

Preliminary Examination of How Human-driven Freshwater Flow Alteration Affects Trophic Ecology of Juvenile Snook (*Centropomus undecimalis*) in Estuarine Creeks

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Abstract Maintaining proper freshwater and marine inputs is essential for estuarine function. Alteration of freshwater flows into small tributaries that traverse the upland-estuarine margin may be especially problematic, e.g., by impacting the nursery areas for juvenile finfish and shellfish. We used stomach contents and stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) to examine effects of freshwater flow alterations on the trophic ecology of juvenile common snook (*Centropomus undecimalis*) in four mangrove creeks with different freshwater flow regimes. Diet diversity in less degraded creeks was greater than in more degraded creeks, and the importance (by % mass) of the top three preys was disproportionately higher in the more degraded creeks. Stable isotope measures of trophic diversity corroborate these trends, suggesting higher intraspecific trophic diversity in less degraded creeks. The difference in diet diversity of juvenile snook may be an indicator of an overall change in ecosystem function and these shifts in food web

structure may affect the rate that juveniles of this and other species with similar habitat requirements successfully join the adult population.

Keywords Food web · Freshwater flow alteration · Intraspecific niche variation · Juvenile fish · Lavage · Trophic ecology

Introduction

Collapse of estuarine and marine fisheries is increasingly acknowledged as one of the gravest global environmental crises (Pauly et al. 1998; Worm et al. 2006). The two primary anthropogenic impacts driving fishery collapse are over-exploitation and habitat loss or degradation (Lotze et al. 2006). In estuarine ecosystems, maintaining the proper balance of freshwater and marine inputs is essential for proper ecosystem function. Habitat degradation through disruption of this hydrologic connectivity (sensu Pringle 2006), e.g., by altering the magnitude or dynamics of freshwater flow into estuaries, may be one of the primary mechanisms through which estuarine fisheries are affected (Layman et al. 2007a).

Anthropogenic alterations of freshwater flows into estuaries are of particular importance to ecosystem function because of potential impacts to the ecological interactions among constituent species within the systems (Sklar and Browder 1998; reviewed in Beach 2002). Whereas some organisms can tolerate wide ranges in salinity, many species have relatively narrow salinity tolerances and remain in a preferred salinity range (Montague and Ley 1993; Sklar and Browder 1998). The increase in impervious surfaces and loss of wetland habitats (both due to coastal development) alter the source, timing, and velocity of freshwater flows

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and thus influence salinity patterns (Sklar and Browder 1998). When >10% of a watershed's acreage is converted to impervious surface, the water bodies can become seriously degraded and may be characterized by losses of faunal diversity, productivity, and overall stability (reviewed in Beach 2002). In the United States, 25% of coastal habitats are expected to be developed by 2025 (Beach 2002) and with increasing coastal development worldwide there is an exigent need to understand how alterations to watersheds and freshwater inflows can impact coastal fishes.

Freshwater flows are especially important to small tributaries that traverse the margin between uplands and estuaries. Oligohaline creeks that serve as estuarine tributaries are important habitats for many juvenile finfish and shellfish (Peters et al. 1998; Baltz et al. 1998; Geary et al. 2001; Poulakis et al. 2002). For example, recruitment of common snook (*Centropomus undecimalis*) larvae to creeks coincides with the wet season, when they are able to utilize higher water inflows to access shallow creeks and the surrounding flooded littoral zone. Likewise, many resident fishes and invertebrates (that are potential prey for juvenile snook) have evolved life history strategies to respond to freshwater flows and associated salinity changes.

In this study, we examined the diet and trophic ecology of juvenile snook in four mangrove creeks that experience different levels of freshwater flow alteration. We tested the hypothesis that juvenile snook diet differs among creek types (H_0 : juvenile snook diet does not differ among creek types). We used non-lethal lavage to collect stomach contents to document instantaneous diet composition and stable isotope analysis to examine juvenile snook trophic ecology as reflected by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. These data provide both "snap-shot" and time-integrated insights into the diet of this important coastal predator species.

Materials and Methods

Study Location

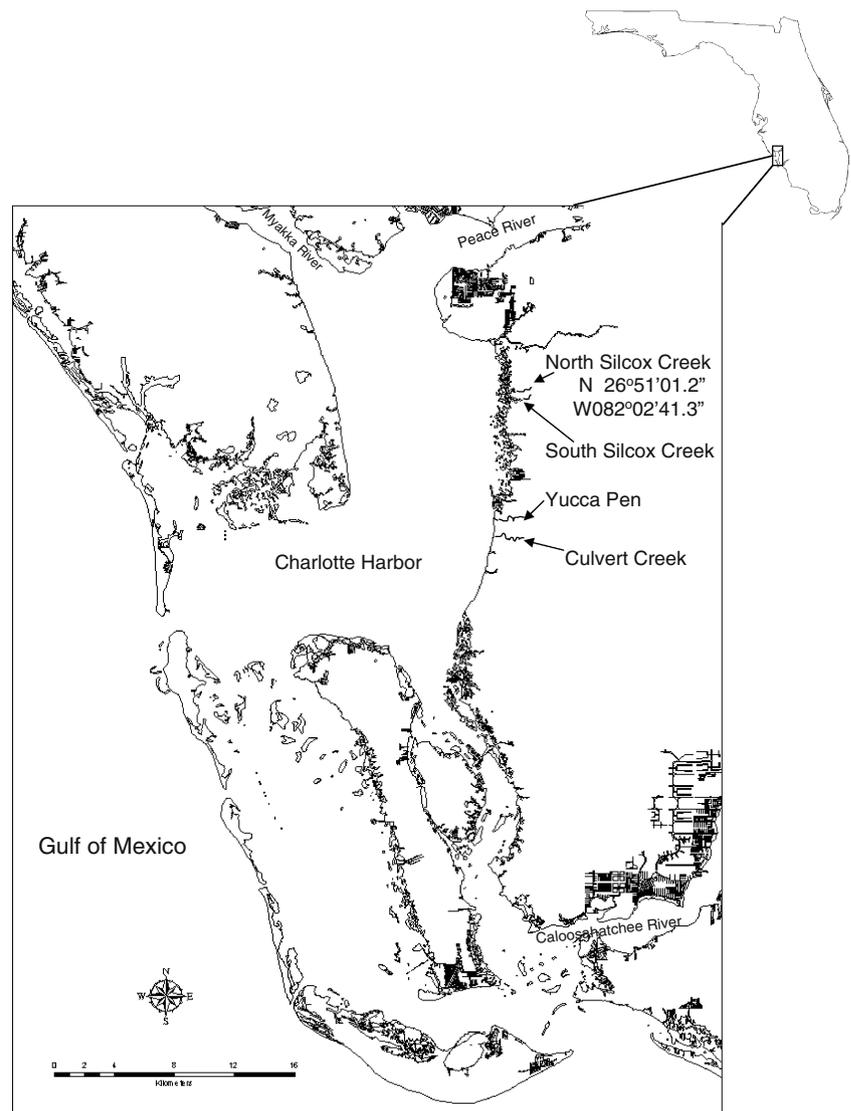
Charlotte Harbor is a 700 km² coastal plain estuarine system in southwest Florida, USA (Hammet 1990; Fig. 1). The Peace, Myakka, and Caloosahatchee rivers, as well as many smaller creeks throughout the drainage, transport large amounts of fresh water into the harbor. The harbor is connected to the Gulf of Mexico through Boca Grande Pass, San Carlos Bay, and three smaller inlets. The climate of Charlotte Harbor is subtropical; mean seasonal water temperatures range from 12° to 36°C, and freezes are infrequent (Poulakis et al. 2003). Seagrass flats (262 km² total coverage, Sargent et al. 1995) and mangrove shorelines (143 km² total coverage; L. Kish, Florida Fish and Wildlife Research Institute, unpublished data) are common

habitats within the estuary, with >80% of mainland shorelines under protection (i.e., no habitat alteration allowed) (R. Repenning, Florida Department of Environmental Protection, personal communication; Hammet 1990). Despite the high level of shoreline protection, anthropogenic development is extensive in certain areas of the watershed and this has altered freshwater flow patterns.

Four mangrove-fringed estuarine creeks, each ~2 km long, on the eastern shoreline of Charlotte Harbor, FL (Fig. 1), were sampled regularly from June through November 2007. For the purposes of this study, two creeks were considered 'less degraded' and two creeks 'more degraded' based upon creek morphology and alterations of freshwater flows within creek watersheds. These watershed alterations are not the extreme urbanization that has occurred in some locations, rather alterations that influence freshwater flows into the creeks such as roads, houses, ditches, and berms that change freshwater flow patterns. The two northernmost creeks (North Silcox Creek and South Silcox Creek; Fig. 2a) were considered 'less degraded'. Creek drainage morphology remains largely intact except for remnant mosquito ditches (compared to 1953 aerial photos). The immediate drainages remain largely undeveloped: the closest road to the creek head (point where the creek can no longer be traveled on foot, and where the creek can no longer be traced using aerial imagery) is 1.9 km for North Silcox and 2.1 km for South Silcox; there are four buildings within 2 km of the North Silcox creek head and three buildings within 2 km of the South Silcox creek head. Other than these land alterations, the watersheds are unaltered. Creek widths range from 2 m in narrow passes to >60 m in wider bays, depth is shallow (<0.5 m except in narrow passes where depths reach 1 m), shorelines are lined entirely by red mangroves *Rhizophora mangle*, and substrate is mixed mud and sand. Submerged aquatic vegetation (primarily shoal grass, *Halodule wrightii*) occurs sporadically throughout the creeks.

The two southern creeks (Yucca Pen and Culvert Creek; Fig. 2b), located 16 km south of the natural creeks, are considered 'more degraded', as their upland drainages and wetlands have been altered for development, altering freshwater flow regimes. In contrast to the less degraded creeks, the immediate creek watersheds are more impacted by roads and houses: the distance from creek head to nearest road is 0.1 km for Yucca Pen and 0 km for Culvert Creek; a housing development with >100 houses begins within 0.5 km of the Yucca Pen creek head, and the Culvert Creek watershed contains >25 houses and a network of roads and containment ponds within 2 km of the creek head. The altered flow regimes cause short, pulsing hydroperiods with concentrated overland sheet flow. The bottoms are mostly hard sand and the submerged aquatic vegetation (*H. wrightii*) is patchy and limited to the lower two-thirds

Fig. 1 Locations of study creeks in Charlotte Harbor, Florida (USA)



of the creeks because of extended periods of low salinity during freshwater runoff periods (Doering and Chamberlain 2000; Ridler et al. 2006). The creeks are narrow (mean = 5 m) for the upper two-thirds and have wider bays (60 m) in their extreme lower portions. Narrow sections are scoured to >2 m depth with undercut banks (presumably due to high flows during freshwater runoff events) and reduced width of the intertidal mangrove prop root habitat.

Anthropogenic coastal development is patchy and variable and is affected by a host of factors, including local and state land planning, environmental protections, infrastructure (roads, sewer, etc), and private vs. government land holdings. Therefore, the impacts of coastal habitat alterations are also patchy, which generally precludes a completely random sample design. This is the case in Charlotte Harbor, where coastal habitats are a patchwork of developed and conservation lands. This patchy nature of coastal development and conservation is reflected in the

sites used in this study—the creek types (less degraded vs. more degraded) are confounded by latitude in that creeks of similar quality are near to one another. However, each creek has a unique watershed that sets the creeks apart (i.e., they are not impacted by the same anthropogenic habitat alteration), which reduces confounding effects of creek locations. Moreover, all four creeks are within the same estuarine hydrological zone (Poulakis et al. 2003), so are unlikely to differ in larval supply or other hydrologically mediated influences from the estuary.

Stomach Content and Tissue Collection

Juvenile snook between 120 and 346 mm standard length (SL) (mean = 242.13, SD = 48.4) were captured by center bag seines (22×1.2 m, 3.2 mm mesh; 30×1.8 m, 25 mm mesh) from June through November 2007. Snook in this size range were sampled because individuals <120 mm

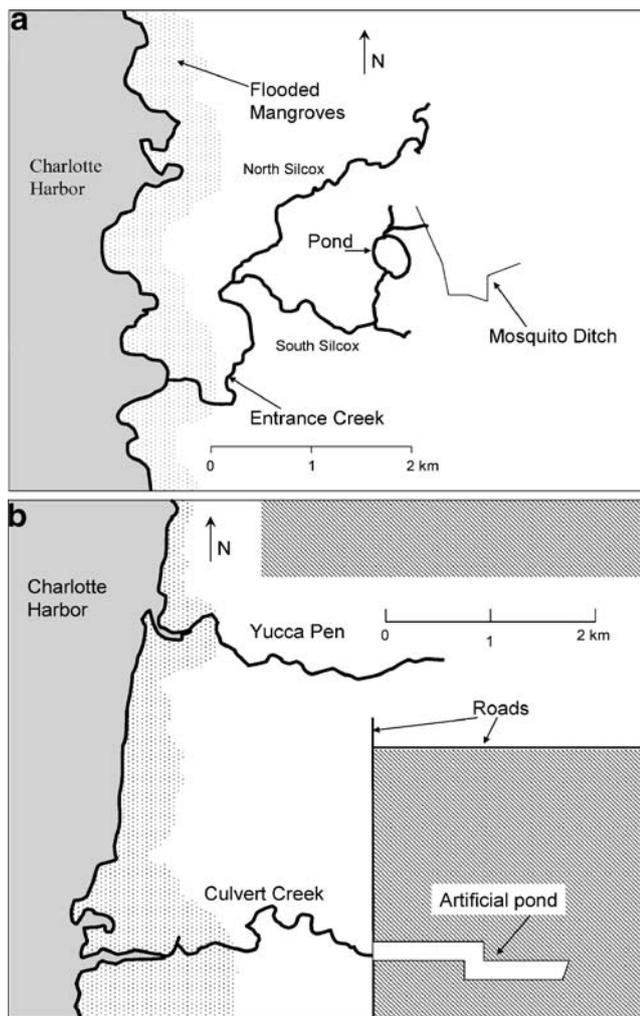


Fig. 2 Diagrams of study creeks (**a** North Silcox and South Silcox = less degraded; **b** Yucca Pen, Culvert Creek = more degraded) showing artificial ponds and altered portions of upland drainages. Heavy stippling in (**b**) denotes land altered by development

experience negative effects of lavage (e.g., distended abdomens and loss of equilibrium after release), and snook >350 mm are no longer creek residents (i.e., they inhabit creeks as well as habitats of the open estuary (Stevens et al. 2007), and are infrequently captured by sampling within creeks (AJA, unpublished data)). A semi-flexible plastic tube was inserted down the esophagus into the stomach of each snook and creek water was pumped into the stomach with a small, submersible pump to force out the stomach contents. Fish were held in a head-down position during lavage to enhance regurgitation. Stomach contents were stored in sealed plastic bags on ice and transferred to 70% ethanol upon return to the lab. To determine efficiency of the lavage procedure (what portion of stomach contents remain in stomachs after the procedure), 34 snook were retained after

lavage and stored on ice. Their stomachs were later removed and stored in 70% ethanol. Once lavage was completed, a 15-mm equilateral triangle (~5 mg) of the soft tissue from the second dorsal fin was removed with scissors and stored in small, sealed, plastic bags on ice. The tissue samples were frozen until processing for stable isotope analysis. All fish, except those retained to test the efficacy of lavage, were released at the site of capture.

Stomach Contents

Stomach contents for each fish were identified to the lowest possible taxon and enumerated. To obtain weights, stomach contents of each fish were separated by taxon, placed into foil trays, and dried in an oven for 12 h at 77°C. Data were used to estimate diet composition of juvenile snook separately for each study creek by frequency of occurrence (F = number of stomachs in which the prey item occurred), percent abundance (N = number of individuals of the prey item divided by the total number of prey items), and percent weight (W = weight of a prey type divided by total weight of all prey types). A Relative Importance Index (RI) (George and Hadley 1979) was calculated as a way to reduce the amount of bias from using N , F , or W alone:

$$RI = 100 * AI_i / \sum AI_i,$$

Where AI_i (Absolute Index of prey taxon i) = $N_i + W_i + F_i$.

Shannon diversity index (H'), evenness (J') (Zar 1984), and species richness of stomach contents were also calculated for each creek based upon prey abundance in juvenile snook stomachs.

Similarity matrices were constructed with Bray–Curtis similarity coefficients generated from square-root transformed percent prey weight data to compare juvenile snook diet among creeks. Percent prey weight data were used in the among-creek comparison because weight most closely approximates the energetic importance of the prey items.

Stable Isotope Analysis

Whereas stomach content analysis provides “snap-shot” characterizations of individuals’ diets, stable isotope analysis allows for time- and space-integrated representations of trophic role (Post et al. 2007; Bearhop et al. 2004; Layman et al. 2007a). This approach to the study of a population’s niche has proven to be a valuable tool in examining impacts of anthropogenic habitat alterations, largely because an organism’s diet reflects a broad suite of local abiotic and biotic conditions (e.g., Campbell et al. 2003; Layman et al. 2007b). Applications of stable isotope ratios in studies of trophic ecology take advantage of natural variation in stable isotope ratios and the underlying aspects of a species’ trophic niche which the variation reflects. For nitrogen, the

ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}\text{N}$) exhibits stepwise enrichment with trophic transfers and is a powerful tool for estimating the relative trophic position of organisms (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002). Ratios of carbon isotopes ($\delta^{13}\text{C}$) vary substantially among primary producers with different photosynthetic pathways (e.g., C3 vs. C4 plants), but change little with trophic transfers (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). Therefore, $\delta^{13}\text{C}$ can be used to determine ultimate sources of dietary carbon.

Fin clips (~5 mg) of dorsal fin tissue were immediately placed on ice in the field and later frozen for subsequent preparation at Florida International University. Samples were dried for >48 h at 40–50°C and ground into a fine powder. Approximately 1.5 mg of each powdered sample was analyzed on a ThermoFinniganDeltaPlus at the Yale Earth System Center for Stable Isotopic Studies. All stable isotope values are reported in the δ -notation where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1,000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Global standard for $\delta^{13}\text{C}$ is PeeDee belemnite and for $\delta^{15}\text{N}$ is atmospheric nitrogen. Since C/N ratios of all samples were relatively low (mean \pm SD, 3.5 ± 0.2) no lipid corrections were necessary (Post et al. 2007). One-way ANOVA on ranks was used to compare mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of individuals among sites.

We depict all individual snook in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 2-D “trophic niche space” following Layman et al. (2007a). Quantitative metrics based on dispersion of individuals in niche space can reveal important aspects of intraspecific niche variation (Layman et al. 2007a, b), especially when interpretations are made in conjunction with direct diet data (Layman and Post 2008). We used the “mean distance to centroid” metric (hereafter *CD*) of Layman et al. (2007a). This value is calculated as the average Euclidean distance of each individual in a population to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ centroid, where the centroid is the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all individuals in a population. This metric provides a measure of the average degree of trophic diversity within a sample. *CD* is influenced by dispersion along both the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ axes, but is less sensitive to sample size than other metrics used to represent trophic diversity within a population (Layman et al. 2007b).

Results

Lavage Efficiency

Thirty-four juvenile snook were sacrificed after lavage (eight from North Silcox, 12 from South Silcox, seven from Yucca Pen, and six from Culvert Creek), and their stomachs examined for any potential contents that had not been regurgitated. Of these fish, 16 had no lavage contents (i.e.,

their stomachs appeared to be empty). Upon dissection, all fish had empty stomachs (regardless of whether there were contents collected during lavage), suggesting that lavage is a suitable procedure for examining juvenile snook stomach contents.

Stomach Contents

Between June and November 2007, stomach contents were collected via lavage from 123 juvenile snook. Of these lavaged fish, 86 (69.9%) had contents in their stomachs. When examined by creek: 34 total fish were lavaged in North Silcox, of which 24 contained prey; 38 in South Silcox (33 contained prey); seven in Yucca Pen (all contained prey), and 44 in Culvert Creek (22 contained prey) (Table 1). Sampling effort in Yucca Pen was at least as extensive as other creeks, but there were few juvenile snook in Yucca Pen during the project period (perhaps also reflecting human impact to the watershed).

Snook stomachs contained a total of 26 prey groups, dominated by teleost fishes and crustaceans. Prey group richness of stomach contents differed among creeks, with more prey groups utilized by juvenile snook in North Silcox (19) and South Silcox (16) than in Yucca Pen (nine) or Culvert Creek (eight). Prey diversity, as estimated by the Shannon diversity index, was also higher in North Silcox ($H' = 0.94$) and South Silcox (0.96) than Yucca Pen (0.70) and Culvert Creek (0.65). Prey evenness was highest in South Silcox ($J = 0.79$), followed by Yucca Pen (0.74), North Silcox (0.73), and Culvert Creek (0.72). Diet diversity of Yucca Pen must be treated with caution because of the low sample size ($n = 7$ snook lavaged). However, sample sizes were sufficiently large in the other creeks, so the trend of greater diet diversity in less degraded creeks appears valid. Among-creek diet differences were not due to snook size, since sizes of sampled snook were not significantly different (Kolmogorov–Smirnov test, $p > 0.05$ for all paired tests: North Silcox mean = 239.41 mm standard length, SD = 17.14; South Silcox mean = 245.43, SD = 33.07; Culvert Creek mean = 239.97, SD = 35.87; and Yucca Pen mean = 246.58, SD = 12.91). The top five (all creeks combined) prey items ranked by the Relative Importance (RI) index were: (1) unidentified teleostei, (2) *Poecilia latipinna* (sailfin molly) (3) *Menidia* spp. (silversides), (4) *Palaemonetes* spp. (grass shrimp), and (5) *Lucania parva* (rainwater killifish) (Table 1). At least three of these prey groups were found in the top five for each creek. Among creeks, the sum RI of the top three prey was higher for more degraded creeks: Culvert Creek = 81.6% of RI; Yucca Pen = 76.9%; North Silcox = 53.4%; and South Silcox = 50.3%.

Overall rank order of percent weight of prey, which indicates the energetic importance of prey in the diet, was

Table 1 Summary of prey items found in stomachs of juvenile snook lavaged in four mangrove study creeks of Charlotte Harbor, FL, USA ($n=123$)

Species	North Silcox					South Silcox					Yucca Pen					Culvert Creek					Total				
	N	W	F	RI	R	N	W	F	RI	R	N	W	F	RI	R	N	W	F	RI	R	N	W	F	RI	R
Unk. Teleostei	21.6	9.6	24.2	18.5	2	35.4	25.4	32.3	31.0	1	41.2	21.3	33.3	31.9	1	36.4	10.9	30.2	25.8	2	30.1	14.2	29.1	24.5	1
<i>Poecilia latipinna</i>	4.5	26.2	9.1	13.3	3	1.5	7.0	3.1	3.9	8	26.5	46.6	20.0	31.0	2	32.3	63.3	27.9	41.2	1	11.3	31.1	12.2	18.2	2
<i>Menidia spp.</i>	29.6	23.0	12.1	21.6	1	10.8	10.2	7.7	9.5	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.8	13.5	6.9	12.1	3
<i>Palaemonetes spp.</i>	10.6	3.9	9.1	7.9	4	3.8	1.9	6.2	4.0	7	14.7	20.5	6.7	14.0	3	19.2	6.0	18.6	14.6	3	10.8	4.5	10.1	8.5	4
<i>Lucania parva</i>	5.5	3.9	7.6	5.7	6	12.3	7.8	9.2	9.8	2	0.0	0.0	0.0	0.0	0.0	3.0	1.5	4.7	3.1	5	6.5	4.2	6.9	5.9	5
<i>Brachyura</i>	0.5	0.2	1.5	0.7	18	6.9	5.8	13.8	8.8	4	2.9	0.4	6.7	3.3	8	2.0	0.7	4.7	2.5	6	2.8	1.7	6.9	3.8	6
<i>Gambusia holbrooki</i>	12.6	3.7	3.0	6.4	5	0.0	0.0	0.0	0.0	0.0	2.9	2.2	6.7	3.9	6	0.0	0.0	0.0	0.0	0.0	5.6	2.1	1.6	3.1	7
<i>Eucinostomus spp.</i>	1.5	9.8	3.0	4.8	7	1.5	1.1	1.5	1.4	15	2.9	1.4	6.7	3.7	7	0.0	0.0	0.0	0.0	0.0	1.3	5.0	2.1	2.8	8
<i>Dendrobranchiata</i>	3.0	1.1	6.1	3.4	8	4.6	0.9	4.6	3.4	10	0.0	0.0	0.0	0.0	0.0	2.0	0.4	2.3	1.6	8	3.0	0.8	4.2	2.7	9
<i>Sesarma spp.</i>	0.5	1.6	1.5	1.2	16	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	11.1	9.3	8.1	4	1.1	3.4	2.6	2.4	10
<i>Cyprinodon variegatus</i>	1.5	3.7	3.0	2.7	10	1.5	2.4	1.5	1.8	14	0.0	0.0	0.0	0.0	0.0	1.0	2.4	2.3	1.9	7	1.3	3.0	2.1	2.1	11
<i>Microgobius gulosus</i>	1.0	2.1	3.0	2.1	11	3.8	5.5	1.5	3.6	9	2.9	3.3	6.7	4.3	5	0.0	0.0	0.0	0.0	0.0	1.7	2.5	2.1	2.1	12
Gobiidae	0.0	0.0	0.0	0.0	0.0	6.2	5.6	7.7	6.5	6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	1.9	2.6	2.1	13
<i>Adinia xenica</i>	0.0	0.0	0.0	0.0	0.0	5.4	15.4	1.5	7.4	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	3.8	0.5	2.0	14
<i>Fundulus grandis</i>	1.0	5.4	3.0	3.1	9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	2.6	1.1	1.4	15
<i>Fundulus spp.</i>	0.0	0.0	0.0	0.0	0.0	0.8	5.1	1.5	2.5	13	2.9	0.4	6.7	3.3	9	0.0	0.0	0.0	0.0	0.0	0.4	1.3	1.1	0.9	16
Unk Invertebrata	0.0	0.0	0.0	0.0	0.0	3.8	0.1	4.6	2.8	11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	1.6	0.9	17
<i>Fundulus confluentus</i>	2.0	0.7	3.0	1.9	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.3	1.1	0.8	18
<i>Farfantepenaeus duorarum</i>	1.5	0.8	3.0	1.8	13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	1.1	0.7	19
Clupeidae	0.0	0.0	0.0	0.0	0.0	0.8	5.1	1.5	2.5	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.3	0.5	0.7	20
<i>Uca spp.</i>	0.5	2.0	1.5	1.3	15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.9	0.5	0.6	21
Isopoda	1.0	0.3	3.0	1.4	14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.1	1.1	0.5	22
<i>Eucinostomus harengulus</i>	1.0	0.8	1.5	1.1	17	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.5	0.5	23
<i>Fundulus similis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	3.9	6.7	4.5	4	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.5	0.3	24
<i>Anchoa spp.</i>	0.5	0.1	1.5	0.7	19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.5	0.3	25
Amphipoda	0.0	0.0	0.0	0.0	0.0	0.8	0.0	1.5	0.8	16	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.5	0.2	26
Detritus	*	*	1.3	*	*	*	*	0.8	*	*	*	*	0.0	*	*	*	*	0.0	*	*	*	*	0.0	*	*
Shannon-Wiener Diversity	0.94					0.96					0.7					0.65					1.01				
Evenness	0.73					0.79					0.74					0.72					0.72				
Number of snook sampled	34					38					7					44					123				
Number of full stomachs	24					33					7					22					86				

Values calculated separately for each creek, except for Total, which is all creeks combined. Detritus was only recorded by frequency of occurrence and was not used in calculations because it was ingested incidentally during feeding

N percent numerical abundance, W percent weight, F percent frequency of occurrence in stomachs, RI Relative Importance ($RI = (N + W + F) / (\Sigma(N + W + F))$) (George and Hadley 1979), R rank order by Relative Importance

* Detritus was considered a byproduct of feeding, and not a food source. Its presence was noted, but it was not included in calculations of diet variables.

dominated by prey that were typically larger in body size but less common numerically. The five highest (all creeks combined) categories by percent weight were (1) *L. parva*, (2) unidentified Dendrobranchiata (shrimp), (3) *Cyprinodon variegatus* (sheepshead minnow) (4) *Fundulus confluentus* (marsh killifish), and (5) *Farfantepenaeus duorarum* (pink shrimp). *L. parva* and unidentified Dendrobranchiata were among the top five prey categories by weight in all four creeks. Similarity analysis (based on percent weight of prey) showed a distinct grouping, with North Silcox and South Silcox grouping together and Yucca Pen and Culvert Creek grouping together (Fig. 3), suggesting diet differences among creeks.

Stable Isotopes

Eighty-four fin clips were processed for stable isotope analysis (n : North Silcox=10; South Silcox=10; Culvert Creek=62; Yucca Pen=2). Fin tissue samples were taken from numerous juvenile snook that were captured and released as part of an ongoing tag–recapture study. Some of these juvenile snook were not lavaged; therefore, sample sizes for stomach contents and stable isotopes differ. Because of low sample size, Yucca Pen samples were excluded from further analysis. Individual values were quite variable; for example, in Culvert Creek, individuals ranged over 8.5‰ in $\delta^{13}\text{C}$ and 2.6‰ in $\delta^{15}\text{N}$ (Fig. 4). Among the three sites, mean $\delta^{13}\text{C}$ signatures differed significantly ($H=8.5$, $df=2$, $p=0.014$) with $\delta^{13}\text{C}$ of individuals more depleted in the less degraded habitats (means: Culvert Creek=-18.2, North Silcox=-19.7, South Silcox=-21.0). There was no significant difference in $\delta^{15}\text{N}$ among sites (means: Culvert Creek=7.8, North Silcox=8.1, South Silcox=8.0; $H=1.9$, $df=2$, $p=0.38$). There was a clear trend

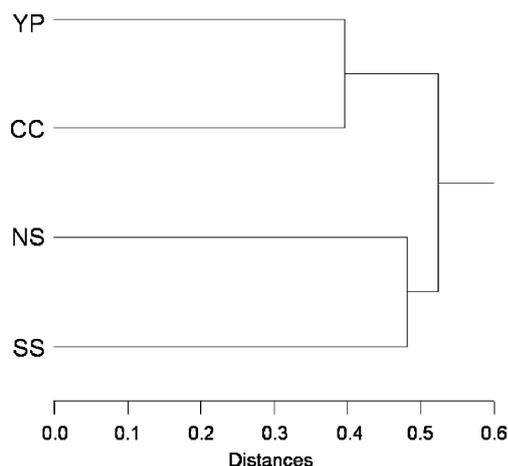


Fig. 3 Dendrogram depicting results of the similarity matrices constructed with Bray–Curtis similarity coefficients generated from square-root transformed percent prey weight data to compare juvenile snook diet among creeks

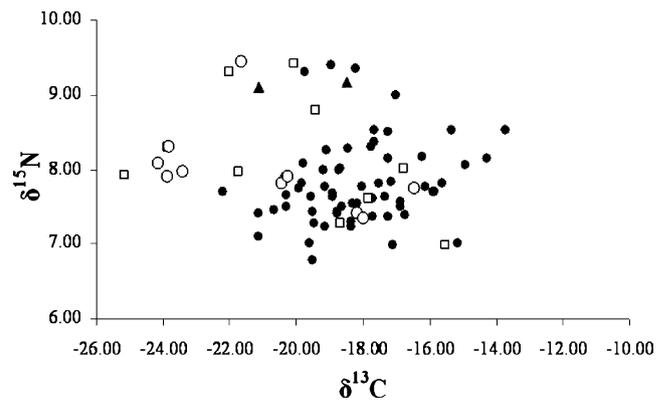


Fig. 4 Figure showing results of stable isotope analysis, shown in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 2-D “trophic niche space”. Each symbol represents an individual juvenile snook. Clear symbols represent ‘less degraded’ creeks (clear square North Silcox Creek, clear circle South Silcox Creek) and solid symbols represent ‘more degraded’ creeks (solid circle Culvert Creek, solid triangle Yucca Pen)

toward greater CD values in less degraded habitats: North Silcox=2.7, South Silcox=2.5, and Culvert Creek=1.6. This suggests greater intra-individual diet variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the less degraded creeks.

Discussion

All variables examined in this study point to a more diverse diet for juvenile snook in the less degraded creeks. This trend is maintained even if Yucca Pen is removed from consideration because of low sample size. When the other creeks are compared, sample sizes are similar for the less degraded creeks (North Silcox (34 juvenile snook sampled, 24 with contents), South Silcox (38, 33)), and for the more degraded creek (Culvert Creek (44, 22)), yet the total number of prey items is more than twice as high in the less degraded creeks (Table 1). In addition, similarity analysis of stomach contents (based on percent weight, an indicator of energetic importance) showed grouping by creek type, with North Silcox and South Silcox as one grouping and Yucca Pen and Culvert Creek as a separate grouping. Juvenile snook in the more degraded creeks appear to rely more heavily on a few prey, likely a reflection of a narrower trophic niche in the more degraded creeks.

The apparent effects of anthropogenic habitat modifications on juvenile snook diet have occurred elsewhere and may indicate a fundamental trophic shift resulting from different types of habitat modifications. The impoundment of marshes (i.e., fragmentation) on the east coast of Florida, for example, appeared to influence juvenile snook diet: the top species of prey fish differed, with a greater diversity of prey fish in pre-impoundment marshes (Harrington and Harrington 1961; Gilmore et al. 1983). Gilmore et al. (1983) also found that diet composition

differed between freshwater and saltwater impoundments: 44% of juvenile snook stomachs in freshwater impoundments contained fish, 21% shrimp, 15% microcrustaceans, and 8% insects, whereas in saltmarsh impoundments, 35% of stomachs contained microcrustaceans, 23% fish, and 19% grass shrimp. Differences between diet of juvenile snook in unfragmented river (30% fish, 65% shrimp, and 10% other) and lagoon (55% fish, 40% shrimp, and 15% crabs) habitats in Puerto Rico were less pronounced (Aliaume et al. 1997). The results of this and previous studies indicate that additional research is needed to determine the full effects of anthropogenic habitat alteration on juvenile snook trophic ecology.

Although comparisons are constrained by substantial sample size differences, stable isotope analysis suggests greater among-individual diet variation in the less degraded creeks. This may reflect the fact that most individuals in the more degraded creeks feed primarily on a few dominant prey items (as supported by diet analysis), whereas individuals in less degraded creeks have a larger scope for diet specializations (*sensu* Bolnick et al. 2003), i.e., focusing on a specific subset of a more diverse prey base. Layman et al. (2007b) found increased among-individual variation in isotopic signatures in less degraded tidal creeks of the Bahamas, likely due to the substantially constrained potential prey base in systems for which hydrologic connectivity was reduced by construction of roads. Analysis of a potentially similar trophic pattern is ongoing for tidal creeks of Charlotte Harbor through a detailed examination of degree of diet specialization, as based on both diet contents and prey isotope values, following Araujo et al. (2007). In general, less enriched mean $\delta^{13}\text{C}$ values in less degraded creeks suggests a fundamental shift in the underlying trophic basis of the creek food webs following human alteration of freshwater flow. Yet because of the myriad potential resource pools in estuarine ecosystems (Layman 2007), more study is needed to elucidate the underlying mechanism driving the apparent shift in mean $\delta^{13}\text{C}$ values of snook among sites.

As stated above, in tidal creeks of the Bahamas, human-induced fragmentation results in drastically simplified food webs (Layman et al. 2007a). Reductions in prey diversity for top predators may be one of the primary causes of reduced growth rates, lower fish condition, and higher parasite loads (Rypel and Layman 2008). In this study, the estuarine habitats maintained connectivity, but experienced different patterns of freshwater flow due to anthropogenic alterations of upland drainages. Similar reductions in prey diversity in the diets of top predators reported herein and by Layman et al. (2007a, b) suggest that different forms of human impacts may have similar, predictable, effects on food web structure in tidal creek ecosystems.

Two alternative sources of variation might explain the diet variation observed in this study. First, it is possible that

juvenile snook traveled between mangrove creeks, so may have obtained prey in multiple creeks and thus this movement may have increased diet variation. This is unlikely, however. Ongoing tag–recapture research shows that juvenile snook can and do move between creeks, but these between-creek movements are not common (<5% of >3,000 tagged juvenile snook were detected in creeks other than where they were tagged) and movements are not typically over long distances (AJA unpublished data). Movements are between nearby creeks, indicating short-distance movements, and are therefore constrained to movement within creek types as addressed in this study (i.e., juvenile snook might move between North Silcox and South Silcox (less degraded) or between Yucca Pen and Culvert Creek (more degraded), but not between less degraded and more degraded creeks, which are more than 16 km apart).

Second, seasonal changes in juvenile snook diet may explain some of the observed variation. Although it is likely that juvenile snook diet changes seasonally, based upon prey abundance and/or availability, it is unlikely that these seasonal changes differed among the creeks. All four study creeks are within the same estuarine hydrological zone (Poulakis et al. 2003), so estuarine-based seasonal differences were assumed to be similar in all four creeks. All four creeks are similar enough in latitude to preclude any latitude-based differences. Furthermore, stable isotope analysis of fish muscle tissue integrates energy assimilation over many months (MacNeil et al. 2006) and thus would not reflect short-term temporal variation in diet.

Given that juvenile snook rely upon creek and marsh habitats, and these coastal habitats are under continuing stress from anthropogenic sources, additional research is needed to determine the extent that shifts in food web structure ultimately affect overall fishery production. Following the framework of Beck et al. (2001), nursery function is a result of a combination of density, growth, and survival of juveniles, and ultimately the entry of individuals into the adult population. Habitats that support fewer individuals or slower growth rates (which may result from a reduction in diet diversity) are generally not ranked as nursery habitats (reviewed in Adams et al. 2006). As with other species that use similar habitats, the difference in diet diversity of juvenile snook may be an indicator of an overall change in ecosystem function (*sensu* Valentine-Rose et al. 2007) and such changes in food web structure may ultimately affect the ability of juveniles to successfully join the adult population.

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References

- Adams, A.J., C.P. Dahlgren, G.T. Kellison, M.S. Kendall, C.A. Layman, J.A. Ley, I. Nagelkerken, and J.E. Serafy. 2006. The juvenile contribution function of tropical backreef systems. *Marine Ecology Progress Series* 318: 287–301. doi:10.3354/meps318287.
- Aliaume, C., A. Zerbi, and J.M. Miller. 1997. Nursery habitat and diet of juvenile *Centropomus* species in Puerto Rico estuaries. *Gulf of Mexico Science* 2: 77–87.
- Araujo, M.S., D.I. Bolnick, G. Machado, A.A. Giarretta, and S.F. dos Reis. 2007. Using delta C-13 stable isotopes to quantify individual-level diet variation. *Oecologia* 152: 643–654. doi:10.1007/s00442-007-0687-1.
- Baltz, D.M., J.W. Fleeger, C.F. Rakocinski, and J.N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental Biology of Fishes* 53: 89–103. doi:10.1023/A:1007471724608.
- Beach, D. 2002. *Coastal sprawl: the effects of urban design on aquatic ecosystems in the United States*. Arlington: Pew Oceans Commission.
- Bearhop, S., C.E. Adams, S. Waldron, R.A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007–1012. doi:10.1111/j.0021-8790.2004.00861.x.
- Beck, M.W., K.L. Heck, K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641. doi:10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.
- Bolnick, D.I., R. Svanbäck, J.A. Fordyce, L.H. Yang, J.M. Davis, C. D. Hulsey, and M.L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28. doi:10.1086/343878.
- Campbell, L.M., R.E. Hecky, and S.B. Wandra. 2003. Stable isotope analyses of food web structure and fish diet in Neapolitan and Winam Gulfs, Lake Victoria, East Africa. *Journal of Great Lakes Research* 29(Supplement 2): 243–257.
- DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341–351. doi:10.1016/0016-7037(81)90244-1.
- Doering, P.H., and R.H. Chamberlain. 2000. Experimental studies on the salinity tolerance of turtle grass, *Thalassia testudinum*. In *Seagrasses: monitoring, ecology, physiology, and management*, ed. S.A. Bortone, 81–98. Boca Raton: CRC Press.
- Geary, B.W., J.R. Rooper, and J.W. Webb. 2001. Utilization of saltmarsh shorelines by newly settled sciaenids in a Texas estuary. *Gulf and Caribbean Research* 13: 37–49.
- George, E.L., and W.F. Hadley. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) young of the year. *Transactions of the American Fisheries Society* 108: 253–261. doi:10.1577/1548-8659(1979)108<253:FAHPBR>2.0.CO;2.
- Gilmore, R.G., C.J. Donohoe, and D.W. Cooke. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook. *Florida Science* 46: 306–313.
- Hammet, K.M. 1990. Land use, water use, streamflow characteristics, and water quality characteristics of the Charlotte Harbor inflow area, Florida. *U. S. Geological Survey Water Supply Paper* 2359 A.
- Harrington Jr., R.W., and E.S. Harrington. 1961. Food selection among fishes invading a high subtropical salt marsh: from onset of flooding through the progress of a mosquito brood. *Ecology* 42: 646–666. doi:10.2307/1933496.
- Layman, C.A. 2007. What can stable isotope ratios reveal about mangroves as fish habitat? *Bulletin of Marine Science* 80: 513–527.
- Layman, C.A., and D.M. Post. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure?: Reply. *Ecology* 89: 2358–2359. doi:10.1890/08-0167.1.
- Layman, C.A., J.P. Quattrochi, C.M. Peyer, and J.E. Allgeier. 2007a. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* 10: 937–944. doi:10.1111/j.1461-0248.2007.01087.x.
- Layman, C.A., D.A. Arrington, C.G. Montaña, and D.M. Post. 2007b. Can stable isotope ratios provide quantitative measures of trophic diversity within food webs? *Ecology* 88: 42–48. doi:10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2.
- Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809. doi:10.1126/science.1128035.
- MacNeil, M.A., K.G. Drouillard, and A.T. Fisk. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 345–353. doi:10.1139/f05-219.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ¹⁵N along food chains: further evidence and the relation between ¹⁵N and animal age. *Geochimica et Cosmochimica Acta* 48: 1135–1140. doi:10.1016/0016-7037(84)90204-7.
- Montague, C.L., and J.A. Ley. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries* 16: 703–717. doi:10.2307/1352429.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* 279: 860–863. doi:10.1126/science.279.5352.860.
- Peters, K.M., R.E. Matheson Jr., and R.G. Taylor. 1998. Reproduction and early life history of common snook, *Centropomus undecimalis* (Bloch), in Florida. *Bulletin of Marine Science* 62: 509–529.
- Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320. doi:10.1146/annurev.es.18.110187.001453.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83: 703–718.
- Post, D.M., C.A. Layman, D.A. Arrington, G. Takimoto, C.G. Montaña, and J. Quattrochi. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152: 179–189. doi:10.1007/s00442-006-0630-x.
- Poulakis, G.R., J.M. Shenker, and D.S. Taylor. 2002. Habitat use by fishes after tidal reconnection of an impounded estuarine wetland in the Indian River Lagoon, Florida (USA). *Wetlands Ecology and Management* 10: 51–69. doi:10.1023/A:1014305310291.
- Poulakis, G.R., D.A. Blewett, and M.E. Mitchell. 2003. The effects of season and proximity to fringing mangroves on seagrass-associated fish communities in Charlotte Harbor, Florida. *Gulf of Mexico Science* 21: 171–184.
- Pringle, C. 2006. Hydrologic connectivity: a neglected dimension of conservation biology. In *Connectivity conservation*, ed. K.R. Crooks, and M. Sanjayan, 233–254. Cambridge: Cambridge University Press.
- Ridler, M.S., R.C. Dent, and D.A. Arrington. 2006. Effects of two hurricanes on *Syringodium filiforme*, manatee grass, within the Loxahatchee River estuary, southeast Florida. *Estuaries and Coasts* 29: 1019–1025.
- Rypel, A., and C.A. Layman. 2008. Degree of aquatic ecosystem fragmentation predicts population characteristics of gray snapper (*Lutjanus griseus*) in Caribbean tidal creeks. *Canadian Journal*

- of Fisheries and Aquatic Sciences* 65: 335–339. doi:10.1139/F07-192.
- Sargent, F.J., T.J. Leary, D.W. Crewz, and C.R. Kruer. 1995. Scarring of Florida's seagrasses: assessment and management options. FMRI Tech. Rep. TR-1. Florida Marine Research Institute, St. Petersburg, FL: 37.
- Sklar, F.H., and J.A. Browder. 1998. Coastal environmental impacts brought about by alterations in freshwater flow in the Gulf of Mexico. *Environmental Management* 22: 547–562. doi:10.1007/s002679900127.
- Stevens, P.W., D.A. Blewett, and G.R. Poulakis. 2007. Variable habitat use by juvenile common snook, *Centropomus undecimalis* (Pisces: Centropomidae): applying a life-history model in a southwest Florida estuary. *Bulletin of Marine Science* 80(1): 93–108.
- Valentine-Rose, L., C.A. Layman, D.A. Arrington, and A.L. Rypel. 2007. Habitat fragmentation affects fish secondary production in Bahamian tidal creeks. *Bulletin of Marine Science* 80: 863–878.
- Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Selkoe, J.J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790. doi:10.1126/science.1132294.
- Zar, J.H. 1984. *Biostatistical analysis*. Englewood Cliffs: Prentice Hall.