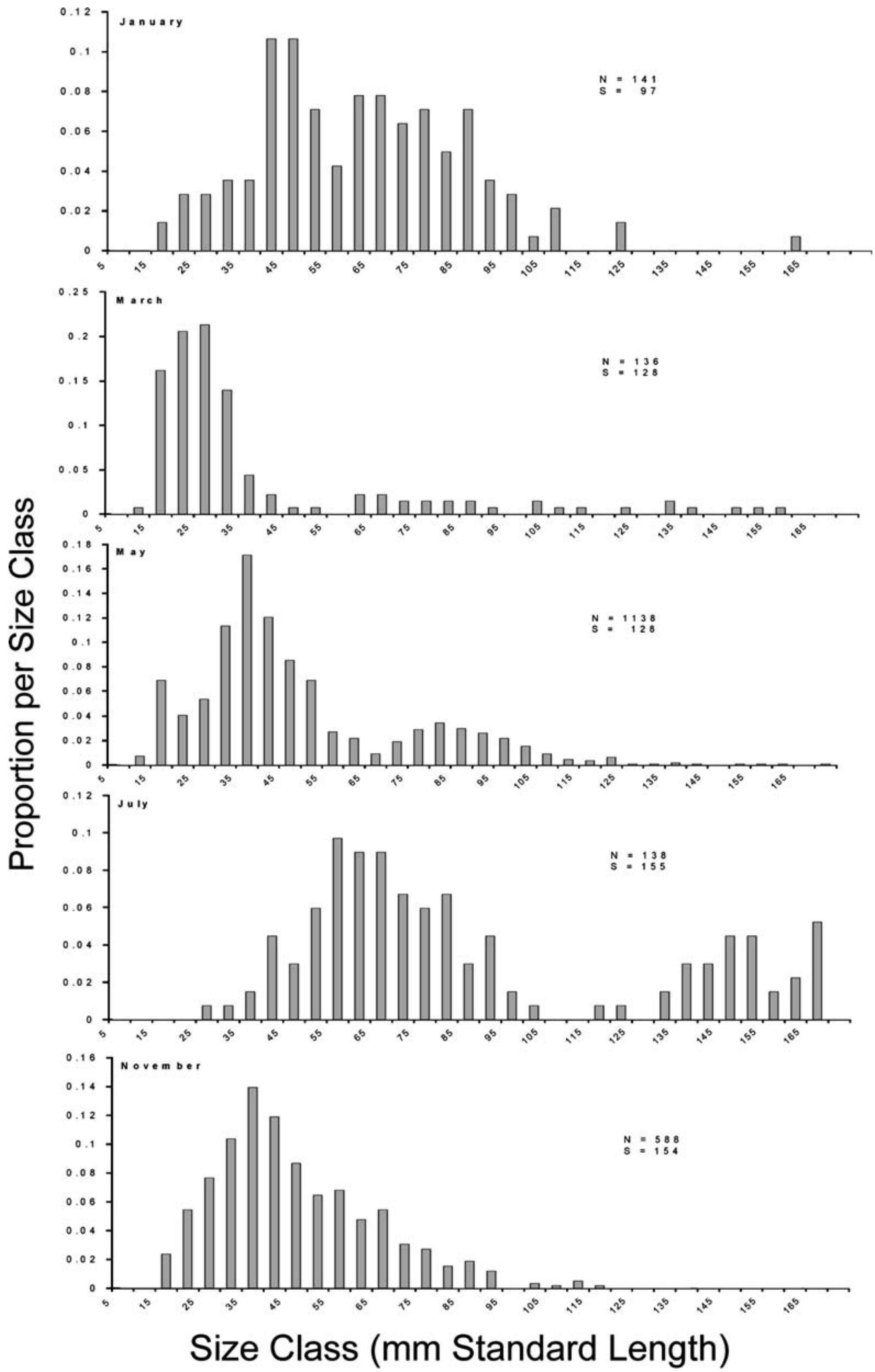
January
N = 141
S = 97
March
N = 136
S = 128
May
N = 1138
S = 128
July
N = 138
S = 155
November
N = 588
S = 154
Proportion per Size Class
Size Class (mm Standard Length)

Figure 3. Length frequency of juvenile permit captured in the Florida Keys, Florida, by month. n = number of juvenile permit captured; *S* = number of samples (21 and 45.5 m seines, combined). Data pooled across years for November (2003 and 2004) and January (2004 and 2005). All other months sampled only in 2004.

sparsely vegetated habitats also concurs with findings from estuarine habitats of southwest Florida (Adams & Blewett 2004), where juvenile permit were captured primarily over sparse seagrass bottom along or near beach shorelines. Thus, windward sandy beaches, and adjacent sparsely vegetated bottoms, are valuable nursery habitats for permit.

The presence of settlement-size permit in windward beach samples and the lack of similar-size individuals in other habitats suggest that permit are actively settling along beaches. Such active settlement should not be surprising since larvae can use olfaction and sound to select settlement habitats (reviewed in Montgomery et al. 2001). Although such cues were not examined in this study, if observed juvenile abundance patterns resulted from non-selective settlement and habitat-specific differential post-settlement mortality, one would expect capture of settlement-size individuals in other habitats.

Numerous other species also use beaches or sparsely vegetated bottom as recruitment habitats. For example, the closely related *T. carolinus* recruits almost exclusively in the surf zone of exposed sandy beaches (Finucane 1969; Naughton & Saloman 1978; Peters & Nelson 1987). Additional species with high juvenile abundance along windward sandy beaches include *Albula* spp (this study) *Menticirrhus* spp (this study, Saloman & Naughton 1979; Peters & Nelson 1987), and *Caranx* spp (this study).

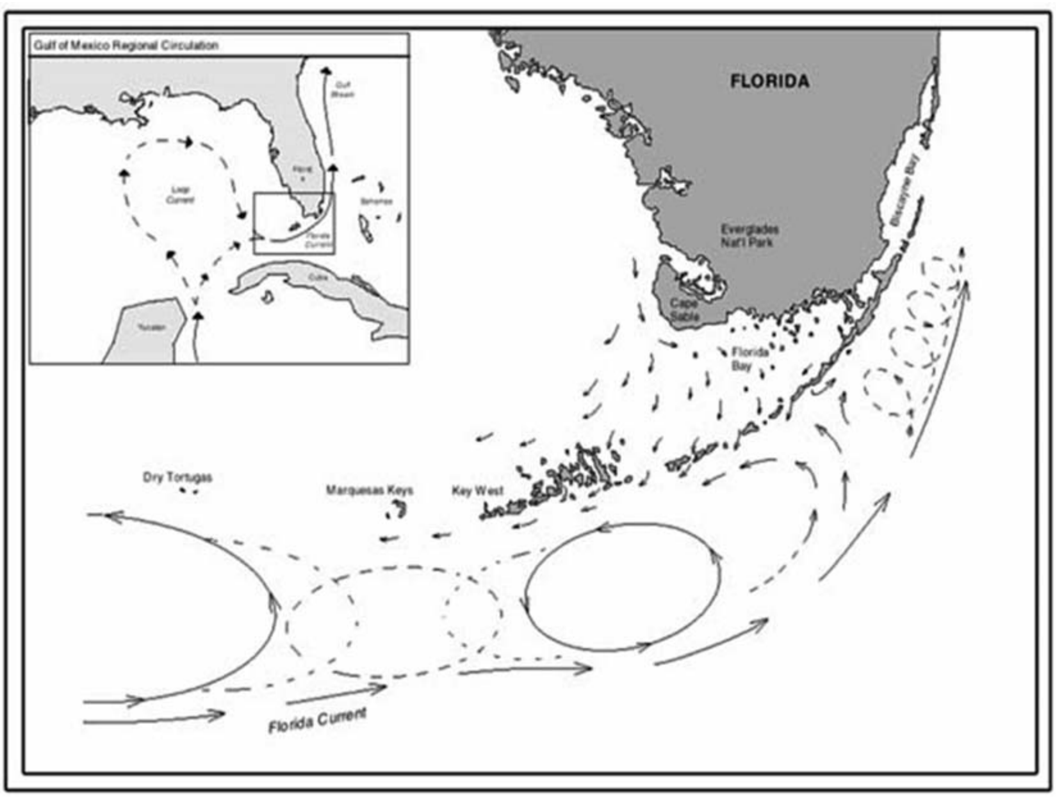

Figure 4. Map showing currents that may transport larvae from Caribbean spawning locations to Florida. The gyres shoreward of the Florida Current can entrain larvae being transported in the Florida Current (e.g. from upcurrent sources) and/or retain locally produced larvae. Figure from United States National Oceanographic and Atmospheric Administration (http://oceanexplorer.noaa.gov/explorations/islands01/background/wind/media/fl_currents.html).

The presence of juvenile permit throughout the year is in conflict with observed gonadal activity related to spawning in Florida (Crabtree et al. 2002). In addition to this study, juvenile permit were also present throughout the year in the U.S. Virgin Islands (Ivan Mateo, U.S.V.I. Division of Fish and Wildlife, personal communication) and in the Florida Keys (Crabtree et al. 2002). However, no previous study addressed size at settlement and early growth of juvenile permit, which left open the possibility that seasonal differences in juvenile growth could explain the observations. Since juvenile permit ≤20 mm are <30 days old from hatch date, and spawning occurs February through October in Belize (Graham & Castellanos 2005) prolonged spawning is likely the major cause of the presence of small juveniles throughout the year.

Seasonal differences in early juvenile abundance, and apparent settlement pulses, suggest three possible scenarios for larval supply to the Florida Keys. First, most larvae are from local sources. For example, permit spawn in Florida from May through July, and highest juvenile abundance in this study was in May (Figure 3). A second scenario is that permit larvae from multiple sources are present for much of the year, and the seasonal spawning of Florida permit merely augments the supply from outside sources. A third possibility is that oceanographic currents differentially deliver larvae irrespective of their source, thus resulting in variability in months of peak settlement and juvenile abundance. For example, in this study a cohort can be followed from March (likely prior to active spawning in Florida) through July (Figure 3).

Oceanographic processes provide pathways for both downstream transport and retention of permit larvae to Florida (Figure 4). The Yucatan Current, which is fed by the Caribbean Current, feeds into the Florida Current (Maul 1977), which moves westward to the south of the southernmost Florida Keys, and then northward along the eastern side of the Florida peninsula, eventually becoming the Gulf Stream. The Gulf Loop current also feeds into the Florida Current (Maul 1977). These current interactions provide a pathway for downstream larval transport from the Caribbean and the Dry Tortugas to the Florida Keys and mainland. Since the relative magnitude of input of the Yucatan Current and Gulf Loop Current into the Florida Current varies (Molinari 1980), the proportion of permit larvae arriving in Florida from upstream sources also likely varies. Retention of larvae spawned in Florida, and the shoreward transport of larvae entrained in the Florida Current are likely facilitated by the Tortugas Gyre (Lee et al. 1994), which varies temporally in size and location, as well as by eddies resulting from meanders in the Florida Current and Gulf Stream (Limouzy-Paris et al. 1997). Future research should examine seasonal characteristics of settlement and juvenile abundance throughout the permit's range with a focus on determining possible source locations and pathways of larval transport.

The presence of young juvenile permit throughout the year in this study is in contrast to seasonal abundance patterns reported in some sub-tropical and warm temperate locations, where juvenile permit are present only during warmer months (Finucane 1969; Naughton & Saloman 1978; Saloman & Naughton 1979; Peters & Nelson 1987; Adams & Blewett 2004). The seasonal distribution of permit observed in those areas could be caused by other factors. For example, larvae could be present year-round, but water temperature drops below larval and juvenile tolerances during winter, restricting juvenile permit presence to warmer summer and fall months. Alternatively, larvae may actively avoid subtropical and warm-temperate latitudes during cold months by staying south of an isotherm, or current patterns may change seasonally so larvae are not delivered to more northern locations.

The lack of juvenile permit >170 mm from samples suggests an ontogenetic shift away from windward beach habitats. It is likely that larger juvenile permit could escape the small seine, but the 45.5 m net was used specifically to capture larger juveniles, so net avoidance does not explain the complete absence of larger juvenile permit. An apparent ontogenetic habitat shift was also observed in a south Florida estuary (Adams & Blewett 2004), and juvenile permit undergo ontogenetic diet shifts (Carr & Adams 1973) that might necessitate habitat shifts.

In conclusion, this information has important conservation and management implications, especially given the lack of published information on early life stages of permit. The multi-habitat comparative sampling and finding of exclusive habitat use conclusively demonstrates that windward sandy beaches are permit nursery habitats. This provides a framework for future research of processes influencing juvenile permit growth, survival, and connectivity to sub-adult and adult life stages, information essential for conservation and management. That settlement occurs through much of the year, whereas spawning occurs only during summer in Florida (Crabtree et al. 2002), suggests population connectivity at a regional scale. Knowledge of larval duration and determination of settlement dates provides direction for future research into larval sources for different nursery habitat locations. Each of these pieces of information provides a target for specific conservation and management measures to ensure a sustainable fishery.

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