Environ Biol Fish (2011) 90:223–233
DOI 10.1007/s10641-010-9734-6

Diet of age-0 tarpon (*Megalops atlanticus*) in anthropogenically-modified and natural nursery habitats along the Indian River Lagoon, Florida

Zachary R. Jud · Craig A. Layman · Jonathan M. Shenker

Received: 5 January 2010 / Accepted: 12 October 2010 / Published online: 3 November 2010

Abstract As human development in coastal areas increases, the role of anthropogenically-created habitats in the life history of marine organisms is becoming increasingly important. We examined the diet of age-0 tarpon, *Megalops atlanticus*, in and around man-made mosquito control impoundments along the Indian River Lagoon in east-central Florida, with a particular focus on identifying dietary patterns associated with tarpon size and nursery habitat type (i.e., between perimeter pool habitats in established impoundments and newly-created restoration marsh habitats). Age-0 tarpon were found to consume a wide variety of prey organisms, and exhibited considerable dietary variation among study sites. Smaller juvenile tarpon consumed a limited number of small prey taxa, while larger individuals fed on a greater range of prey taxa and sizes. Overall, copepods and fishes were the dominant prey items; however, the consumption of these organisms varied considerably among size classes and sites. There was no clear difference in tarpon diet between the two types of habitat we examined. The ability of juvenile tarpon to utilize such a diverse range of prey organisms may allow populations to inhabit a variety of habitats, including man-made marshes. When natural systems have been degraded or destroyed, human-altered habitats can assume a nursery role for the species.

Keywords Dietary plasticity · Habitat fragmentation · Mosquito control impoundments · Optimal foraging · Predator-prey interactions · Mangrove marsh restoration

Introduction

Florida's coastal wetlands play an important role in the recruitment of tarpon, *Megalops atlanticus* (Wade 1962; Crabtree et al. 1995; Shenker et al. 2002). The most important nursery habitats for tarpon in the continental United States are located in Florida, as it is the only state where winter water temperatures consistently remain within the species' tolerance range (Howells 1985). Because adult tarpon are highly valued by the sport fishing industry, most of the research conducted on the species has been targeted at mature individuals. Much less is known about the early life history stages, when tarpon rely on threatened coastal wetlands. In particular, little is known about the diet of juvenile tarpon following settlement. A better understanding of how certain

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Z. R. Jud (✉) · C. A. Layman
Department of Biological Sciences, Marine Sciences Program, Florida International University,
3000 NE 151st Street,
North Miami, FL 33181, USA
e-mail: zackjud@gmail.com

J. M. Shenker
Department of Biological Science,
Florida Institute of Technology,
150 W University Blvd,
Melbourne, FL 32901, USA

early life history traits develop across a range of nursery habitats is critical for the conservation of the species, as natural nursery habitats are being modified by humans at a rapid rate.

Along the east coast of Florida, man-made mosquito control impoundments have become increasingly important to tarpon recruitment because a large percentage of the region's natural marshes were impounded for mosquito control purposes from the 1950s to 1970s (Brockmeyer et al. 1997; Poulakis et al. 2002; Stevens et al. 2007). Historically, mosquito control impoundments were highly fragmented ecosystems that lacked connections with the surrounding marine environment. In recent decades, hydrologic connectivity has been restored to most of Florida's impounded marshes (Brockmeyer et al. 1997). Transient fish species begin to utilize impoundments immediately following reconnection (Vose and Bell 1994; Llanso et al. 1998; Poulakis et al. 2002), and in many ways, reconnected impoundments appear to function much like natural marshes (Stevens et al. 2006; Lewis and Gilmore 2007). In addition to reconnecting existing mosquito control impoundments, state and regional agencies have started creating man-made restoration marshes (Lewis and Gilmore 2007). Juvenile tarpon have been observed in these newly-created marsh habitats less than 1 year after construction (Z. R. Jud, unpubl. data).

Our objective was to characterize the diet of age-0 tarpon in established mosquito control impoundment habitats and newly-constructed restoration marshes. Although the limited body of work on the trophic ecology of age-0 tarpon identified considerable variability in diet (Harrington and Harrington 1960, 1961; Catano and Garzon-Ferreira 1994; Chacon-Chaverri 1994), it is not clear how these dietary patterns are affected by anthropogenic habitat modification. Prey species composition, size, and diversity were compared among different size classes of age-0 tarpon. We then made dietary comparisons among several study sites, and specifically examined diet differences between mosquito control impoundment and restoration marsh habitats.

Methods

Between September and November of 2007, 15 east-central Florida mosquito control impoundments and restoration marshes were examined daily for the presence of age-0 tarpon. These wetlands, located in Indian River and St. Lucie counties, are hydrologically connected to the Indian River Lagoon, a bar-built estuary that parallels Florida's Atlantic coast. Age-0 tarpon were captured at a total of seven study sites (Table 1). Tarpon Hole (TH) and Site Six (#6) were characterized as perimeter pool habitats within established mosquito control impoundments (Fig. 1a, b). Perimeter pools are mangrove-lined depressions scoured into the marsh surface by the pumps that were historically used to fill impoundments. These habitats are decades old, have well-established plant and animal communities, and are surrounded by a complex network of mature red mangrove (*Rhizophora mangle*) prop roots. Perimeter pool habitats remain inundated during all tidal stages, and serve as an important refuge for fish during periods of low water.

Three additional collection sites, Restored Creek (RC), Restored Creek North (RCN), and Beach Pool (BP) were located in newly-constructed restoration marsh habitats (Fig. 1c, d). These man-made marshes had been constructed during the previous year by the St. Lucie County Mosquito Control District in an effort to provide increased marsh habitat for fishes and wildlife. The restoration marshes were dug using heavy equipment, and were designed to mimic the structure and hydrology of natural mangrove creek systems. The absence of mature red mangrove trees and prop roots, coupled with smooth, muddy shorelines, resulted in low structural complexity compared to perimeter pool habitats. All of these man-made marshes were hydrologically connected to the Indian River Lagoon or existing mosquito control impoundments.

Age-0 tarpon were also opportunistically collected at two natural (i.e., not anthropogenically-created) sites in the Indian River Lagoon. These sites (Tarpon Hole East—THE, and Blind Creek—BC) were located in close proximity to perimeter pool and restoration marsh habitats, and were included to provide some comparison between man-made and natural habitats. Although tarpon from these two sites were not used in our primary analysis (i.e., comparing diet between perimeter pool and restoration marsh habitats), they were included in the general description of tarpon diet and the analysis of diet vs. tarpon length.

Table 1 Description of age-0 tarpon collection sites, where n=the number of tarpon retained for dietary analysis

Site Name	Abbreviation	Habitat Type	Location	n
Site Six	#6	Perimeter Pool	27º21′49″ N 80º14′59″ W	8
Tarpon Hole	TH	Perimeter Pool	27º48′42″ N 80º25′36″ W	30
Restored Creek	RC	Restoration Marsh	27º24′48″ N 80º16′24″ W	20
Restored Creek North	RCN	Restoration Marsh	27º24′49″ N 80º16′24″ W	6
Beach Pool	BP	Restoration Marsh	27º22′41″ N 80º15′15″ W	21
Tarpon Hole East	THE	Natural Indian River Lagoon	27º48′42″ N 80º25′35″ W	5
Blind Creek	BC	Natural Indian River Lagoon	27º22′42″ N 80º15′16″ W	7

In order to reduce the potential influence of seasonal variation, sampling was restricted to a 2 month period in the fall of 2007. This time frame was selected to coincide with the end of the peak recruiting period for tarpon (Harrington 1958; Shenker et al. 2002), when maximum numbers of age-0 fish would be expected to be present in the mosquito control impoundments. Tarpon were captured using cast nets (4.3 m diameter, 13 mm mesh) and seines (15.2×1.8 m, 3 mm mesh). Standard lengths (SL) were measured to the nearest 1.0 mm, and the fish were weighed to the nearest 0.01 g. Tarpon were then euthanized and the entire digestive tract was immediately removed and placed into 10% formalin. All tarpon greater than 215 mm SL were released alive, as they could have been either age-0 or age-1 individuals (Harrington 1958; Chacon-Chaverri 1994; Crabtree et al. 1995; Zerbi et al. 2001).

In the laboratory, tarpon digestive tracts were removed from 10% formalin after one week and

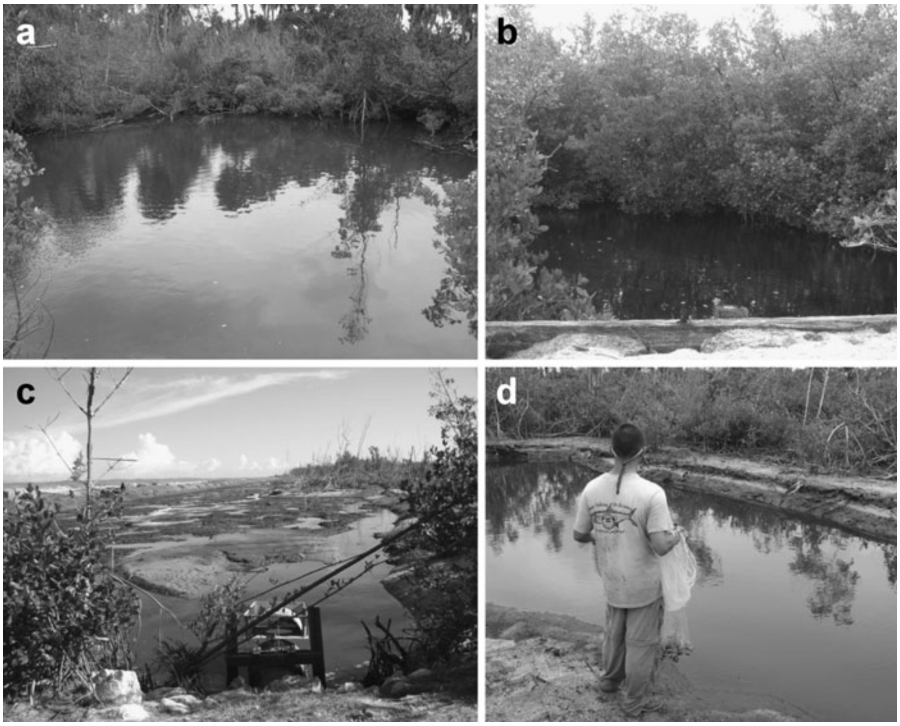


Fig. 1 Photographs of study sites, illustrating perimeter pool and restoration marsh habitats. **a** Site Six (perimeter pool). **b** Tarpon Hole (perimeter pool). **c** Beach Pool (restoration marsh). **d** Restored Creek (restoration marsh)

placed into 96% ethanol. Stomachs were processed individually under a stereomicroscope. Before each stomach was dissected, visceral fat deposits (an indicator of nutrition) were noted on a presence/absence basis. Prey organisms contained in the stomachs were identified to the lowest possible taxonomic level. Prey items were counted and weighed to the nearest 0.001 g on a digital balance (wet weight). Some microscopic prey taxa were too abundant to count individually; in these cases, prey abundance was estimated by counting individuals in a diluted sub-sample on a 1.0 ml Sedgwick-Rafter counting cell at 40 X magnification. For organisms that were too small to be weighed individually, entire samples were filtered out of solution and weighed as a group.

To obtain an overall description of juvenile tarpon diet, the following values were calculated for each prey taxon: the percent frequency of occurrence of prey taxon *i* among all stomachs in the sample ($\%O_i$ = percent frequency of occurrence), the proportion of the number of prey items present in a prey taxon *i* to the total number of prey items present in all stomachs ($\%N_i$ = percent of total diet by number), and the proportion of the aggregate wet weight of a prey taxon *i* to the total wet weight of all prey items ($\%W_i$ = percent of total diet by weight). Based on these values, an Index of Relative Importance (IRI) was calculated for each prey taxon *i*, where $IRI_i = \%O_i(\%N_i + \%W_i)$. The IRI is a compound index that incorporates quantity, weight, and frequency of occurrence into a single numerical measure, facilitating dietary comparisons and providing a more accurate estimate of "dietary importance" of prey items (Hynes 1950; Hyslop 1980; Cortes 1997; Treloar et al. 2007; Adams et al. 2009). To standardize comparisons among prey taxa, we converted IRI_i values into $\%IRI_i$ by dividing each taxon's IRI_i value by the sum of IRI_i values for all prey taxa combined (Cortes 1997).

Juvenile tarpon were pooled across all sites to determine how dietary composition may have changed through ontogeny. All tarpon that had identifiable food items in their guts were assigned to 20 mm size classes. For all size classes, $\%O_i$, $\%N_i$, $\%W_i$, and %IRI were calculated for each prey taxon. We used a 1-way analysis of similarities (ANOSIM) to test for significant differences in dietary composition among size classes (PRIMER v6.1.9 software). Prey weight values used for ANOSIM were fourth root transformed to down-weight abundant prey taxa. To determine whether different size classes of age-0 tarpon consumed different-sized prey items, the median (± median absolute deviation) of mean weights of individual prey items consumed by each tarpon were compared among size classes using a Kruskal-Wallis test. A Kruskal-Wallis test was also used to determine whether different size classes of age-0 tarpon exhibited variation in the number of individual prey taxa consumed (median ± median absolute deviation).

Stomach contents were analyzed to determine whether dietary composition of age-0 tarpon varied among study sites, as well as between established perimeter pool habitats and newly-constructed restoration marsh habitats. To avoid confounding site-related dietary differences with size-related dietary differences, we tested whether tarpon from each site were significantly different in length. A Kruskal-Wallis test was conducted to determine whether median tarpon size varied among sites. For each site, $\%O_i$, $\%N_i$, $\%W_i$, and %IRI were calculated for all prey taxa. A 1-way ANOSIM (Bray-Curtis similarity matrix, fourth root transformed prey weight values) was then used to test whether the diet of age-0 tarpon varied among all sites. Finally, a 2-way nested ANOSIM was used to test whether the dietary composition of age-0 tarpon differed within and between perimeter pool habitats (mosquito control impoundments) and restoration marsh habitats, where sites were nested within the two habitat types.

Results

A total of 366 tarpon were captured during the fall of 2007. Ninety-seven of these fish were ≤215 mm and were retained for stomach content analysis. The remaining fish were released unharmed. The harvested fish ranged in standard length from 64 to 215 mm, with a mean (± SD) of 143.8±35.5 mm. Seventy-one of the 97 collected stomachs contained identifiable prey items, representing 22 different taxa (Fig. 2). Only five prey taxa were found in more than 10% of the tarpon. Fishes (Teleostei) occurred with the greatest frequency, followed by copepods (Copepoda), water boatmen (Corixidae), shrimp (Caridea), and backswimmers (Notonectidae). Eleven of the 22

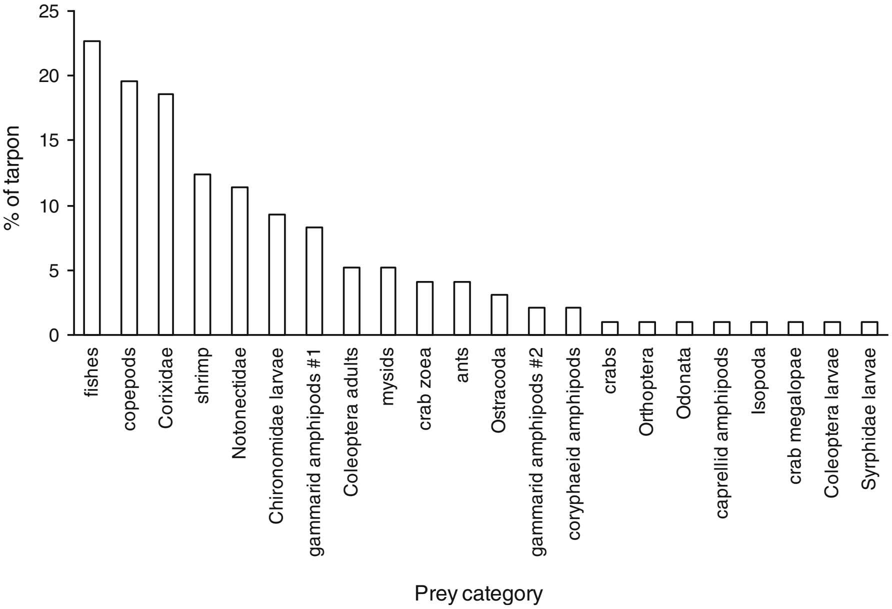


Fig. 2 Frequency of occurrence of 22 prey taxa in 71 tarpon that contained identifiable prey items

prey categories were identified in three or fewer individual tarpon.

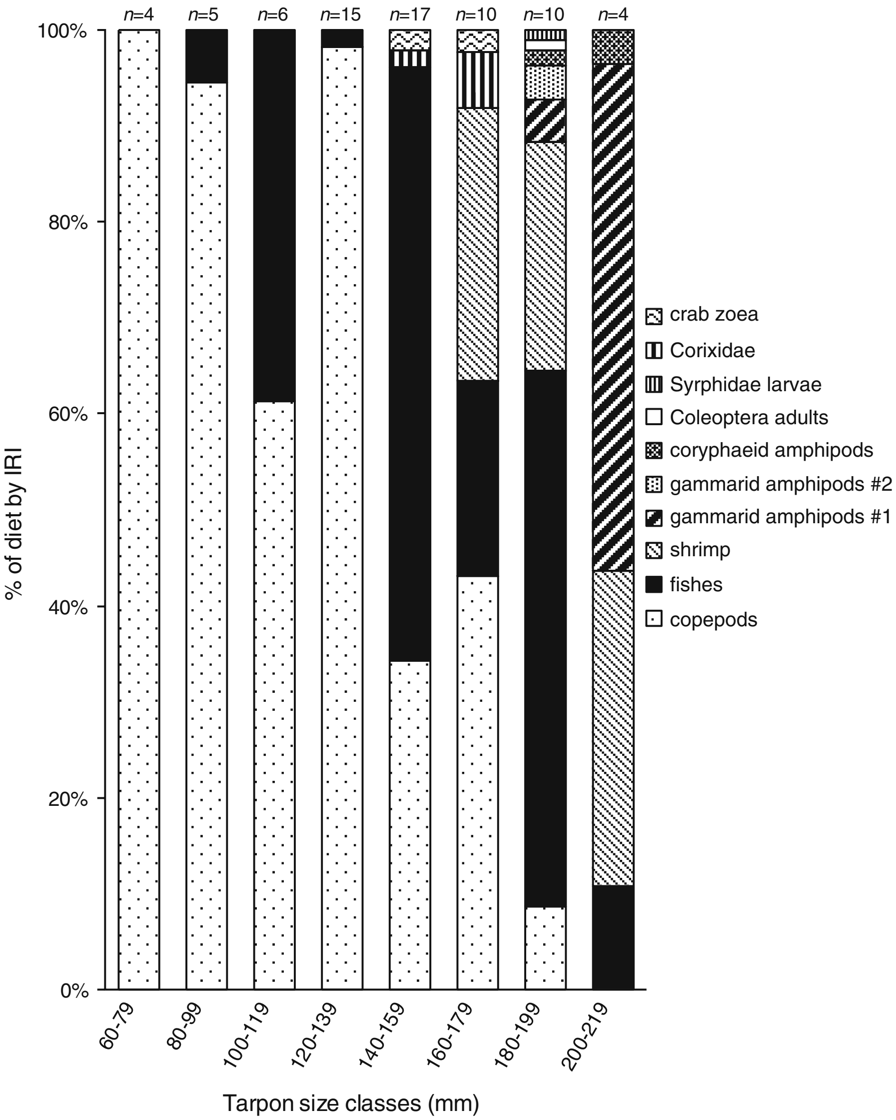
Copepods were the numerically dominant prey taxon, accounting for 97% of the prey consumed by number. More than 300,000 copepods were identified in the 19 tarpon stomachs that contained this prey item. The remaining 21 prey taxa combined contributed to less than 3% of tarpon diet by number. By weight, fishes (51%), shrimp (20%) and copepods (18%) were the three most dominate prey items. These were the only prey taxa that exceeded 3% of tarpon diet by weight. When taking into account quantity, weight, and frequency of occurrence, copepods had the highest relative IRI value, followed by fishes, shrimp, and corixids. The remaining prey taxa had %IRI values lower than 0.5%.

Analysis of %IRI values for the gut contents of age-0 tarpon revealed patterns of prey consumption related to tarpon length (Fig. 3). Some prey taxa (e.g., copepods) dominated the diets of smaller tarpon, while other prey taxa (e.g., shrimp) were only consumed by larger tarpon. Although the smallest size class of tarpon (i.e., 60–79 mm) only consumed copepods, this prey item remained an important dietary component in tarpon up to the 160–179 mm size class, and was consumed to a lesser degree by tarpon as large as 183 mm. Some individual fish consumed copepods in huge numbers (i.e., >50,000/tarpon). Fishes were consumed by all but the smallest tarpon (i.e., 60–79 mm), but %IRI values for fishes varied considerably among tarpon size classes.

The results of a 1-way ANOSIM identified significant differences in prey composition among size classes (R=0.07, p=0.02). There was no significant difference in the mean weight of individual prey items consumed per tarpon among size classes (Kruskal-Wallis; H=13.2, p=0.07) or the number of prey taxa consumed per tarpon among size classes (Kruskal-Wallis; H=12.6, p=0.08). However, as tarpon length increased, there was an increase in the variation (median absolute deviation) of prey weight and the absolute number of prey taxa consumed per fish (Fig. 4). Larger tarpon fed on a wide range of prey sizes, whereas smaller tarpon typically consumed only small prey items. Additionally, larger tarpon fed on a more diverse range of prey organisms. The stomach contents of all tarpon <100 mm contained no more than one prey taxon, while individuals ≥100 mm contained from one to five prey taxa, with a mean (± SD) of 1.98±1.3 prey taxa per tarpon.

Since the above analyses established that diet varied with tarpon size, comparisons among sites would be most relevant if all sites contained tarpon of similar size. The median size of tarpon from Tarpon Hole was significantly smaller than four of the other sites (Kruskal-Wallis; H=46, p<0.001), but there was no significant difference in tarpon size among the remaining six sites. Dietary differences identified at

Fig. 3 Percent of diet by IRI (%IRI) for all tarpon that contained identifiable prey items. Data are presented based on 20 mm size classes. Only %IRI values greater than 0.9% are shown



Tarpon Hole must be viewed with caution since the smaller size of tarpon at this site may have influenced diet, independent of habitat type.

Dietary patterns varied significantly among the seven study sites (1-way ANOSIM; $R=0.24$, $p=0.001$), including pairs of sites separated by ≤25 m. Even within a single site on a single sampling date, the diets of individual tarpon were often dominated by different prey taxa, suggesting high levels of within-site variation in prey consumption. None of the 22 prey taxa we identified were present in tarpon diets at all seven sites. Some prey taxa (e.g., crab zoea) were only found in tarpon diets at one or two sites and may have represented a locally available food source. Other prey categories (e.g., fishes) were consumed at nearly all of the study sites.

Tarpon diets at Site Six, a perimeter pool site, were dominated by shrimp and amphipods (Fig. 5). Although 14 different prey taxa were consumed at the Restored Creek restoration marsh site (more than any other site), copepods were the dominant dietary item, with the remaining 13 taxa being consumed in low quantities. At Restored Creek North, a restoration marsh habitat located just 25 m from Restored Creek, crab zoea and amphipods were the dominant prey items. Diets at the third restoration marsh site, Beach Pool, were dominated by copepods, corixids, and fishes. At Tarpon Hole, the perimeter pool habitat

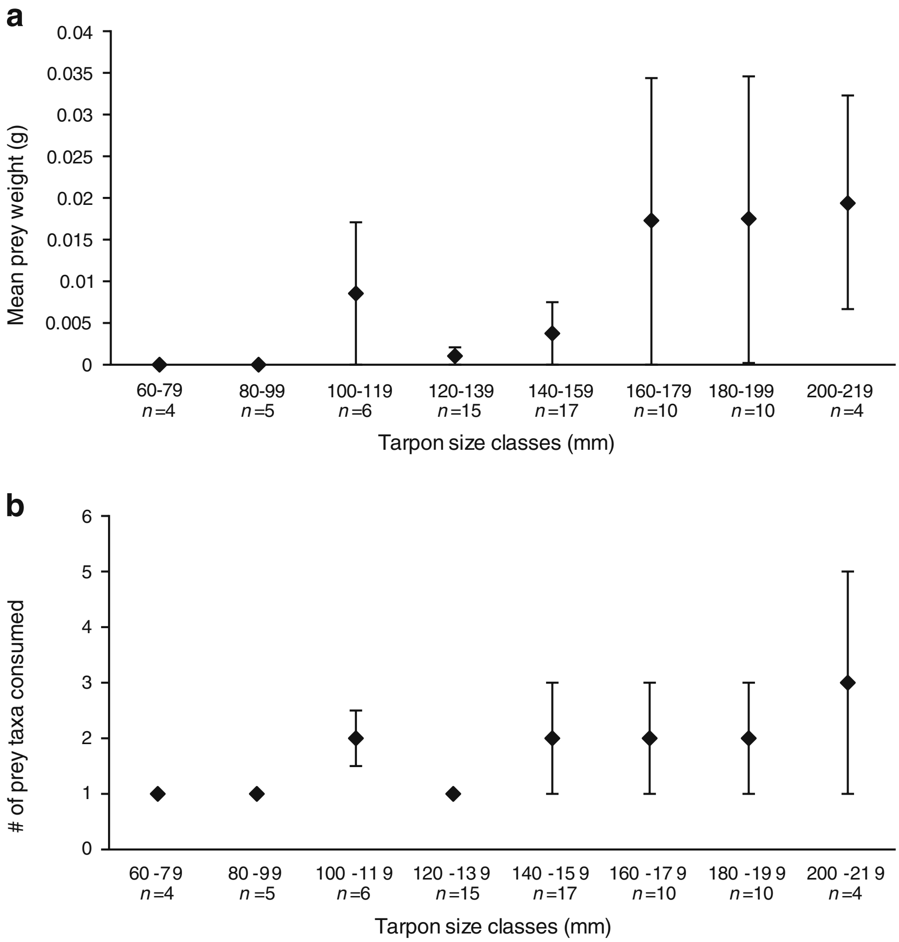


Fig. 4 Length-based dietary characteristics of age-0 tarpon. **a** Tarpon length vs. the mean weight of each prey item consumed (median ± median absolute deviation). **b** Tarpon length vs. the number of different prey taxa consumed per tarpon (median ± median absolute deviation). In both cases, there was no significant difference among size classes, but variation tended to increase with tarpon length

with smaller tarpon, copepods and fishes were the dominant prey taxa.

Age-0 tarpon from the two natural IRL sites had different dietary patterns than individuals from the perimeter pool or restoration marsh sites. Diets of tarpon at Blind Creek were almost entirely composed of fishes, while at Tarpon Hole East, shrimp were the most important prey taxon. These were the only two sites where diets were dominated by large prey organisms. At the time of dissection, visceral fat deposits were noted in 18 of 21 tarpon (86%) from Beach Pool and six of seven tarpon (86%) from Blind Creek. Only two of the 69 tarpon (3%) captured at the remaining five sites had visceral fat deposits.

A 2-way nested ANOSIM was used to determine whether diets differed within and between the two main habitat types: 1) perimeter pools in established mosquito control impoundments, and 2) newly-constructed restoration marshes. A significant difference in diets was identified among sites within the two habitat types (R=0.26, p=0.001); however, there was no significant difference between the two habitat types (R=0.08, p=0.4). Variation in tarpon diet among sites within the two habitats was greater than variation between the two habitats.

Discussion

Age-0 tarpon exhibited considerable dietary variability among size classes and study sites. The size-based dietary shifts we observed in age-0 tarpon were likely caused by an increase in prey capture ability resulting from changes in morphology or feeding kinematics (Guigand and Turingan 2002). A reduction in gape limitation and an increase in swimming speed and efficiency may allow larger age-0 tarpon to consume larger, more evasive (i.e., harder to capture) prey organisms. Previous studies identified a shift from copepod consumption to piscivory as juvenile tarpon reached 75–100 mm (Harrington and Harrington 1960; Catano and Garzon-Ferreira 1994; Chacon-Chaverri 1994). We observed a similar dietary shift in tarpon from mosquito control impoundments and restoration marshes; however, the shift occurred at larger body sizes, and a variety of other prey taxa (i.e., not just fishes) were consumed by these larger individuals (Fig. 3). The consumption of copepods by relatively large juvenile tarpon was unexpected, and may be unique to the man-made habitats we studied. The presence of huge quantities of copepods in the diets of some age-0 tarpon suggests that the fish may employ a combination of suction and ram feeding (Guigand and Turingan 2002) while rapidly swimming through swarms of copepods, essentially filtering prey out of the water column. Filter feeding has not previously been described in juvenile tarpon; however, the presence of long, tightly-spaced gill rakers supports dietary observations that suggest this feeding strategy may be employed (Langeland and Nøst 1995).

The rapid growth experienced during the juvenile phase in many organisms can lead to a continuously-shifting niche (Werner and Gilliam 1984). In the case of age-0 tarpon, changes in the composition and size of prey items consumed as body size increases may function to reduce intraspecific competition, particularly when prey abundance is limited. Since recruitment of juvenile tarpon occurs in pulses throughout the summer (Shenker et al. 2002), it is not uncommon to find several different size classes of tarpon simultaneously occupying the same nursery habitat. Size-based shifts in diet may allow multiple size classes of age-0 tarpon to coexist in confined nursery habitats.

A variety of factors may explain the dietary differences we observed among sites and between habitat types. Within estuaries, prey communities can vary considerably among different habitats (Layman and Silliman 2002; Valentine-Rose et al. 2007). Although we did not sample prey organisms at our study sites, the high complexity of perimeter pool habitats may have supported a different prey base than the structurally-simple restoration marsh habitats. Additionally, our study sites possessed different levels of connectivity to adjacent mangrove forests and surrounding bodies of water. Habitats with higher levels of connectivity often support a greater variety of prey species (Poulakis et al. 2002; Layman et al. 2007; Lewis and Gilmore 2007). Further, physical parameters (e.g., turbidity, salinity, temperature, dissolved oxygen levels, etc.) can vary widely, even at small spatial scales. In addition to affecting prey abundance and diversity, these factors may also influence prey selection or capture efficiency. In turbid waters, for example, age-0 tarpon may be more successful at capturing certain prey organisms (e.g., prey organisms that flee at the sight of a predator), while in low turbidity habitats, other prey organisms (e.g., cryptic prey organisms) may be located and captured more easily (Shoup and Wahl 2009). The interplay between these factors is complex and difficult to quantify, but their combined effects on prey base and prey capture ability likely shape the diet of tarpon.

While we anticipated that the diet of tarpon within mosquito control impoundment sites would differ from restoration marsh sites, we found no clear pattern between diet and habitat type. There appeared to be obvious physical and biological differences between the two main habitat types we examined, but we did not quantitatively determine whether all sites actually fit into this simple dichotomy. Our grouping of sites together as perimeter pool habitats and restoration marsh habitats may have underestimated the actual biotic and abiotic variability among sites, which, in turn, could have influenced diet.

The tarpon collected at Beach Pool, a restoration marsh site, present one possible explanation of how juvenile tarpon utilize newly-constructed marshes. These tarpon had the greatest percentage of empty stomachs out of all seven sites, yet they also possessed visceral fat deposits. Stored fat is indicative of high nutrition (Borcherding et al. 2007), but superficially, this doesn't correspond well to the empty stomachs found at the site. The fish-dominated diets of tarpon captured at Blind Creek, an adjacent natural Indian River Lagoon site, may explain why the restoration marsh fish showed signs of high nutrition, despite having frequently empty stomachs. It appears that tarpon periodically move through the short culvert connecting Beach Pool to Blind Creek, leaving the sanctuary of the nursery marsh to make brief feeding forays into the Indian River Lagoon estuary. If man-made restoration marshes do function to provide shelter for age-0 tarpon between feeding bouts, the creation of these habitats may actually benefit juvenile tarpon recruitment.

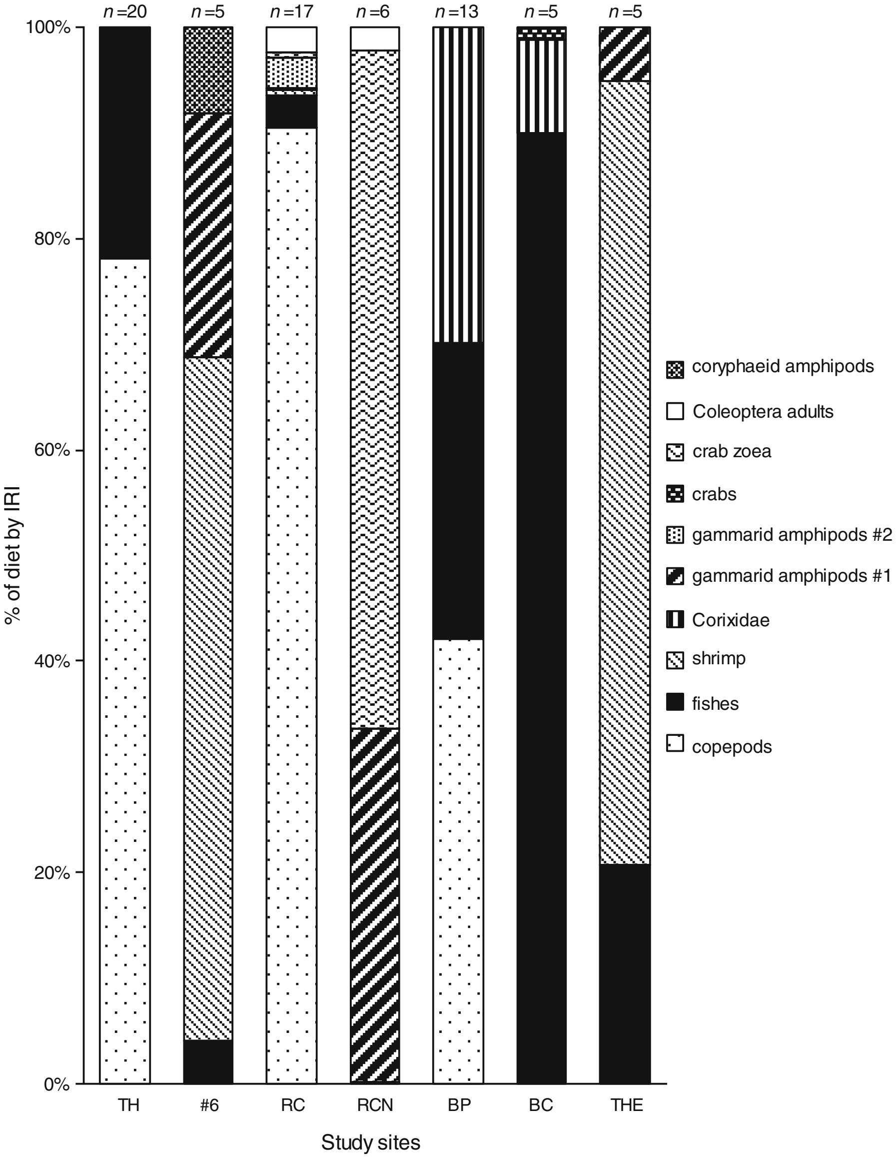


Fig. 5 Percent of diet by IRI (%IRI) for all tarpon that contained identifiable prey items. Data are categorized by study site. Only %IRI values greater than 0.9% are shown

Although dietary variation can be a result of genetic differences across a species' range, variation in diet for highly dispersive species like tarpon (McMillen-Jackson et al. 2005) is likely a result of localized feeding plasticity (Turingan et al. 1995; Crabtree et al. 1998; Cutwa and Turingan 2000). The ability of age-0 tarpon to feed on many different prey organisms may allow the species to inhabit a range of nursery habitats, including man-made marshes, despite potential shifts in prey abundance and diversity associated with anthropogenic disturbance. The classic notion that pristine ecosystems are the only valuable nursery habitats for marine organisms may not apply to all species. We have shown that when natural systems have been degraded or destroyed, human-altered habitats can assume a nursery role. As coastal areas become increasingly modified by man, the amount of natural nursery marsh habitat available to recruiting tarpon will continue to decline. Juvenile tarpon may become even more dependent on man-made mosquito control impoundments and restoration marshes as the degradation of coastal habitats continues.

Acknowledgments This research was funded in part through grants provided by Bonefish and Tarpon Trust, the Don Hawley Foundation, and the Florida Fly Fishing Association, as well as a teaching assistantship provided by Florida Institute of Technology. We are particularly grateful for the generous support and unlimited access provided by Jim David and the St. Lucie County Mosquito Control District. The fieldwork carried out during this study would not have been possible without the assistance of John O'Connell, Leslie Martin, Kate Heckman, Mike Gerlach, and Rick Oldham. Tarpon were collected pursuant to Florida Fish and Wildlife Conservation Commission Permit # 06SR-035.

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