

# Transport and connectivity modeling of larval permit from an observed spawning aggregation in the Dry Tortugas, Florida

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**Abstract** Large aggregations of adult permit (*Trachinotus falcatus*) were consistently observed since 2004 by divers in a collaborative fishery-independent reef fish visual census survey during May and June on the western-most edge of the Dry Tortugas Bank, Florida, in coral reef habitat, indicating proximal spawning sites. We investigated the possible fate and connectivity of larvae spawned at this location in the Dry Tortugas and two other published aggregation sites through a drift analysis using the ocean circulation and transport dynamics simulator HYCOM (Hybrid Community Ocean Model). New age-length data facilitated the determination of larval durations and rates of juvenile growth. Modeled larval transport data from spawning sites in the Dry Tortugas, Belize and Cuba were evaluated and compared to a spatially-extensive empirical juvenile permit data set from Florida. Our study revealed that unique oceanographic processes provided pathways for both downstream larval transport and juvenile retention, to and from Florida waters. These

simulation results indicated that the Dry Tortugas region is a key source of permit recruits to southeast Florida stretching from the Florida Keys and up Florida's east coast, and to a much lesser extent the west Florida shelf. Simulations from Belize and Cuba spawning sites revealed high local retention with low connectivity to Florida, emphasizing the importance of local resource management throughout the permit's range.

**Keywords** *Trachinotus falcatus* · Larval transport and fate · Drift · Recruitment · Juvenile age and growth · Population dynamics · Fishery management

## Introduction

The coupled biological-physical environmental mechanisms regulating the recruitment, population dynamics and productivity of marine fishes are not particularly well understood (Rothschild 1986; Mullin 1993; Sammarco and Heron 1994; Caley et al. 1996; Bakun 1996; Cowen et al. 2000; Mann and Lazier 2005; Levin 2006). This is also true for permit (*Trachinotus falcatus*), a large game fish species of the western central Atlantic Ocean belonging to the Carangidae family (jacks). Permit range from Massachusetts to southern Florida, throughout the Bahamas, Caribbean Sea south to Brazil (Robins et al. 1986; Smith-Vaniz 2002). In the USA, permit are most common in southern Florida. Adults are coastal fishes that inhabit seagrass and tidal sand flats and channels, either as solitary individuals or small schools, but are also found offshore on coral reefs

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and artificial structures. They feed on crabs, shrimps, clams and smaller fishes and have a specialized plate at the back of their mouth that helps them crush hard-shelled animals (Jory 1986). Permit can reach 100 cm FL and the all-tackle world record is 27 kg (IGFA 2015).

An iconic and lucrative sport fishery targeted by flyfishers occurs in the shallow clear-water flats of south Florida and the Florida Keys, and there is also a conventional gear fishery on offshore coral reefs and artificial structures. More than 98 % of the flyfishing and saltwater line class world records of permit came from southern Florida and the Florida Keys (IGFA 2015). Other well-known locations for permit include The Bahamas, Cuba, Mexico and several Caribbean nations. There is also a relatively small commercial fishery on the West Coast of Florida. Permit are especially coveted by catch-and-release recreational anglers for their beauty and fighting abilities, and by extractive fishers for their unique taste and dollar value.

There are inevitable conflicts to achieve sustainability in a fishery with such dichotomous resource use perspectives. In Florida, permit harvest is regulated through gear restrictions, catch and size limits, and a spatially restricted seasonal closure. Currently permit stock status is unknown throughout their range, and despite their widespread tropical distribution and high economic values in Florida and Caribbean countries, there is no information on population connectivity from which to base management decisions. This is further complicated by the fact that for many reef fish species, little is known about location and timing of spawning, and most importantly, the ultimate fate of larval fish (e.g., Paris et al. 2005; Botsford et al. 2009). Such lack of knowledge hinders the efforts of fisheries management because of the weak definition of unit stock, “a closed inter-breeding unit” (Beverton and Holt 1957). In that regard, substantial confusion persists concerning permit spawning periodicity and larval dynamics.

In Florida, Crabtree et al. (2002) reported permit spawning period typically lasted from April to September, but peaked during May to July. In Cuba and Belize, permit spawning season has been reported from March to September, and February to October, respectively (García-Cagide et al. 2001; Graham and Castellanos 2005). During spawning season along the southern Florida coast, mature adult permit are seen in large aggregations on offshore natural and artificial structures. After drifting as fertilized eggs and larvae for a duration of about

25 to 30 days, settling post-larval and juvenile permit are subsequently found in sheltered seagrass beds, among mangrove roots, and along sandy beaches (Crabtree et al. 2002; Adams and Blewett 2004; Félix et al. 2007; Snodgrass and Harnden 2009). Based on spatially restricted and limited sampling effort, Fields (1962) noted the presence of juvenile permit (< 12 mm SL) throughout the year in south Florida, which he believed indicated a prolonged spawning period. More recently, seine surveys along beaches in south Florida also found juvenile permit year round (Adams et al. 2006; Snodgrass and Harnden 2009). However, these authors speculated that observed “out of phase” winter recruitment may have been derivative of permit spawning in other northern Caribbean locations (Lee et al. 1992; Crabtree et al. 2002; Adams et al. 2006). Until recently, no spawning aggregations in Florida had ever been positively identified.

In this paper, we first describe empirical observations of large aggregations of permit seen seasonally in the same area in the Dry Tortugas, Florida, for over a decade. We hypothesized that these aggregations of permit may be on or around a potential regional spawning site(s). To examine this hypothesis, we evaluated the relationship of the seasonal occurrence of permit juveniles throughout Florida with a large empirical Florida-wide fishery-independent data set to evaluate year round presence of juveniles. New samples of recently recruited permit were aged to estimate larval duration. These various pieces of information were assimilated and used as inputs to a state-of-the-art ocean currents and transport simulation model to evaluate the fate of developing eggs and larvae spawned at the observed Dry Tortugas site and from various published spawning aggregations sites in Cuba and Belize. Drift simulation results were then compared to the empirical field data on permit juvenile densities to assess the importance of these sites to recruitment of juvenile permit in Florida.

## Methods

### Study area

The Florida Keys coral reef extends 400 km southwest along an island archipelago from Key Biscayne near Miami to the Dry Tortugas, a region located

113 km west of Key West encompassing seven islands surrounded by 326 km<sup>2</sup> of mapped coral reef habitat that supports an incredibly diverse and productive community of corals and tropical fish species (Davis 1982; Franklin et al. 2003; Ault et al. 2006, 2013; Smith et al. 2011). Unique topographic and oceanographic conditions in the region help sustain the highly productive Florida Keys coral reef ecosystem. Oceanographic dynamics are influenced by the Loop Current extending through the Straits of Yucatan between insular Cuba and the continental Belize-Mexico coastline into the southeastern Gulf of Mexico. The rich marine environment of the Dry Tortugas is a product of the unique geophysical setting which promotes dynamic oceanographic conditions such as incursions and perturbations driven by the Gulf of Mexico's Loop Current which emerges in the Straits of Florida as the Florida Current near the Dry Tortugas and then flows parallel to the barrier reef through the Straits of Florida towards Miami. This dynamic oceanography helps create intricate recirculating gyres and cyclonic eddies that are responsible for larval retention throughout the Florida Keys (Lee et al. 1992; Fratanoni et al. 1998; Sponaugle et al. 2005), and surface currents with some of the highest current speeds in the world (Stommel 1976; Olson 2001). The region contains known reef fish spawning grounds, and its upstream location in the Florida Current facilitates advective dispersion and transport of eggs and larvae to the rest of the Keys and southern Florida (Lee and Williams 1999; Dahlgren and Sobel 2000; Domeier 2004; Burton et al. 2005). In part, due to its upstream location in the Florida Current and distance from the nearest human population center (i.e., Key West), several large marine reserves have been created in the area to improve the conditions and sustainability of reef fisheries throughout the Florida Keys (Bohnsack and Ault 1996; Ault et al. 2006, 2013).

#### Reef fish visual census (RVC)

Fishery-independent reef fish visual census (RVC) surveys using a two-stage stratified random sampling design (Smith et al. 2011) have been conducted since 1979 throughout the Florida Keys, and since 1999 throughout the Dry Tortugas, Florida, to assess the sustainability status of the exploited coral reef fish community (Ault

et al. 1998, 2005, 2014), and to evaluate the design and resource restoration efficacy of marine protected areas (Meester et al. 2004; Ault et al. 2006, 2013). The RVC is a standard, non-destructive, in situ monitoring protocol in which a stationary diver records reef-fish data (numbers at sizes of each species) while centered in a circular plot of 15 m dia (Brandt et al. 2009; Smith et al. 2011). Each year, from Miami to the Dry Tortugas hundreds of random sites are surveyed in coral reef habitats <30 m depth. In the course of these annual surveys, large schools of permit indicative of spawning aggregations have been sighted, recorded and photographed in the Dry Tortugas. The entire (1979–2012) RVC data set was analyzed to place these permit aggregation events in context with other sightings and to determine the frequency, location and timing of these events throughout the Florida Keys coral reef ecosystem.

#### Daily ages at lengths

Larval duration and juvenile growth rates were determined from samples collected from June to August 2013 at Key Biscayne, Florida. Sagittal otoliths from these fish were sent to [www.tropicalfishageing.com.au](http://www.tropicalfishageing.com.au) for age determination. Otoliths were prepared for daily increment counting using the method of Secor and Dean (1992). Sagittal otoliths were first embedded in an epoxy resin block and allowed to cure for 10 h at 60 °C. A 400 µm traverse section was cut from each block using a Buehler low-speed saw where the otolith core was exposed. Each section was then mounted on a separate glass microscope slide with thermoplastic cement and polished with 1200-grit wet-dry sanding paper. Each section was viewed under a light transmitted compound microscope at 40–400× magnification. Daily increments were counted along the dorsal axis where possible, as the increments were generally more distinct in this region of the otolith sections. Settlement marks, which indicated the time (in d) in which a particular fish recruited to benthic nearshore habitats, allowed for explicit determination of larval duration.

#### Juvenile permit field sampling

Size-structured relative abundance of early juvenile phase ( $\leq 40$  mm SL) permit were acquired from three separate sampling program datasets. By far, the largest spatiotemporal dataset came from the Florida Fish and Wildlife Conservation Commission's Fisheries-

Independent Monitoring Program (FIM), which has since 1985 conducted fisheries-independent sampling along the entire state of Florida marine coastline. The data utilized for our analyses encompassed sampling from 1996 through 2011 of six major estuarine systems between Apalachicola in the western panhandle in the Gulf of Mexico, to Jacksonville on the Atlantic coast (Fig. 1 and Table 1). In each location, sampling effort was relatively consistent by month throughout the year. The FIM utilized several gear types throughout its history to monitor the relative abundance of fishery resources in major coastal habitat zones of the temperate to subtropical regions of Florida. Since we were interested in early juvenile phase permit, we constrained our study to evaluation of only two gear types: (1) 21.3 m center bag seine with 3.1 mm mesh that was hauled in waters of <1.6 m depth; and, (2) 183 m center bag seine with 37.5 mm mesh. Sampling stations with salinities <2 psu were removed from this study as no early juvenile phase permit were ever caught at these salinities.

The second dataset was a survey of shoreline fishes conducted by the South Florida Regional Laboratory of FWRI from 1994 to 1997 using a 21.3 m seine with 3.1 mm mesh (Snodgrass and Harnden 2009). A third dataset spanning 2003 to 2004 was from the oceanside beaches of Key Biscayne that also used 21.3 m seine with 3.1 mm mesh. For all surveys, the SL was measured for all permit. Lengths were proportionally assigned to fish not measured by those that were measured in each haul. Since permit look very similar to and are frequently caught with pompano (*Trachinotus carolinus*), permit were positively identified by counting dorsal and anal fin rays because these meristics are distinct from pompano (Robins et al. 1986). Regional empirical data were grouped geographically into zones for comparison with analytical simulation results (Fig. 1). Percent occurrence and catch per unit effort (CPUE) of juveniles  $\leq 40$  mm SL were calculated for each region. CPUE was standardized among gear types to number of permit per 100 m<sup>2</sup>.

Transport model, drift simulations and larval trajectories

Lagrangian “drift” simulations were conducted using assimilated surface currents from HYCOM model (Cummings 2005; Chassignet et al. 2007) from April 2008 to October 2010 for permit spawning that was presumed to occur monthly at every 3rd quarter moon (Graham and Castellanos 2005) at three regional locations

where spawning aggregations are known or hypothesized: (1) Dry Tortugas Florida (this paper); (2) Turneffe Island, Belize (Graham and Castellanos 2005); and, (3) western Cuba (García-Cagide et al. 2001) (Fig. 1). Each drift simulation entailed continuous Lagrangian tracking in time and space. A total of 1000 passive particles (“larvae”) were initially released into the model domain at the specific spawning site, and then transported in the model at hourly steps for 30 days. During the course of a simulation, particles located in environments with substrate depths shallower than 50 m were considered to have been successfully recruited. The principal metric employed was the percentage of released particles recruited on day 30 in each of the six coastal environmental zones defined in Fig. 1; (1) east Florida (EF); (2) south Florida (SF); (3) west Florida (WF); (4) Gulf of Mexico and western Caribbean (GM); (5) Caribbean (CA); and, (6) The Bahamas (BA).

## Results

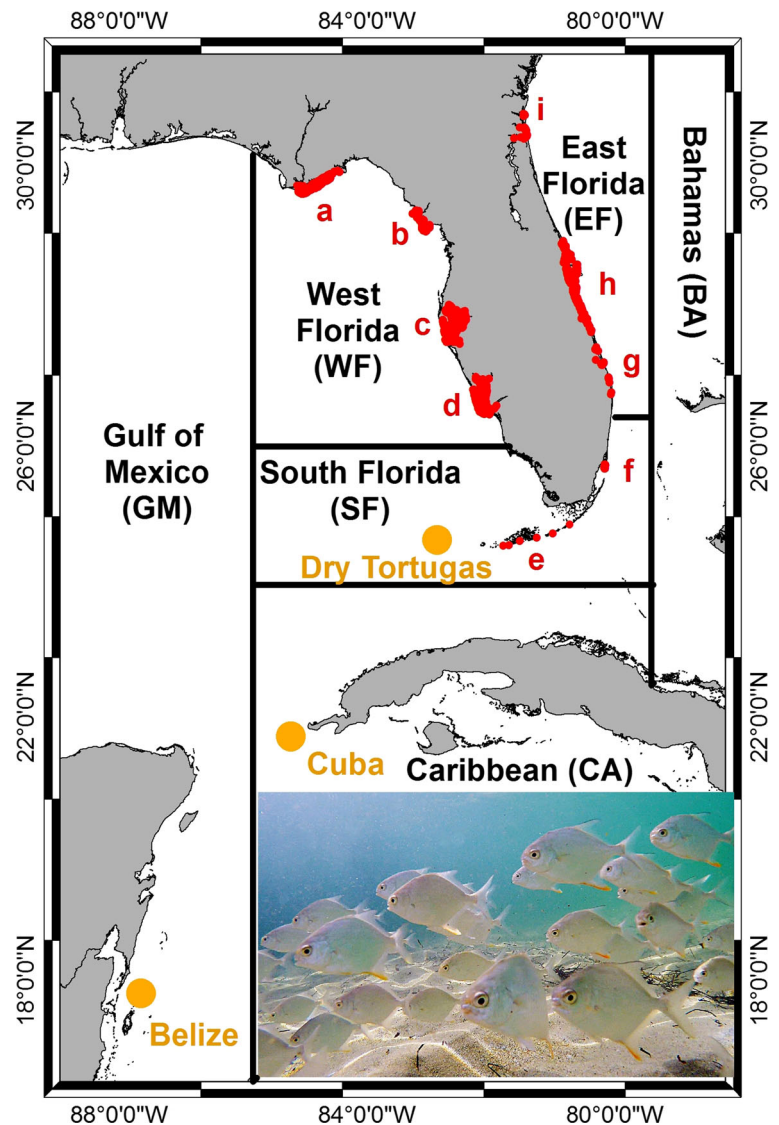
### RVC

Individual permit, especially schools with more than 10 fish, were extremely rare along the Florida coral reef tract in depths <30 m (Table 2). In the Florida Keys, only three schools of permit with >10 individuals were observed during 33 (1979–2012) years of the RVC program which represented close to 13,000 diver survey samples. Despite the rarity of large schools in the Keys, during the months of May and June, particularly large aggregations of permit have been repeatedly observed on the western edge of Dry Tortugas bank during four separate years (2004, 2008, 2010 and 2012) by multiple divers in the survey team (Figs. 2 and 3). The general location of these permit schools were consistent and adjacent to a steep drop off. These schools of permit typically consisted of a thousand or more fish swimming in a spiral fashion in the water column with a dark marking on their sides, which although often observed in shallow water when feeding, has also been documented on spawning fish (Fig. 3; Graham and Castellanos 2005).

### Daily ages at lengths

A subsample of 27 juvenile specimens collected from the 2013 Key Biscayne June–August sampling was processed for daily aging. Lengths ranged from 15.5 to

**Fig. 1** Map of northwestern Caribbean Sea, the Gulf of Mexico and the Florida Straits. Red dots along the Florida coast represent juvenile permit sampling sites: **a** Apalachicola, **b** Cedar Key, **c** Tampa Bay, **d** Charlotte Harbor, **e** Florida Keys, **f** Key Biscayne, **g** Tequesta, **h** Indian River, and **i** Jacksonville. Orange dots indicate observed or hypothesized permit spawning sites which were the starting points of larval drift simulations. The lines delineate the spatial zones used for analysis of passive particle distributions. Inserted is a photograph of a small school of juvenile permit (30–60 mm SL) on Key Biscayne, FL (photo by J. Luo)



**Table 1** Summary results of juvenile ( $\leq 40$  mm SL) permit haul seine sampling. CPUE units are permit per 100 m<sup>2</sup>

Location/Region	Years	No. Hauls	Percent Occurrence	No. Permit	CPUE
Jacksonville	2001–2011	5336	2.6	694	0.0093000
Indian River	1998–2011	10,612	1.5	642	0.0045600
Tequesta	1997–2011	2501	0.1	4	0.0000388
Key Biscayne	2003–2004	180	24.4	143	0.5700000
Florida Keys	1994–1997	136	61.5	1487	7.8700000
Charlotte Harbor	1996–2011	11,752	0.4	149	0.0009500
Tampa Bay	1996–2011	13,160	0.3	150	0.0009100
Cedar Key	1996–2011	7419	0.9	240	0.0021100
Apalachicola	1998–2011	6124	0.7	148	0.0011500



**Table 2** Total number of reef fish visual samples, sites with permit observed, and sites with >10 permit observed in the Florida Keys (1979–2012 combined) and Dry Tortugas by year from 1999 to 2012

Description	Florida Keys	Dry Tortugas						
	1979–2012	1999	2000	2004	2006	2008	2010	2012
Number of samples	12,953	428	437	594	485	644	706	799
Number of sites observed	142	4	3	17	2	24	27	24
Sites with >10 permit	3	0	0	8	0	6	2	1

35.5 mm SL, and ages from 34 to 61 d (Fig. 4). Of the 27 fish subsampled, five otoliths showed a settlement mark at ages ranging from 25 to 28 d. From this information, larval duration was set to 30 d in the drift simulation model.

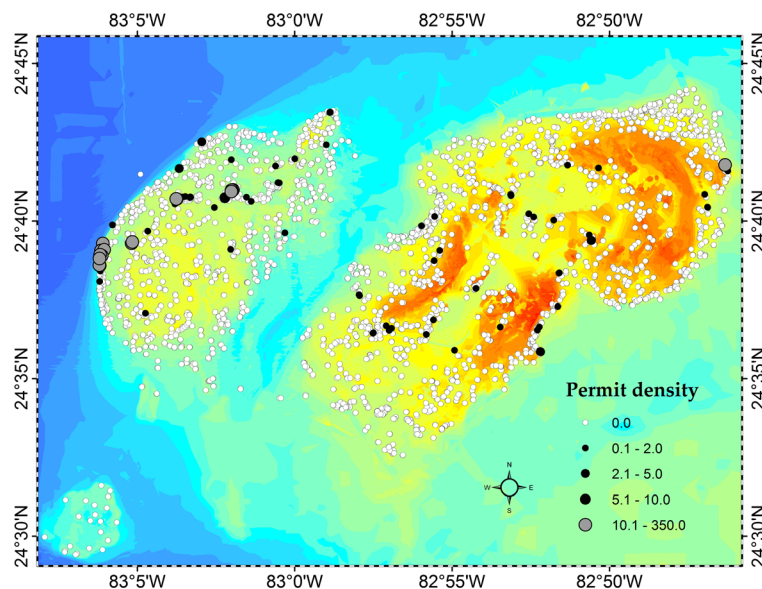
### Juvenile permit field sampling

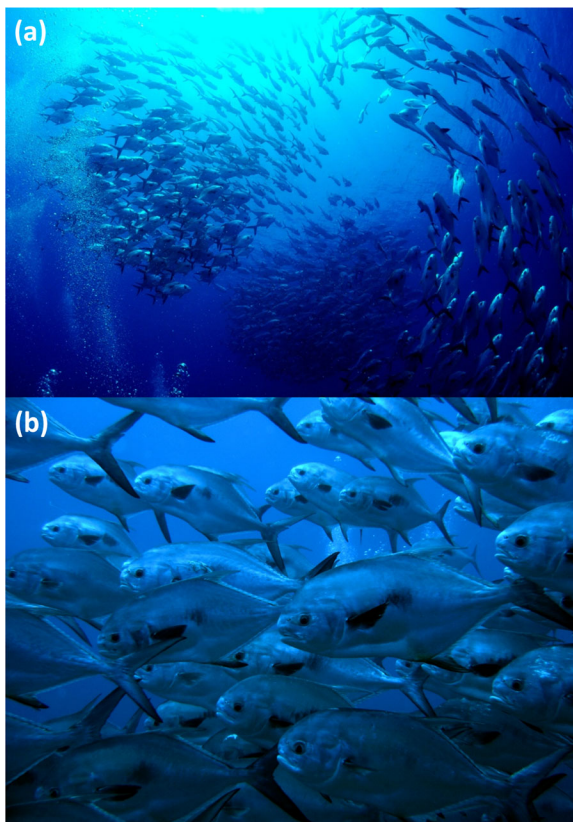
CPUE of early juvenile permit was several orders of magnitude higher in south Florida (SF) as compared to either east coast (EF) or West Coast (WF) of Florida (Table 1). Monthly CPUEs of juveniles  $\leq 40$  mm SL indicated that permit recruitment occurred year-round in SF (Fig. 5), where a peak in recruitment occurred in the spring, followed by lower CPUE from June to August, and then another peak in fall. For the EF and WF regions, CPUE of  $\leq 40$  mm SL permit peaked in fall, with highest

values during October. In EF and WF there was a modicum of juvenile recruitment during late winter to early spring.

### Larval transport and drift simulations

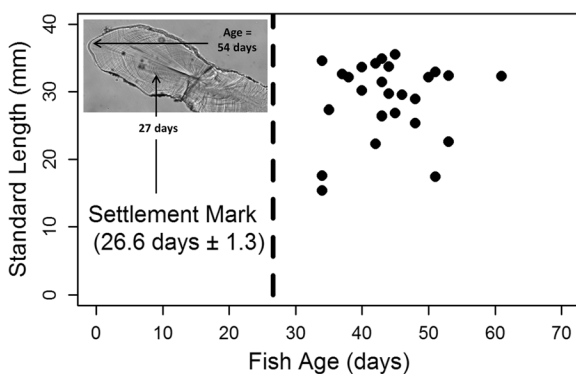
Lagrangian drift simulations of permit recruitment showed that larval particles released from the Dry Tortugas were significantly more likely to recruit in Florida after 30 days than those released from either Belize or Cuba spawning sites (Figs. 6 and 7). On average 19.8, 10.9 and 5.6 % of Dry Tortugas releases settled in SF, EF and WF, respectively. Particles released from Belize were most likely to have remained in the GM zone, while those released from Cuba remained in the CA zone. However, the percentage of larval recruitment in Florida had large temporal variations depending

**Fig. 2** Bathymetric map of Dry Tortugas, Florida with location of sample sites and permit density (per 177 m<sup>2</sup>) from reef fish visual surveys during years 1999–2012



**Fig. 3** Photographs of large aggregations of permit (*Trachinotus falcatus*) (60–90 cm FL) observed during reef fish visual surveys in the Dry Tortugas (west Tortugas Bank) in: **a** June 2010 (photo by J. Luo), and **b** June 2004 (photo by D. Bryan)

on spawning dates (Fig. 8). For example, simulated recruitment from the Dry Tortugas spawning site to the SF recruitment zone ranged from 0 to 80.1 %. Both the



**Fig. 4** Daily age as a function of standard length from 27 otoliths collected in 2013 in Key Biscayne, Florida. Dashed vertical line represents average settlement mark (26.2 days  $\pm$  1.3 SD) from 5 otoliths. Insert is a 26 mm SL permit otolith at 40 $\times$

western Cuba and Belize spawning sites each had a single observation with >10 % recruitment in SF (Figs. 9 and 10) during the simulated time period.

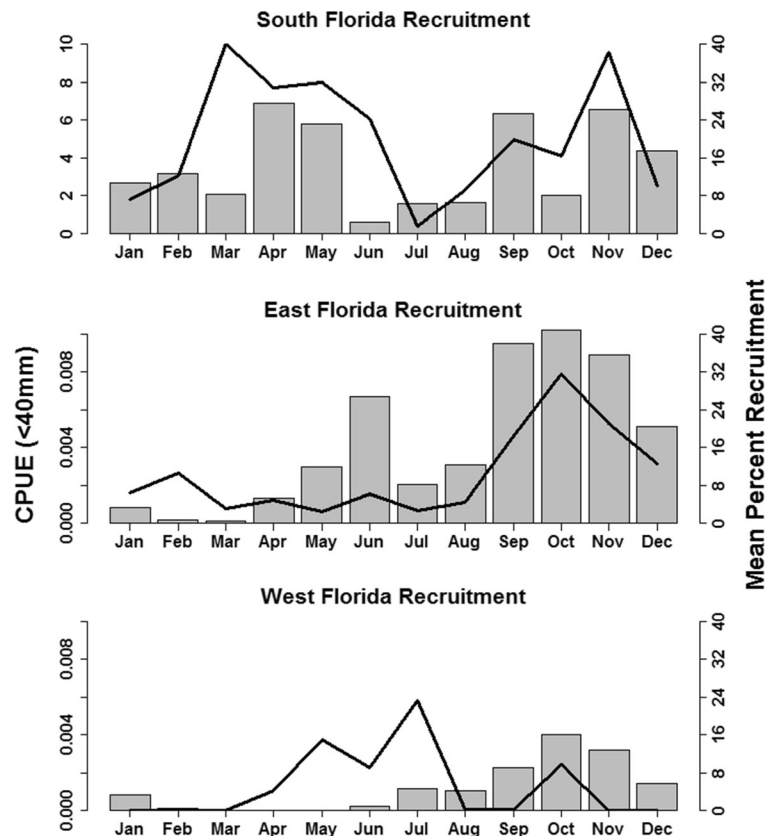
In the WF zone, the potential of larval recruitments from any of the three spawning sites was low. There were 6 events from the Dry Tortugas spawning site with simulated recruitment >5 %, and no events from the Belize or Cuba had recruitments >1 %.

Simulated monthly mean recruitment from the Dry Tortugas site showed a bimodal pattern in SF with peaks in spring and late fall, similar to the empirical CPUE data (Fig. 5). Simulated monthly recruitment to EF also followed the same pattern as the empirical CPUE with a peak recruitment in the fall. On WF, simulated recruitment peaks occurred in summer, which was contrary to observed CPUEs.

## Discussion

Permit are a major component of a highly valuable recreational fishery in Florida and the western Caribbean, yet there is limited scientific data available from which to inform management decision making (Armstrong et al. 1996). Improved understanding of population dynamics and connectivity is vital for the successful management of this or any fishery, as the degree of connectivity at both the larval and adult life stages guide prudent management actions (Botsford et al. 2009). In this study, ocean drift models, new information on larval duration, empirical data on spatial distribution and seasonality of juvenile permit occurrence, and spawning site identification in Florida suggests: (i) permit spawn throughout the year in SF, likely in the Dry Tortugas region; and (ii) population connectivity with other locations in the northern Caribbean is very low and with self-recruitment as a principal feature for Florida.

Juvenile permit were present year-round in Florida with elevated CPUE at SF sites when compared to other Florida locations. Daily aging results showed that these juveniles were between one and two months old, confirming the notion that permit must have spawned year-round to produce these recruits. The reproduction work of Crabtree et al. (2002) that indicated a March–August spawning season in Florida, led earlier authors to speculate that winter spawning may occur in other Caribbean locations and that perhaps these populations were connected to Florida providing year-round recruits (Crabtree et al. 2002; Adams et al. 2006). However, our



**Fig. 5** Monthly CPUE of juvenile permit ( $\leq 40$  mm SL) by zone in gray bars. Dark line indicates the mean percent by month of simulated drift particles that settled in each zone from the Dry Tortugas spawning site

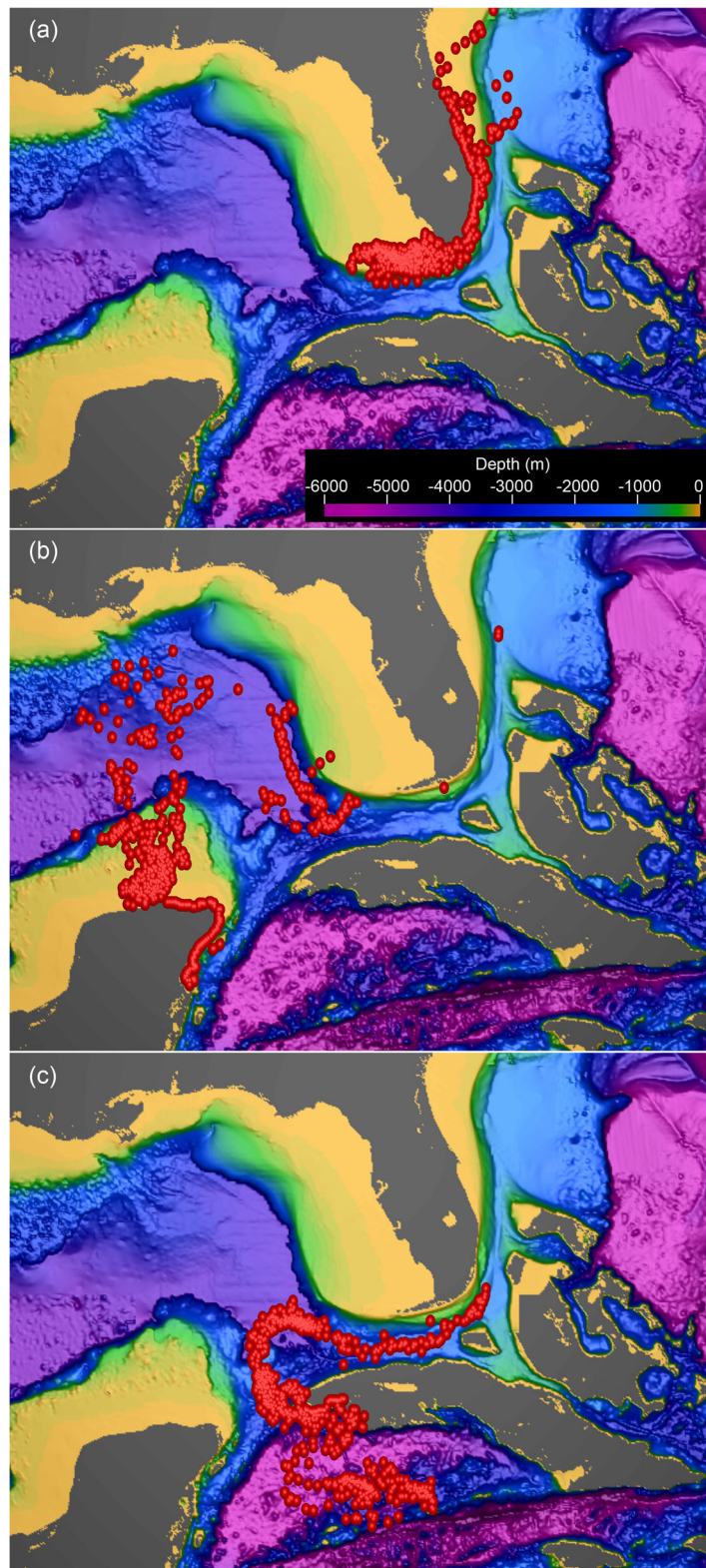
intensive 30 d larval drift simulations showed that the two other known spawning sites in the Caribbean could have only provided very small and inconsistent supplies of recruits. These results indicated that the bulk of Florida permit recruits throughout the year must have come from spawning sites within Florida, such as the Dry Tortugas site.

Reef fish spawning sites are typically located near geological prominences coupled with favorable oceanic conditions that promote larval survival (Domeier and Colin 1997; Heyman and Kjerfve 2008). Riley's Hump, a known spawning aggregation site for mutton snapper and other reef fishes (Lindeman et al. 2000; Burton et al. 2005), is only 10 km south of the Dry Tortugas western bank. Recently a group of permit was observed along with several other snapper species (Lutjanidae) in what appeared to be spawning behaviors (Feeley et al., Spawning migration movements of mutton snapper in the Dry Tortugas, Florida: spatial dynamics within a marine reserve network, in review). Environmental

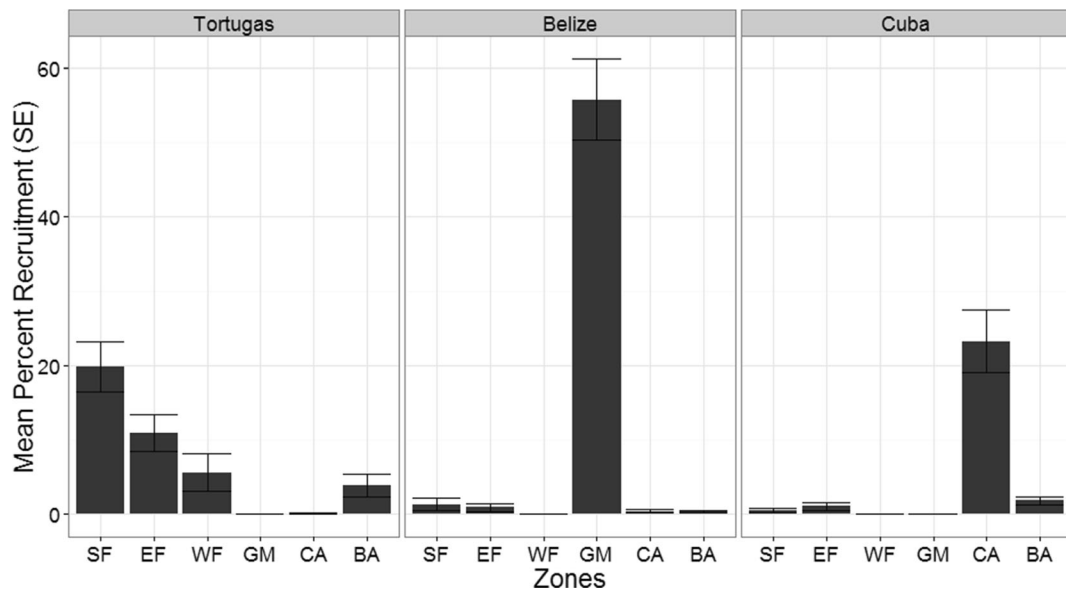
and physical oceanographic conditions present on the western Tortugas bank are similar to those at Riley's Hump, so it is not particularly surprising that permit would also aggregate at that location to spawn.

Earlier research has shown that the oceanographic features in south Florida, including the Florida Current, its associated meanders and eddies, and the Tortugas and Pourtales gyres, foster the retention of Dry Tortugas larvae and facilitate recruitment throughout the Florida Keys coral reef tract (Lee et al. 1992, 1994; Domeier 2004). Our drift simulations further confirmed this notion and allowed us to closely examine seasonal trends in recruitment. Constant year-round releases of simulated "larvae" from the Dry Tortugas region showed a bimodal pattern of recruitment in SF, with spring and late fall peaks. A single mode in recruitment was observed in the fall in EF. These results compared favorably with the empirical CPUE data on juvenile permit for each of the respective zones in Florida.





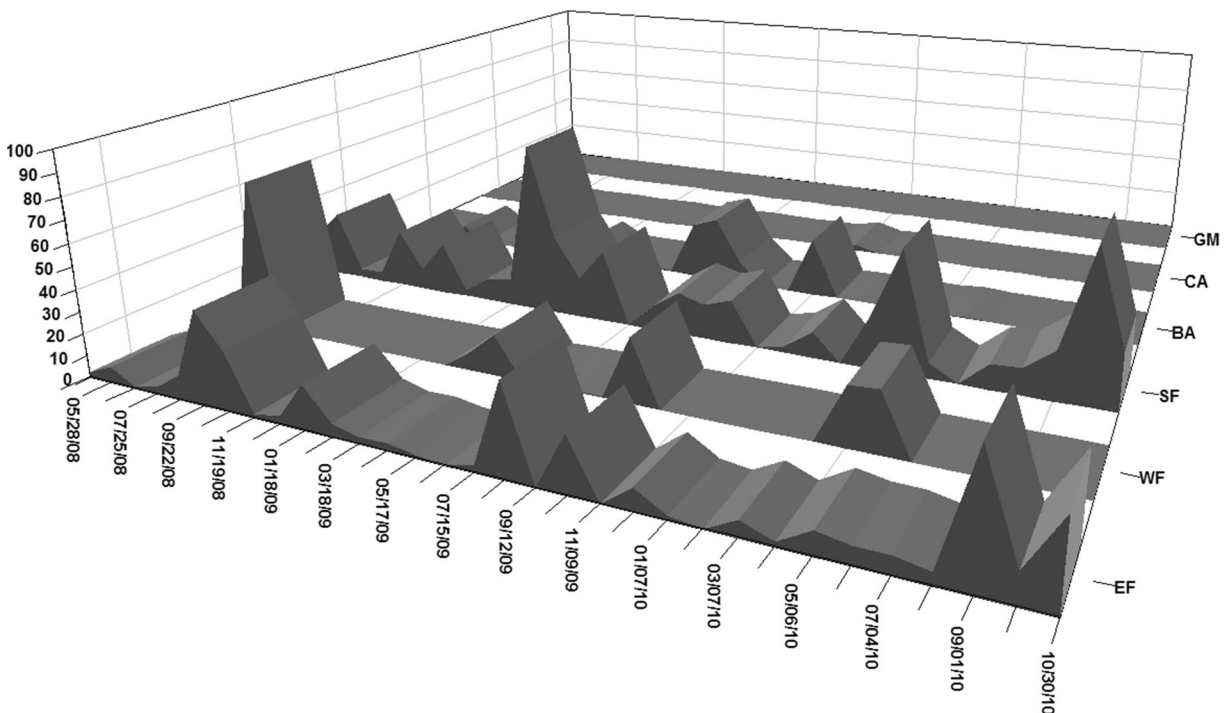
**Fig. 6** Location of larval drift particles after 30 d simulation runs. Release from: **a** Dry Tortugas on Oct. 2010, **b** Belize on Aug. 2008, and **c** Cuba on Oct. 2010



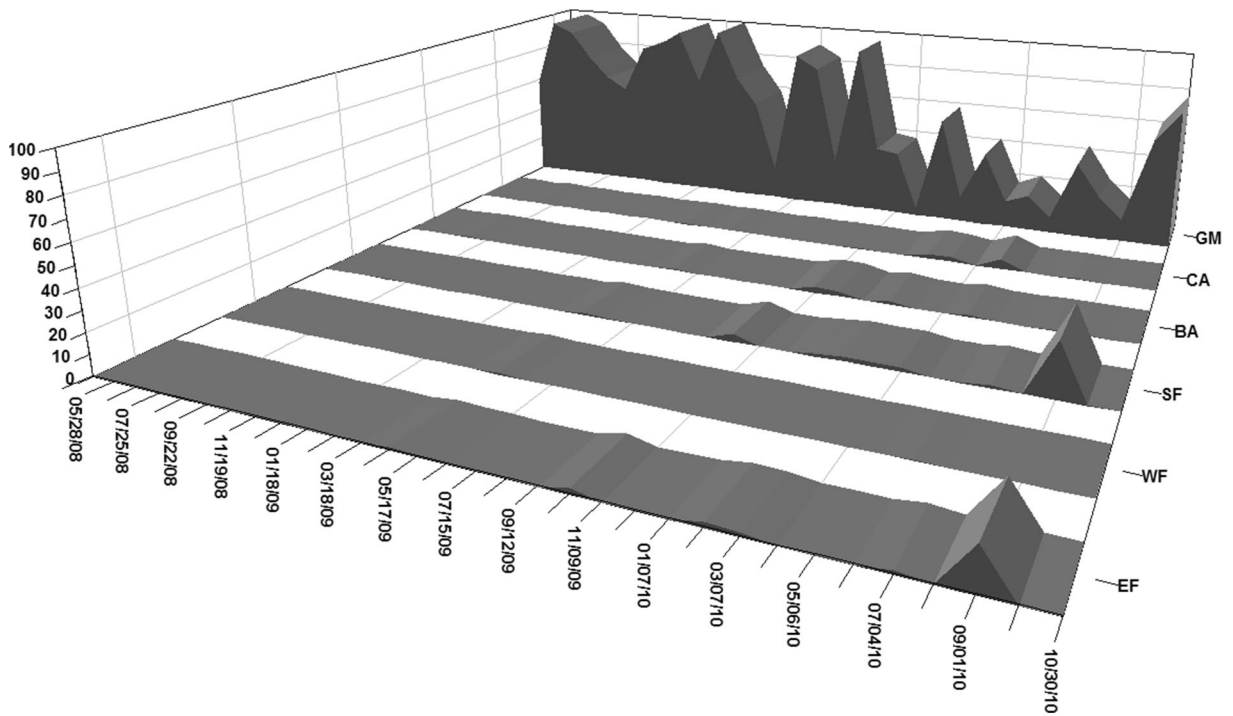
**Fig. 7** Mean percent recruitment (with SE) of simulated particles into six geographical zones from three different spawning locations: South Florida (SF), East Florida (EF), West Florida (WF), Gulf of Mexico and Western Caribbean (GM), Caribbean (CA) and The Bahamas (BA)

We believe this supports the theory that permit recruitment in both SF and EF may be driven by the timing of oceanographic events and intensity of spawning in the Dry Tortugas. Recruitment in WF

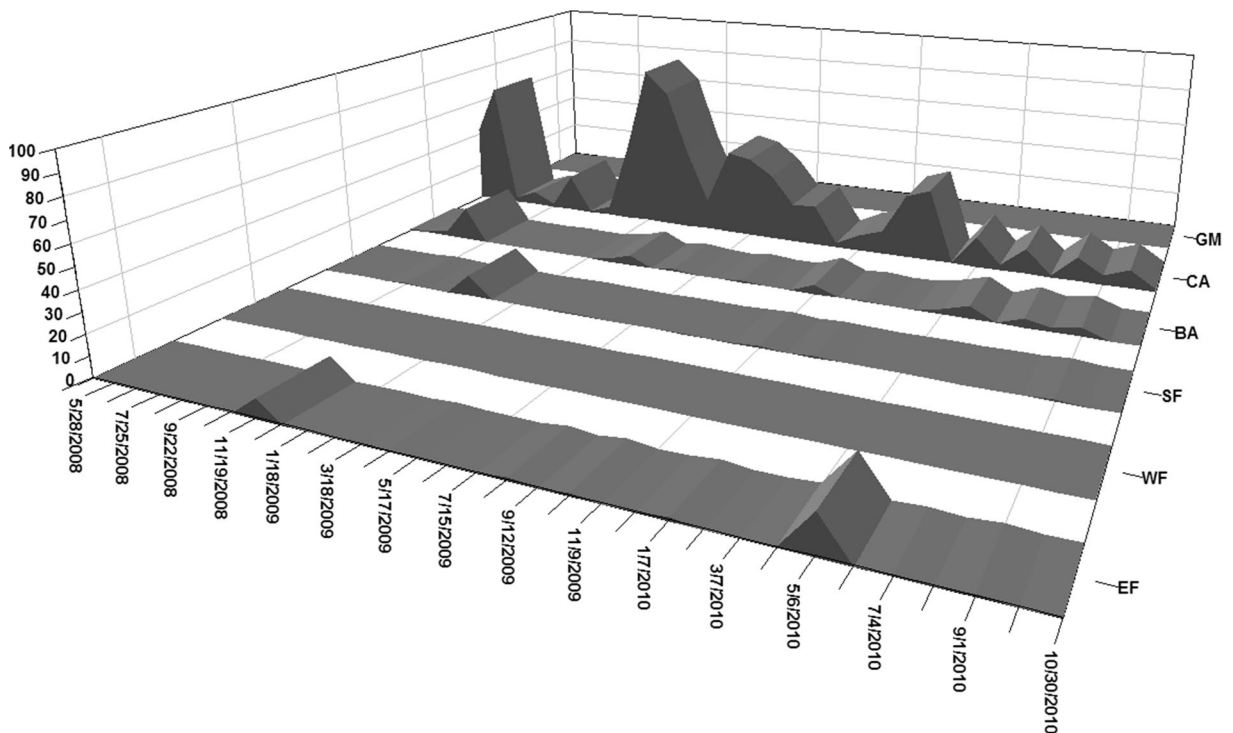
from larvae spawned in the Dry Tortugas, on the other hand, indicated a summer peak as compared to fall for the CPUE data. Along the southern portion of the WF zone and at the more northern sites on the



**Fig. 8** Percent of simulated particles (z axis) recruited in each zone by release date from the Dry Tortugas spawning site. Zone abbreviations: East Florida (EF), West Florida (WF), South Florida (SF), Bahamas (BA), Caribbean (CA), and Gulf of Mexico and Western Caribbean (GM)



**Fig. 9** Percent of simulated particles (z axis) recruited in each zone by release date from the Belize spawning site. Zone abbreviations: East Florida (EF), West Florida (WF), South Florida (SF), Bahamas (BA), Caribbean (CA), and Gulf of Mexico and Western Caribbean (GM)



**Fig. 10** Percent of simulated particles (z axis) recruited in each zone by release date from the Cuba spawning site. Zone abbreviations: East Florida (EF), West Florida (WF), South Florida (SF), Bahamas (BA), Caribbean (CA), and Gulf of Mexico and Western Caribbean (GM)

east and west coasts of Florida, permit recruitment most likely has additional contributions from “other” unknown Florida spawning sites.

The larval drift simulation modeling here emphasized the importance of a focused “local” perspective for Florida fishery management of permit. Recruitment from outside of Florida was estimated to be sporadic and weak, and typically constituted only a very small fraction of ‘larvae’ produced by the spawning permit in Cuba or Belize. Although these infrequent “outside” recruitment events to Florida from the greater Caribbean may ensure apparent genetic homogeneity throughout the region over time-scales that range from centuries to millennia, they likely have little ecological or population dynamic significance to management since these times are only relevant in years to decades. Our conclusions are strikingly similar to those of Paris et al. (2005) who stated that snapper spawning aggregations in Cuba do not significantly contribute recruits to Florida. In addition, Karnauskas et al. (2011) found that spawning sites in Belize had oceanic conditions favorable for retention, rather than dispersion, of larvae. Our work adds to the growing body of scientific literature that indicates the prevalence of self-recruitment in reef fish populations (Cowen et al. 2000; Cowen and Sponaugle 2009; Jones et al. 2009).

Increased knowledge of the timing and location of spawning events, their regional impact on recruitment and how they regulate regional population dynamics is central to effective fishery management (Lindeman et al. 2000). The results presented here demonstrated minor to no apparent larval connectivity between the Florida and the wider Caribbean. This emphasizes the need to consider the regional impacts of Florida fisheries and attendant environmental changes on the long-term sustainability of Florida fishery resources, as has been shown by the importance of the Dry Tortugas for sustainability of Florida coral reef fishes (Ault et al. 2013, 2014). Additionally, this suggests a need for intensified examination and estimation of Florida permit stock abundance, and much closer examination of traditional controls on permit recreational harvests through size, season and bag limits, coupled with more effective controls on the commercial catches that ensure sustainability of this valuable fishery resource. However, the present paucity of required data on the exploited adult population makes it difficult at this time to effectively evaluate the potential performance of such management alternatives. Future research should strive to improve data

assimilation and estimation capabilities to accurately estimate population abundance and size structure to ensure the social and economic benefits of a sustainable permit fishery.

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## References

- Adams AJ, Blewett DA (2004) Spatial patterns of estuarine habitat use and temporal patterns in abundance of juvenile permit, (*Trachinotus falcatus*). *Gulf and Carib Res* 16:129–139
- Adams AJ, Wolfe RK, Kellison GT, Victor BC (2006) Patterns of juvenile habitat use and seasonality of settlement by permit, *Trachinotus falcatus*. *Environ Biol Fish* 75:209–217
- Armstrong MP, Hood PB, Murphy MD, Muller RG (1996) A stock assessment of permit, *Trachinotus falcatus*, in Florida waters. *FL DEP FMRI IHR* 1996-005:50
- Ault JS, Bohnsack JA, Meester GA (1998) A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fish Bull* 96:395–414
- Ault JS, Bohnsack JA, Smith SG, Luo J (2005) Towards sustainable multispecies fisheries in the Florida USA coral reef ecosystem. *Bull Mar Sci* 76:595–622
- Ault JS, Smith SG, Bohnsack JA, Luo J, Harper DE, McClellan DB (2006) Building sustainable fisheries in Florida’s coral reef ecosystem: positive signs in the Dry Tortugas. *Bull Mar Sci* 78:633–654
- Ault JS, Smith SG, Bohnsack JA, Luo J, Zurcher N, McClellan DB, Ziegler TA, Hallac DE, Patterson ME, Feeley MW, Ruttenburg BI, Hunt J, Kimball D, Causey B (2013) Assessing coral reef fish changes and marine reserve dynamics in the Dry Tortugas, Florida USA. *Fish Res* 144:28–37
- Ault JS, Smith SG, Browder JA, Nuttle W, Franklin EC, Luo J, DiNardo GT, Bohnsack JA (2014) Indicators for assessing the ecological and sustainability dynamics of southern Florida’s coral reef and coastal fisheries. *Ecol Indic* 44:164–172
- Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. Monterey, California Sea Grant College System and NOAA



- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Fishery Investigations Series II, vol. 19. Ministry of Agriculture, Fisheries and Food, Lowestoft, UK
- Bohnsack JA, Ault JS (1996) Management strategies to conserve marine biodiversity. *Oceanography* 9:73–82
- Botsford LW, Brumbaugh DR, Grimes C, Kellner JB, Largier J, O'Farrell MR, Ralston S, Soulanille E, Wespestad V (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Rev. Fish Bio. Fish.* 19:69–95
- Brandt ME, Zurcher N, Acosta A, Ault JS, Bohnsack JA, Feeley MW, Harper DE, Hunt J, Kellison GT, McClellan DB, Patterson ME, Smith SG (2009) A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem. Natural Resource Report NPS/SFCN/NRR—2009/150. National Park Service, Fort Collins, Colorado
- Burton ML, Brennan KJ, Muñoz RC, Parker RO Jr (2005) Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas south ecological reserve. *Fish Bull* 103:404–410
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27:477–500
- Chassignet EP, Hurlburt HE, Smedstad OM, Halliwell GR, Hogan PJ, Wallcraft AJ, Baraille R, Bleck R (2007) The HYCOM (Hybrid Coordinate Ocean Model) data assimilative system. *J Mar Syst* 65:60–83
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466
- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287:857–859
- Crabtree RE, Hood PB, Snodgrass D (2002) Age, growth, and reproduction of permit (*Trachinotus falcatus*) in Florida waters. *Fish Bull* 100:26–34
- Cummings JA (2005) Operational multivariate ocean data assimilation. *Quart J Royal Met Soc* 131:3583–3604
- Dahlgren CP, Sobel J (2000) Designing a Dry Tortugas ecological reserve: how big is big enough?... To do what? *Bull Mar Sci* 66:707–719
- Davis GE (1982) A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bull Mar Sci* 32:608–623
- Domeier ML (2004) A potential larval recruitment pathway originating from a Florida marine protected area. *Fish Oceanogr* 13:287–294
- Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. *Bull Mar Sci* 60:698–726
- Félix FC, Spach HL, Moro PS, Schwarz R, Santos C, Hackradt CW, Hostim-Silva M (2007) Utilization patterns of surf zone inhabiting fish from beaches in Southern Brazil. *Panam J Aquat Sci* 2:27–39
- Fields HM (1962) Pompanos (*Trachinotus* spp.) of south Atlantic coast of the United States. *Fish Bull* 62:89–222
- Franklin EC, Ault JS, Smith SG, Luo J, Meester GA, Diaz GA, Chiappone M, Swanson DW, Miller SL, Bohnsack JA (2003) Benthic habitat mapping in the Tortugas region, Florida. *Mar Geo* 26:19–34
- Frattoni PS, Lee TN, Podesta GP, Muller-Karger FE (1998) The influence of loop current perturbations on the formation and evolution of Tortugas eddies in the southern straits of Florida. *J. Geo. Res.* 103:24759–24779
- García-Cagide A, Claro R, Koshelev BV (2001) Reproductive patterns of fishes of the Cuban shelf. In: Claro R, Lindeman KC, Parenti LR (eds) *Ecology of the marine fishes of Cuba*. Smithsonian Institution Press, Washington DC, pp. 73–114
- Graham RT, Castellanos DW (2005) Courtship and spawning behaviors of carangid species in Belize. *Fish Bull* 103:426–432
- Heyman DH, Kjerfve B (2008) Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit. *Belize Bull Mar Sci* 83:531–551
- IGFA (2015) IGFA world record game fishes: freshwater, saltwater and flyfishing. International Game Fish Association, Dania Beach, Florida
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307–325
- Jory DE (1986) An incident of predation on queen conch, *Strombus gigas* L. (mollusca, strombidae), by Atlantic permit, *Trachinotus falcatus* L. (Pisces, carangidae). *J Fish Biol* 28:129–131
- Karnauskas M, Chérubin LM, Paris CB (2011) Adaptive significance of the formation of multi-species fish spawning aggregations near submerged caps. *PLoS ONE* 6: e22067
- Lee TN, Williams E (1999) Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bull Mar Sci* 64:35–56
- Lee TN, Rooth C, Williams E, McGowan M, Szmant AF, Clarke ME (1992) Influence of Florida current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. *Cont Shelf Res* 12:971–1002
- Lee TN, Clarke ME, Williams E, Szmant AF, Berger T (1994) Evolution of the Tortugas gyre and its influence on recruitment in the Florida Keys. *Bull Mar Sci* 54:621–646
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282–297
- Lindeman KC, Pugliese R, Waugh GT, Ault JS (2000) Developmental pathways within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bull Mar Sci* 66:929–956
- Mann KH, Lazier JRN (2005) *Dynamics of marine ecosystems: biological-physical interactions in the ocean*, 3rd edn. Blackwell Publishing, London
- Meester GA, Mehrotra A, Ault JS, Baker EK (2004) Designing marine reserves for fishery management. *Manag Sci* 50: 1031–1043
- Mullin MM (1993) Webs and scales: physical and ecological processes in marine fish recruitment. Books in recruitment fishery oceanography. Washington Sea Grant Program, Seattle
- Olson DB (2001) Biophysical dynamics of western transition zones: a preliminary synthesis. *Fish Oceanogr* 10:133–150
- Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (lutjanidae)

- spawning aggregations based on biophysical modeling. *Mar Ecol Prog Ser* 296:93–106
- Robins CR, Ray GC, Douglas J (1986) A field guide to Atlantic coast fishes. The Peterson Field Guide Series. Houghton Mifflin Co., Boston
- Rothschild BJ (1986) Dynamics of marine fish populations. Harvard University Press, Cambridge
- Sammarco PW, Heron ML, eds (1994) The bio-physics of marine larval dispersal. Coastal and Estuarine Studies 45. American Geophysical Union. Washington, DC.
- Secor DH, Dean JM (1992) Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. *Can J Fish Aquat Sci* 49:1439–1454
- Smith SG, Ault JS, Bohnsack JA, Harper DE, Luo J, McClellan DB (2011) Multispecies survey design for assessing reef-fish stocks, spatially-explicit management performance, and ecosystem condition. *Fish Res* 109:25–41
- Smith-Vaniz WF (2002) Carangidae. In: Carpenter KE (ed) The living marine resources of the western central Atlantic. Volume 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals. FAO, Rome, pp 1426–1468
- Snodgrass D, Harnden CW (2009) Composition of fish species on ocean-side beach habitats in the Florida Keys. *Fl Sci* 72:153–170
- Sponaugle S, Lee T, Kourafalou V, Pinkard D (2005) Florida current frontal eddies and the settlement of coral reef fishes. *Limnol Oceanogr* 50:1033–1048
- Stommel H (1976) The Gulf Stream: a physical and dynamical description, 2nd edn. University of California Press, Berkeley