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ARTICLE

Feeding Ecology of Dolphinfish in the Western Gulf of Mexico

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Abstract

Dolphinfish *Coryphaena hippurus* support important commercial and recreational fisheries in the Gulf of Mexico. Understanding the feeding ecology of this economically important pelagic fish is key to its sustainable management; however, dietary data from this region are sparse. We conducted a comprehensive diet study to develop new trophic baselines and investigate potential ontogenetic and sex-related shifts in Dolphinfish feeding ecology. The stomach contents of 357 Dolphinfish (27.6–148.5 cm TL) were visually examined from fishery-dependent sources off Port Aransas, Texas. Our analyses revealed a highly piscivorous diet with Actinopterygii comprising 70.44% of the stomach contents by number. The most commonly observed taxa were carangid (12.45%*N*) and tetraodontiform (12.08%*N*; families Balistidae, Monacanthidae, and Tetraodontidae) fishes. Malacostracans were also common (24.83%*N*), mostly in the form of pelagic megalopae. Other prey categories included squid and the critically endangered Kemp's Ridley sea turtles *Lepidochelys kempii*. Although increasingly common in larger fish, *Sargassum* spp. was found across a range of sizes in Dolphinfish, indicating that these fish feed from this drifting macroalgae throughout ontogeny. An ontogenetic shift from primary consumption of carangids and brachyurans in smaller size-classes to tetraodontids, monacanthids, and squid in larger size-classes was also observed. No sex-related difference in diet was observed. The overall infection rate for gastric parasites was 54%, an order of magnitude increase from that previously reported in the region, but consistent with recent studies from other areas. Trematode parasites in the genus *Dinurus* were found in 55% of stomachs and nematode parasites of the family Raphidascarididae in 16% of stomachs. Overall, Dolphinfish in the western Gulf of Mexico are highly opportunistic carnivores with a gastrointestinal parasite burden consistent with that reported in other ocean basins. These data will be important for sustainable management of this economically important species.

Numerous studies have demonstrated the key role of top predatory fishes in structuring marine communities (Bascompte et al. 2005; Frank et al. 2005; Heithaus et al. 2008; Baum and Worm 2009; Shackell et al. 2010). However, for logistical reasons, many of these studies have focused on coastal or

nearshore ecosystems, leaving a major gap in our understanding of how offshore species regulate food web dynamics in the more remote pelagic habitats. Such data limitations impede management of these economically important pelagic fish species and confound predicting potential ecosystemwide effects of

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removing these predators from pelagic ecosystems. Thus, more diet information on pelagic predators is needed to understand trophic interactions in these poorly studied environments.

The Dolphinfinch *Coryphaena hippurus* is an epipelagic fish with circumglobal distribution in tropical to subtropical waters (Gibbs and Collette 1959) and represents a model species in which feeding habits of pelagic predators can be examined. This species is fast growing and short lived, with an average life span of approximately 3–4 years (Schwenke and Buckel 2008). Dolphinfinch reach sexual maturity at around 50 cm TL (Massuti and Morales-Nin 1997; Schwenke and Buckel 2008) which correlates to an age of approximately 6 months for fish in the western Gulf of Mexico (Young 2014). Dolphinfinch grow rapidly in the first year, reaching lengths from 80 to 150 cm TL; afterwards growth slows, and an estimated maximum of 160–200 cm TL is reached by approximately age 3 (Palko et al. 1982; Lasso and Zapata 1999; Schwenke and Buckel 2008; Young 2014). Dolphinfinch in the Gulf of Mexico and the Caribbean Sea tend to have faster growth rates than those in other regions (Schwenke and Buckel 2008). However, the cause of this accelerated development and its relation to diet is unknown.

Perhaps due to their fast-growing nature, Dolphinfinch are known to be voracious eaters with a high metabolic rate (Benetti et al. 1995). The diet of Dolphinfinch has been examined in various ocean basins, including the Mediterranean Sea (Bannister 1976; Massuti et al. 1998), Arabian Sea (Varghese et al. 2013), Caribbean Sea (Oxenford and Hunte 1999), western Atlantic Ocean (Manooch et al. 1984; Rudershausen et al. 2010), and eastern Pacific Ocean (Olson and Galván-Magaña 2002; Torres-Rojas et al. 2014; Tripp-Valdez et al. 2015). However, only one study has examined Dolphinfinch diets in the Gulf of Mexico (Manooch et al. 1984), and this was conducted several decades ago. Thus, there is a lack of recent, region-specific, dietary information. However, Dolphinfinch are piscivorous predators with a diverse diet (Gibbs and Collette 1959; Manooch et al. 1984; Massuti et al. 1998; Oxenford and Hunte 1999; Castriota et al. 2007; Rudershausen et al. 2010; Varghese et al. 2013). In total, over 34 families of fish have been reported in the Dolphinfinch diet (Manooch et al. 1984; Varghese et al. 2013).

Dolphinfinch are primarily surface feeders that associate with floating offshore objects such as fish-aggregating devices (Castriota et al. 2007; Taquet et al. 2007) or floating beds of *Sargassum* spp. (Manooch et al. 1984; Rudershausen et al. 2010). Fish size can influence the foraging strategy of Dolphinfinch and in some areas larger size-classes may not rely on flotsam for food resources. Specifically, larger, older fish appear to display more complex behaviors when foraging, such as swimming in circles or surfing on waves while hunting elusive prey, while smaller and younger Dolphinfinch are more reliant on prey associated with flotsam (Nunes et al. 2015). Additionally, sex-related differences in feeding behavior have been observed. For example, in some regions such

as the western Atlantic Ocean and the Caribbean Sea, males tend to consume more open-water species than do females that consume more flotsam-associated prey (Rose and Hassler 1974; Oxenford and Hunte 1999). Conversely, in the eastern Pacific Ocean, there is apparently no difference in the diet between sexes (Castriota et al. 2007; Tripp-Valdez et al. 2010). To date, there is little understanding of dietary or trophic differences with ontogeny or sex in the western Gulf of Mexico.

High species richness and a high intensity of parasite infection are common in epipelagic fishes (Marcogliese 2002). Dolphinfinch are host to a diverse and unique community of gastric parasites (Burnett-Herkes 1974; Raptopoulou and Lambertsen 1987; Dyer et al. 1997; Carbonell et al. 1999; Williams and Bunkley-Williams 2009). Specifically, Dolphinfinch are the definitive host for digenean parasites of the genus *Dinurus*, which are commonly found in large numbers in the stomach cavity (Carbonell et al. 1999; Williams and Bunkley-Williams 2009). However, *Dinurus* parasites are not considered to be significant pathogens that would negatively impact the host's quality of life (Raptopoulou and Lambertsen 1987), but they are common endoparasites of Dolphinfinch in both the Mediterranean Sea and the western Atlantic Ocean (Raptopoulou and Lambertsen 1987; Carbonell et al. 1999), which demonstrates the potential connectivity between these distant habitats. Thus, the presence of certain parasites in stomachs can act as biological tags and yield information on fish migration and feeding ecology (Carbonell et al. 1999). Presently, the characterization of gastric parasites of Dolphinfinch has been limited in the Gulf of Mexico, impeding our understanding of potential infection rates and interbasin connectivity.

In the western Gulf of Mexico, Dolphinfinch support economically important recreational and commercial fisheries (Thompson 1999), but the dietary resources enabling Dolphinfinch to sustain their relatively high growth rates are not well studied. Such data have become very relevant in this region, where the oil spill from the Deepwater Horizon in 2010 exposed early life stages of several pelagic predatory fishes, including Dolphinfinch, to crude oil and dispersants (Rooker et al. 2013). Exposure of larval and juvenile fish to these toxicants may have impaired swimming performance (Mager et al. 2014), which has implications for increased mortality. Given their great capacity for large-scale migration (Merten et al. 2014a), Dolphinfinch have a high potential to integrate contaminants across the Gulf of Mexico. These findings suggest a need for more information on the feeding biology of these fish in the Gulf of Mexico, as this stock is potentially recovering from a poor 2010 cohort (Kitchens and Rooker 2014).

Our overall goal was to develop new baselines of Dolphinfinch feeding ecology in the northwestern Gulf of Mexico region and provide data to support the sustainable management of this species. Specifically, we sought to

produce a specific survey of diets for Dolphinfish in the western Gulf of Mexico and quantify their prey in relation to ontogeny and sex. Further, a preponderance of gastric parasites in stomach contents provided us with an additional opportunity to assess the prevalence of infection in Dolphinfish.

METHODS

Dolphinfish ($n = 357$) were collected from fish processing houses in Port Aransas, Texas, from October 2010 to December 2011. All fish were captured in Gulf of Mexico waters near Port Aransas. Fish were measured for FL and TL to the nearest centimeter. Fish were sexed by visual inspecting external morphology (Beardsley 1967) and dissected reproductive organs when available. Due to the fishery-dependent nature of the sampling, collection dates were unavailable for some fish. Whole weight (WW) was directly obtained for 32 individuals, while estimates for the remaining individuals were calculated using FL–WW conversions following that of Young (2014):

$$WW = 1.5696 - 0.0915 \times FL + 0.0017 \times FL^2.$$

Stomachs were removed from individuals, placed intact into perforated plastic bags, and fixed in 10% formalin for 48 h. Fixed stomachs were transferred to 70% ethanol for long-term storage. Prey items were identified to the lowest possible taxon (LPT), enumerated, and weighed (mg). Stomachs containing only parasites were considered “empty” as defined by Manooch et al. (1984); however, these stomachs were still used to assess overall vacuity. Percent by weight (%W), percent by number (%N), and percent frequency of occurrence (%O) were calculated for each LPT. Because some metrics can overinflate the importance of small, numerous prey items (Hyslop 1980), a percent index of relative importance (%IRI) was also calculated (Cortes et al. 1997):

$$\%IRI_a = \frac{100 \times IRI}{\sum_{a=1}^n IRI},$$

where $IRI_a = (\%N + \%W) \times \%O$ and a represents samples from 1 to n . Gastric endoparasites were identified and the overall prevalence of infection was quantified.

Sample-size sufficiency across ontogeny was assessed with a cumulative prey curve (Ferry and Caillet 1996). The curve was created in PRIMER version 6 and determined the maximum number of expected prey taxa (S_{max}) and the actual number of prey taxa across samples (S_{obs}) based on the LPT level of identification. To remove the effect of sampling chronology on curve smoothness, the order was randomized across 999 permutations. Sample-size sufficiency in explaining dietary breadth (i.e., asymptotic characteristics) was examined by visual inspection.

Ontogenetic and sex-associated trends in diet composition were assessed using multivariate techniques. We conducted these analyses on prey weights, which were standardized to fish size by dividing the weight of each individual prey item by the individual body weight of the fish (Ajemian and Powers 2012). Standardized prey group weights and numbers were imported into PRIMER, fourth-root transformed, and used to develop a Bray–Curtis similarity matrix. A two-way, crossed permutational, multivariate analysis of variance (PERMANOVA) was used to evaluate differences in diet composition among the various size-classes and sexes (Anderson 2001). Individual Dolphinfish were assigned to one of five size-classes based on 25-cm increments. These size-classes were chosen as they may represent potential ontogenetic shifts that occur with different year-classes and sexual maturity (Young 2014). Binning allowed for an adequate number of samples for each class and a comparison with those of Manooch et al. (1984) who used 20-cm bins. All tests were permuted 999 times under a reduced model (Anderson 2001). Significant factors were further analyzed using PERMANOVA pairwise comparisons, and similarity percentage (SIMPER) analysis was employed to examine the prey items most responsible for the separation among factors (Clarke 1993). We accompanied our analysis with a distance-based test for homogeneity of multivariate dispersions (PERMDISP) to determine possible reasons for the rejection of the null hypothesis (no differences in diet composition) by PERMANOVA, as this test can be sensitive to sample dispersion (Anderson 2006).

RESULTS

Of the 357 stomachs collected 281 contained identifiable prey items. For each size-class the following sample sizes were analyzed: 25–49 cm ($n = 44$), 50–74 cm ($n = 199$), 75–99 cm ($n = 70$), 100–124 cm ($n = 23$), and 125–149 cm ($n = 21$). The cumulative prey curve approached an asymptote, which suggested that the sample size was sufficient to describe the diet (maximum number of unique taxa, or $S_{obs} = 33$, $S_{max} = 33.74$; Figure 1). Fish size ranged from 27.6 to 148.5 cm TL (Figure 2). Sex distribution was 205 females (57%), 134 males (38%), and 18 (5%) undetermined. No prey items were found in 77 individuals (22%). The majority of empty stomachs were from fish of unidentifiable sex (72%), followed by female fish (20%) and males (18%). The smallest size-class (25–49 cm) had the greatest percentage of empty stomachs (32%), followed by the largest size-class (125–149 cm, 29%), the 50–74-cm size-class (22%), the 75–99-cm size-class (16%), and the 100–124-cm size-class (13%; Figure 2). Four major taxonomic classes of prey were identified: Cephalopoda, Malacostraca, Osteichthyes, and Testudines (Table 1). Overall, sargassum occurred in 26% of all stomachs. Sargassum was most common item in the largest size-class (125–149 cm; 43%), followed by the 100–124-cm (30%), 50–74-cm (25%), 75–99-cm (24%), and 25–49-cm (20%) size-classes. Sargassum was more common in males (31%), than in females (24%).

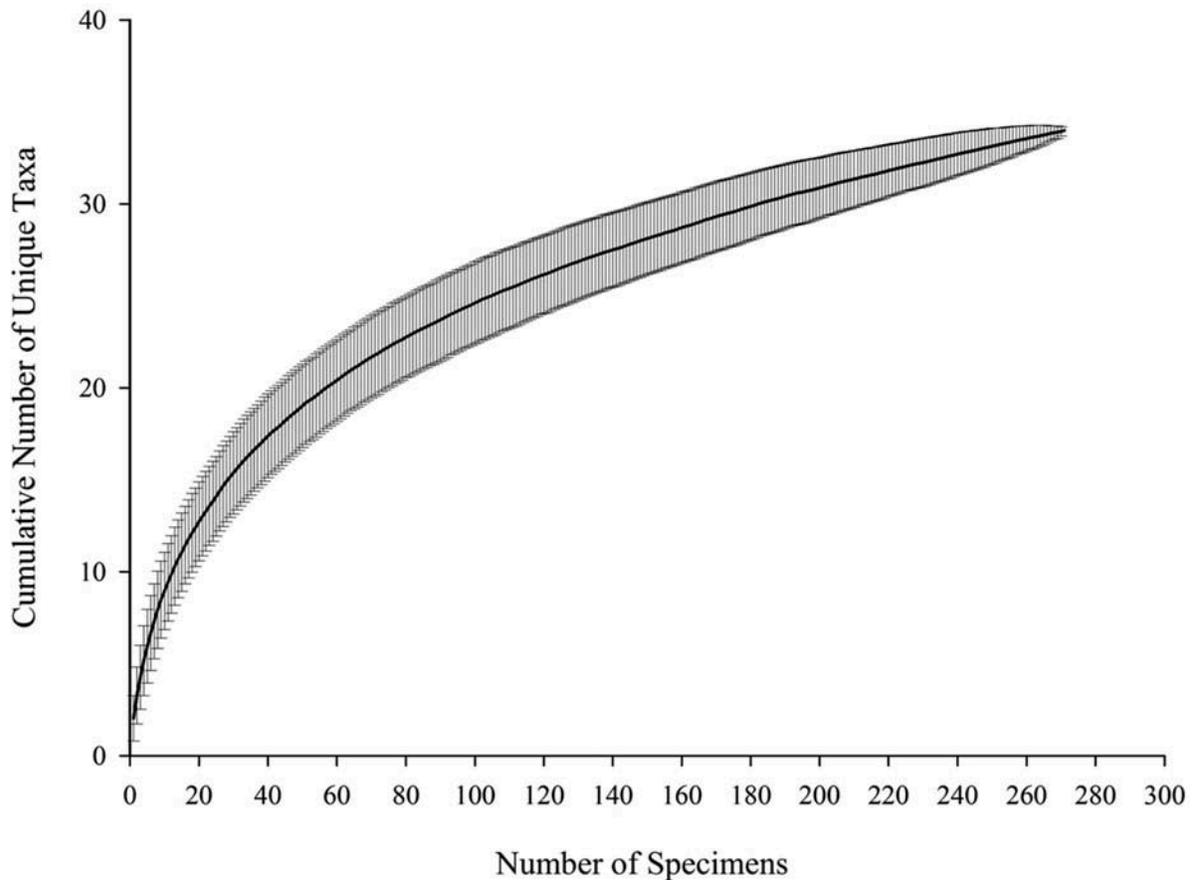


FIGURE 1. Cumulative prey curve plotting mean (\pm SE) of unique prey items and number of specimens examined for Dolphinfish ($n = 357$) collected in the western Gulf of Mexico ($S_{\text{obs}} = 33$, $S_{\text{max}} = 33.74$).

Pooled data for all size-classes of Dolphinfish indicated a diet dominated by bony fishes (Osteichthyes), regardless of the metric used. By number, Osteichthyes was the most important prey class (70.57% N ; Table 1), followed by Malacostraca (24.85% N), Cephalopoda (3.45% N), and Testudines (1.28% N). Within Osteichthyes, the most dominant fish families by number were Carangidae (9.53% N), Tetraodontidae (4.88% N), Monacanthidae (4.88% N), and Balistidae (2.63% N). By weight, Osteichthyes was also the most important prey class (80.80% W), followed by Testudines (2.05% W), Malacostraca (1.15% W), and Cephalopoda (0.47% W ; Table 1). Osteichthyan families contributing the most by weight included Carangidae (17.17% W), Monacanthidae (7.42% W), Tetraodontidae (5.43% W), and Balistidae (2.98% W). Using the compound metric %IRI, Osteichthyes was the most important prey class (96.51%IRI), followed by Malacostraca (3.15%IRI), Cephalopoda (0.31%IRI), and Testudines (0.01%IRI; Table 1). The Osteichthyes family with the highest %IRI was Carangidae (4.86%IRI), followed by Monacanthidae (1.26%IRI), Tetraodontidae (1.04%IRI), and Balistidae (0.49%IRI; Figure 3).

When diets were analyzed by size-class (25-cm bins), an ontogenetic shift was observed. By number, Malacostraca was

the most important prey item (68.17% N) for the smallest size-class (25–49 cm). However, by weight, this prey group was less important (7.24% W ; Table 2). Malacostraca was dominated by small megalopae, classified as Brachyura (39.46% N), which were often consumed in large quantities (Table 2), as well as other small, unidentifiable crustaceans (Decapoda, 26.01% N). For all but the smallest size-class, the diet was over 50% Osteichthyes by number, with a much lower percentage of malacostracans (Table 2). While Osteichthyes was the primary prey category in most size-classes (except 25–49 cm) for all metrics, we observed variability in the importance of different fish families among size-classes. Based on %IRI, Carangidae was the most important identifiable fish family for the smallest size-classes (25–49 cm, 50–74 cm, and 75–99 cm); however, for the 100–124-cm size-class, Balistidae was the most important (3.93%IRI) and for 125–149-cm size-class, Tetraodontidae (17.10%IRI) and Monacanthidae (12.57%IRI) were most important (Figure 3). One incident of cannibalism was observed in the 50–74-cm size-class (0.02%IRI). Consumption of nine juvenile Kemp's Ridley sea turtles *Lepidochelys kempii* was found in a single individual measuring 148 cm TL (3.92%IRI). The turtles ranged in size from 35.4 to 47.5 mm in carapace length.

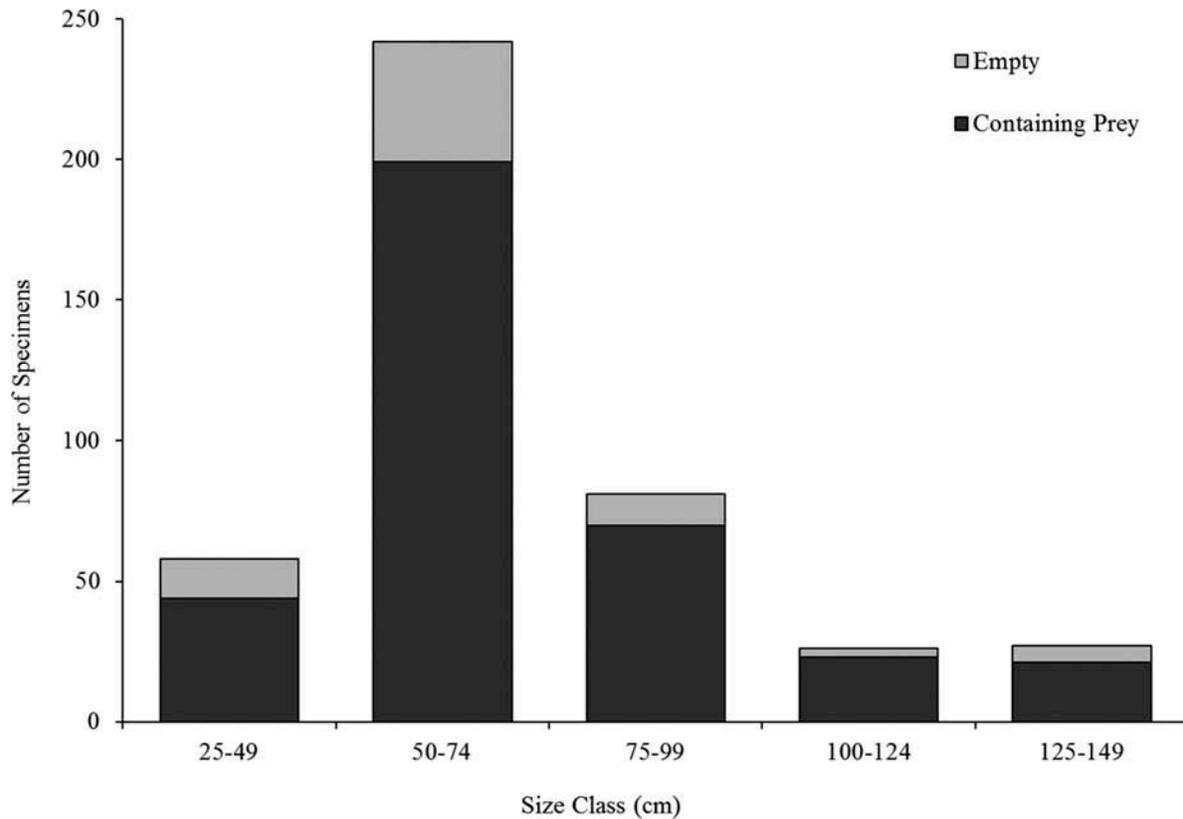


FIGURE 2. Distribution by size-class (25-cm bins) for TLs (cm) of Dolphinfish collected showing empty stomachs and stomachs containing prey; size-classes were 25–49 cm ($n = 44$), 50–74 cm ($n = 199$), 75–99 cm ($n = 70$), 100–124 cm ($n = 23$), and 125–149 cm ($n = 21$).

A two-way crossed PERMANOVA on standardized weights of LPT found no significant interaction between the factors sex and size-class (PERMANOVA: Pseudo- $F_{4, 171} = 1.341$, $P = 0.059$; Table 3). Assessing the two factors individually, sex was not significant (PERMANOVA: Pseudo- $F_{1, 171} = 1.044$, $P = 0.383$); however, size-class was significant (PERMANOVA: Pseudo- $F_{4, 171} = 3.269$, $P = 0.001$; Table 3). Subsequent pairwise comparisons indicated that all size-classes were significantly different from each other except the two largest, 100–124 cm and 125–149 cm (PERMANOVA: $t = 1.2123$, $P = 0.155$; Table 4). The PERMDISP analysis found that these size-class differences were not explained by sample dispersion (PERMDISP: $P = 0.479$), and all size-classes had similar mean deviations from the centroid. The SIMPER analysis showed the main contributors to the dissimilarities between the smallest (25–49 cm) and the three largest size-classes (75–99, 100–124, and 125–149 cm) to be a greater abundance of brachyurans and carangids in the diet of the smaller fish (Table 4). The presence of squid in diets of the 100–124-cm size-class and tetraodontids in the 125–149-cm size-class also contributed to these dissimilarities (Table 4).

The overall gastric parasite infection rate was 68%. Prevalence varied by size-class, and there was a general trend of increased parasite burden with increased TL

(Figure 4). However, percent occurrence was highest for the 100-cm bin. Two endogastric parasites were identified: the hemurid digenean, *Dinurus* sp., (55.16% rate of infection) and the nematode, *Hysterothylacium pelagicum*, (16.37% rate of infection). There were two occurrences of a digenean parasite that could not be identified beyond subclass.

DISCUSSION

Similar to other locations, Dolphinfish in the western Gulf of Mexico are opportunistic predators with a diet dominated by fishes. The diet of this very mobile fish includes a wide array of fish families from the pelagic realm, which is congruent with its habitat use patterns as Dolphinfish are known to spend 60% of their time in the surface layer of the ocean (Merten et al. 2014b). We found ontogenetic shifts in prey for both fish and nonfish prey items; however, unlike some other locations, there were no sex-related differences observed in the diet for this region. Overall, though there were notable dietary changes throughout ontogeny, Dolphinfish in the Gulf of Mexico appear highly dependent on the pelagic environment for food resources.

An ontogenetic shift was observed around sexual maturity (50–74 cm) for both males and females, where diets transitioned from brachyurans, carangids, and balistids to tetraodontids,

TABLE 1. Overall composition of Dolphinfish ($n = 357$) diet by prey class and lowest possible taxon showing percent frequency of occurrence (% O), percent by number (% N), percent by weight (% W), and index of relative importance (%IRI). Calculations for %IRI were performed without innumerable contents (i.e., sargassum, marine trash, and unidentified contents). Values in bold text represent totals for prey class. NI = not identifiable beyond major taxon.

Prey class	Major taxon	Lowest possible taxon	% O	% N	% W	%IRI
Cephalopoda	Teuthida	Teuthida	2.66	3.20	0.47	0.31
Malacostraca			14.97	23.00	1.15	3.15
	Amphipoda, NI	Amphipoda	1.12	1.18	0.04	0.04
	Brachyura	Brachyura	7.13	11.67	0.41	2.71
	Caridea	Caridea	0.14	0.70	0.01	<0.01
	Decapoda, NI	Decapoda	1.54	4.17	0.04	0.20
	Hippolytidae	<i>Latreutes parvulus</i>	0.28	0.14	<0.01	<0.01
	Isopoda, NI	Isopoda	2.10	1.46	0.04	0.10
	Penaeidae	<i>Farfantepenaeus</i> sp.	0.28	0.14	0.24	<0.01
	Portunidae	<i>Callinectes sapidus</i>	0.14	0.21	0.07	<0.01
		Portunidae	0.84	1.39	0.17	0.04
		<i>Portunus sayi</i>	0.42	0.21	0.07	<0.01
	Stomatopoda, NI	Stomatopoda	0.98	1.74	0.06	0.06
Osteichthyes			67.27	65.25	80.01	96.49
	Actinopterygii, NI	Actinopterygii	37.34	38.99	33.59	88.60
	Balistidae	Balistidae	2.94	2.29	2.75	0.49
		<i>Canthidermis sufflamen</i>	0.14	0.139	0.23	<0.01
	Belonidae	Belonidae	0.14	0.07	0.68	<0.01
	Carangidae	Carangidae	7.41	8.83	10.61	4.74
		<i>Caranx crysos</i>	0.14	0.07	0.30	<0.01
		<i>Caranx</i> sp.	0.28	0.278	1.36	0.02
		<i>Chloroscombrus chrysurus</i>	0.14	0.069	0.01	<0.01
		<i>Decapterus punctatus</i>	0.14	0.14	1.30	0.01
		<i>Decapterus</i> sp.	0.28	0.21	0.72	0.01
		<i>Hemicaranx amblyrhynchus</i>	0.98	1.53	0.36	0.06
		<i>Oligoplites saurus</i>	0.14	0.14	0.14	<0.01
		<i>Selar crumenophthalmus</i>	0.42	0.21	0.75	0.01
		<i>Seriola rivoliana</i>	0.14	0.07	1.62	0.01
	Clinidae	Clinidae	0.14	0.14	0.10	<0.01
	Clupeidae	Clupeidae	0.56	0.28	2.15	0.05
		<i>Jenkinsia lamprotaenia</i>	0.14	0.07	1.07	0.01
	Coryphaenidae	<i>Coryphaena hippurus</i>	0.14	0.07	1.28	0.01
	Diodontidae	<i>Diodon holocanthus</i>	0.70	0.49	0.01	<0.01
		<i>Diodon hystrix</i>	0.28	0.14	0.05	<0.01
		<i>Diodon</i> sp.	0.14	0.07	0.31	<0.01
	Exocoetidae	Exocoetidae	1.26	0.70	1.92	0.11
	Haemulidae	<i>Orthopristis chrysoptera</i>	0.14	0.07	0.51	<0.01
	Hemiramphidae	Hemiramphidae	0.14	0.07	0.57	<0.01
		<i>Hemiramphus brasiliensis</i>	0.28	0.14	0.88	0.01
	Istiophoridae	<i>Istiophorus platypterus</i>	0.14	0.07	<0.01	<0.01
	Kyphosidae	<i>Kyphosus sectatrix</i>	0.14	0.07	<0.01	<0.01
	Monacanthidae	<i>Aluterus scriptus</i>	0.14	0.14	0.43	<0.01
		<i>Aluterus</i> sp.	0.14	0.07	<0.01	<0.01
		<i>Cantherhines</i> sp.	4.48	3.06	4.95	1.19
		Monacanthidae	0.84	0.49	2.03	0.07
		<i>Oxymonacanthus longirostris</i>	0.14	0.07	<0.01	<0.01
		<i>Stephanolepis hispidus</i>	0.14	0.07	0.01	<0.01
	Pomatomidae	<i>Pomatomus saltatrix</i>	0.14	0.14	0.26	<0.01

TABLE 1. Continued.

Prey class	Major taxon	Lowest possible taxon	%O	%N	%W	%IRI
	Scaridae	Scaridae	0.14	0.28	0.04	<0.01
	Scombridae	Scombridae	0.56	0.35	0.18	0.01
	Sparidae	<i>Lagodon rhomboides</i>	0.28	0.21	1.96	0.02
		Sparidae	0.14	0.07	0.58	<0.01
	Syngnathidae	<i>Hippocampus</i> sp.	0.14	0.07	0.02	<0.01
	Tetraodontidae	<i>Lagocephalus laevis</i>	0.14	0.28	0.35	<0.01
		<i>Sphoeroides</i> sp.	0.28	0.83	0.09	0.01
		Tetraodontidae	3.78	3.27	4.98	1.03
	Tetraodontiformes, NI	Tetraodontiformes	0.56	0.28	0.05	0.01
	Trichiuridae	<i>Trichiurus lepturus</i>	0.14	0.07	0.15	<0.01
	Triglidae	Triglidae	0.28	0.14	0.66	0.01
Testudines	Cheloniidae		0.28	1.18	2.05	0.01
		Cheloniidae	0.14	0.56	0.01	<0.01
		<i>Lepidochelys kempii</i>	0.14	0.63	2.04	0.01
Phaeophyceae	Sargassaceae	<i>Sargassum</i> sp.	12.87	6.39		
Marine trash			1.96	0.97		
Unidentified					15.50	

monocanthids, and squid (teuthida). This dietary shift may be a result of ontogenetic changes in habitat use. Mature Dolphinfish make deep dives as night, which may provide increased opportunities for larger fish to find more diverse prey resources (Merten et al. 2014b). It is also possible that squid are being consumed as they make diel vertical migrations towards the surface at night (Passarella and Hopkins 1991), which may make them more available to epipelagic fishes.

In our study, the prevalence of the two of the most commonly observed fish families, Carangidae and Monacanthidae, in the diets had divergent trends with Dolphinfish TL. Specifically, carangids were most common in diets of the smallest size-class, while monocanthids increased in importance with the larger size-classes. This dietary shift may be the result of changing foraging strategies with age (Nunes et al. 2015) or simply gape limitation. Ontogenetic shifts in Dolphinfish diets have been observed in other regions; however, specific trends in feeding have varied by location (Manooch 1984; Tripp-Valdez 2015). Our study suggests that Dolphinfish feeding ecology and habitat use are highly dynamic and vary ontogenetically throughout the species' range.

We also observed dietary shifts when examining nonfish prey items. Brachyuran megalopae were numerically dominant in smaller size-classes, where large quantities of these small prey items (up to 53 individuals) were often consumed. Other studies from the Gulf of California have shown Dolphinfish consume large quantities of megalopae, presumably due to availability and ease of capture (Tripp-Valdez et al. 2010), both of which may be important for these faster-growing,

small size-classes. Conversely, in larger size-classes of Dolphinfish, swimming crabs (Portunidae) were numerically dominant for the prey class Malacostraca. Dolphinfish may require more skill to capture these more elusive prey than drifting planktonic megalopae. These findings emphasize that ontogenetic change in feeding ecology may also be driven by the increased feeding agility of fish from larger size-classes, as reported by Nunes et al. (2015).

This is the first documented report of the presence of endangered Kemp's Ridley sea turtles in the Dolphinfish diet. Although sea turtles were found in only a single Dolphinfish in the present study, reports from regional online fishing boards have also documented sea turtle consumption in the Gulf of Mexico (e.g., see <http://www.thefishingwire.com/features/224956>). The proximity of Texas to the only known natural Kemp's Ridley sea turtle nesting site (Rancho Nuevo, Tamaulipas, Mexico) and local statewide head start (Caillouet et al. 2015) and other hatchling release programs may cause Dolphinfish to encounter relatively higher densities of hatchlings as they disperse from nests along Gulf of Mexico shorelines. Indeed, turtles observed in this study were at hatchling size (Marquez 1994). Similarly, sea turtle hatchling predation has also been documented in the Atlantic Ocean in the diet of Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae* (Delorenzo et al. 2015). These young sea turtles are also known to associate with pelagic sargassum in this region (Witherington et al. 2012), which may aggregate them in preferred Dolphinfish habitat (see below). Additionally, anecdotal reports from commercial fishers in Oaxaca, Mexico, describe sea turtle predation by Dolphinfish as a fairly

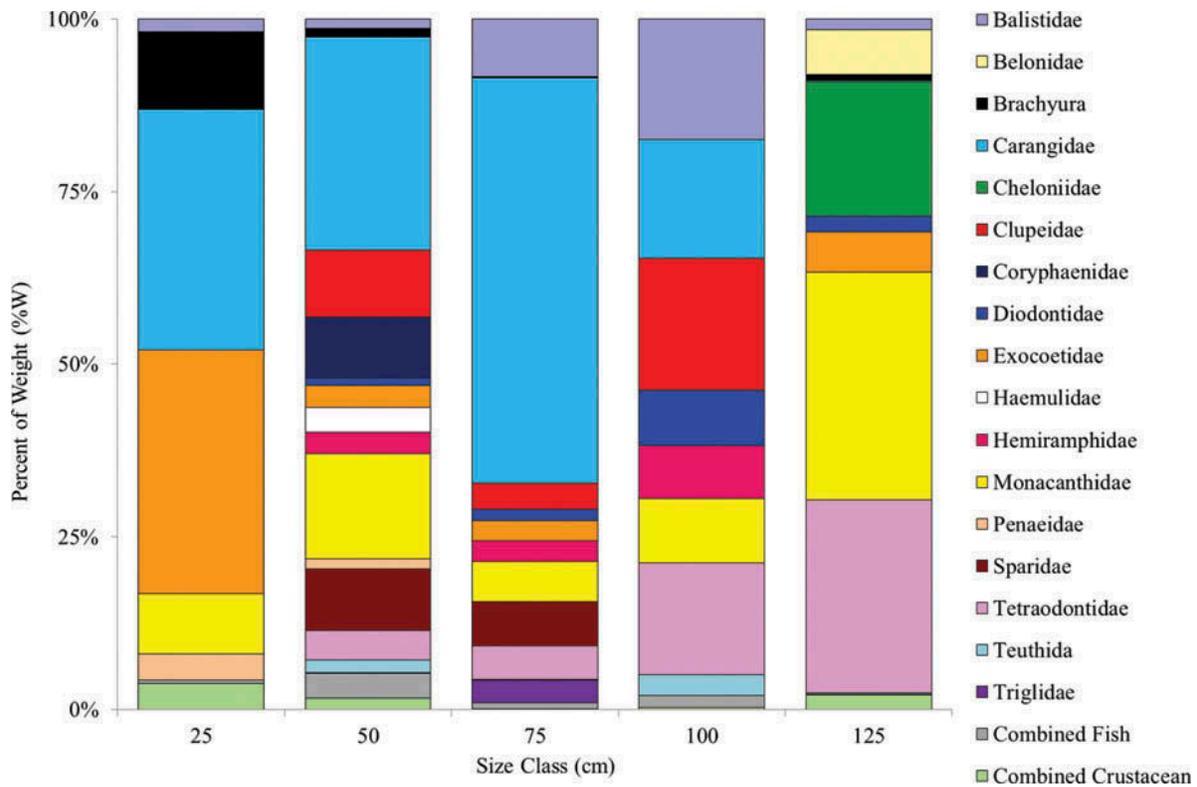


FIGURE 3. Percent by weight (%W) for prey families or lowest possible taxon (LPT) observed in Dolphinfish diets by size-class (cm TL); size-classes were 25–49 cm ($n = 44$), 50–74 cm ($n = 199$), 75–99 cm ($n = 70$), 100–124 cm ($n = 23$), and 125–149 cm ($n = 21$). LPTs contributing <5% were combined by taxonomic class: Combined Fish (Clinidae, Istiophoridae, Kyphosidae, Pomatomidae, Scaridae, Scombridae, Sygnathidae, Tetradontiformes, and Trichiuridae) and Combined Crustaceans (Amphipoda, Caridea, Decapoda, Hippollitidae, Isopoda, Portunidae, and Stomatopoda).

common occurrence in the eastern Pacific Ocean as well (F. Galguera, Puerto Angel, personal communication). These convergent findings suggest that the Dolphinfish is an important chelonian predator and may feed on more diverse resources than previously considered.

The nondiscriminatory feeding habits of Dolphinfish are evidenced by the fairly common occurrence of nonfood items in the stomach contents. Such items included pieces of rope, plastic ribbons, hard plastic bits, and a badminton shuttlecock. This nondiscriminatory feeding style has also been described in many other locales (Gibbs and Collette 1959; Rose and Hassler 1974; Manooch et al. 1984; Rudershausen et al. 2010; Varghese et al. 2013). The most common nonfood item, sargassum, was observed in 26% of stomachs analyzed, and the presence of sargassum in stomach contents was found to increase with Dolphinfish TL. These findings suggest that Dolphinfish increase their use of sargassum habitat with age. However, all fish size-classes had prey items associated with sargassum habitats in the Gulf of Mexico (Wells and Rooker 2004b; Hoffmayer et al. 2005; Taylor et al. 2015). Therefore, it is likely that sargassum is ingested while feeding on fish and other organisms using this floating structure as habitat, and this may be more conspicuous in larger individuals capable of

ingesting larger pieces of this macroalgae. It is also possible that some nutrition may be gained from the ingestion of plant material as suggested by Bethea et al. (2007) in their analysis of Bonnethead *Sphyrna tiburo* diets. Therefore, future diet studies may want to further investigate the nutritional contribution of sargassum to Dolphinfish. Sargassum forms large lines and mats offshore and supports a diverse community of transient and juvenile fishes and invertebrates that comprise an important prey base for pelagic fish predators (SAFMC 2002; Wells and Rooker 2004b; Hoffmayer et al. 2005; Taylor et al. 2015). In previous studies the presence of sargassum was observed to be a common occurrence in Dolphinfish stomach contents, ranging from 28% (Rose and Hassler 1974) to 48% (Manooch 1984), and throughout size-classes (Rudershausen et al. 2010). Our findings and previous work documenting consumption of floating nonfood items and sargassum confirm Dolphinfish reliance on dynamic pelagic habitats. As per Manooch et al. (1984), this feeding behavior may make this economically important species vulnerable to anthropogenic impacts, such as oil spills, along the ocean surface.

We observed no differences in prey consumed between sexes; however, in the Gulf of Mexico, slower growth rates and younger sexual maturity have been estimated for females

TABLE 2. Continued.

Taxonomic group	Percent by number (%N)				Percent by weight (%W)				Index of relative importance (%IRI)						
	25	50	75	100	125	25	50	75	100	125	25	50	75	100	125
Scaridae		0.54				0.13						<0.01			
Scombridae	0.45	0.40	0.41			0.18		0.41			0.02		0.01		
Sparidae		0.27	0.82			3.75		3.52				0.02		0.15	
Syngnathidae		0.13				0.05						<0.01			
Tetraodontidae		3.76	3.67	8.93	15.79	1.78		2.67	6.87	19.88		0.40		0.73	17.10
Tetraodontiformes		0.27	0.41		0.88	0.04		0.08		0.09		<0.01		0.01	0.07
Trichiuridae		0.13				0.45						<0.01			
Triglidae		0.13	0.41			0.03		1.83				<0.01		0.04	
Testudines, Cheloniidae					14.91					13.77					3.92
Sargassum	4.04	7.38	9.80	7.14	8.77										
Unidentified	8.55	11.65	15.33	13.33	11.11	14.60	13.94	13.04	28.34	13.76	16.95	12.51	19.47	35.11	22.39

TABLE 3. Results from a two-way crossed PERMANOVA of Dolphinfish dietary composition among size-classes (25-cm bins) and sex; SS = sum of squares, MS = mean sum of squares.

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (permutation)	Unique permutations
Size-class	4	51,446	12,861	3.269	0.001	999
Sex	1	4,106.2	4,106.2	1.044	0.383	997
Size-class × Sex	4	21,101	5,275.2	1.341	0.059	995
Residual	162	6.37×10^5	3,934.8			
Total	171	7.21×10^5				

(Young 2014). As diet composition was similar between sexes, differing growth rates suggest that females in this region are devoting energy to processes other than somatic growth. For example, female Dolphinfish in the Gulf of Mexico may be dedicating more energy towards reproduction than males. In the Pacific Ocean, females can reach maturity at smaller sizes (Alejo-Plata et al. 2011), and in that region similar feeding ecology between sexes has also been observed through stomach content (Tripp-Valdez et al. 2010; Torres-Rojas et al. 2014) and stable isotope analysis (Tripp-Valdez et al. 2015). As such, despite varying growth rates and potential differences in energetic requirements, males and females still appear to occupy similar ecological feeding niches across a large portion of the species' range.

We found Dolphinfish to have a high gastric parasite burden that increased with fish size, congruent with the findings of Burnett-Herkes (1974) and Manooch (1984). The endoparasites present in this research were similar to those found in other locales globally (Carbonell et al. 1999). The most prevalent gastric parasite we observed, *Dinurus*, has been observed in Dolphinfish from the Mediterranean and Caribbean seas (Carbonell et al. 1999) and is a characteristic parasite of the species (Williams and Bunkley-Williams 2009). The proposed life cycle for *Dinurus* suggests that either benthic gastropods or planktivorous fishes (e.g., clupeids) act as intermediate hosts, of which Dolphinfish are the definitive host (Carbonell et al. 1999). This scenario appears plausible in the Gulf of Mexico given that the size-class with the highest occurrence of clupeid fish in the diet (i.e., 100–124 cm) had the greatest prevalence of *Dinurus* infection. The second most commonly observed parasite, *Hysterothylacium pelagicum*, is also endemic to Dolphinfish (Williams and Bunkley-Williams 2009) and has been previously observed in the Gulf of Mexico, Atlantic and Pacific oceans, and Caribbean Sea (Deardorff and Overstreet 1982; Manooch 1984; Dyer et al. 1997). The intermediate hosts of parasites from the genus *Hysterothylacium* are not well defined, although the parasites are thought to reach sexual maturity in the digestive tract of bony fishes or other vertebrates (Marcogliese 1995). In this study, only the stomach was examined. Thus, any additional parasites occupying the intestines would not have been accounted for. As *H. pelagicum* inhabits both the stomach cavity and intestines (Williams and Bunkley-Williams 2009),

the prevalence observed in this study is likely an underestimation. Nonetheless, the overall percentage of gastric parasitism observed (54%) was higher than the 5% found by Manooch et al. (1984) in the same region. This difference could be due to increases in prevalence of the parasite for the region over the last 30 years, or to our larger sample size (122 versus 357 individuals, respectively). Parasite species have the potential to be identified using molecular methods. Unfortunately, since all stomachs in this study were fixed in formalin, which degrades DNA, this approach was not possible. Future studies may consider alternative stomach and intestinal fixation protocols in order to apply molecular methods to further refine these parasite and dietary analyses. A complete parasitic assessment in this region would allow for a better understanding of the health of the Dolphinfish population as well as its trophic position in the offshore food web.

The families of fish that dominated the observed diet in this study (Carangidae, Balistidae, Monacanthidae, and Tetraodontidae) are common to offshore, pelagic habitats (SAFMC 2002; Wells and Rooker 2004b; Taylor et al. 2015). However, these families also have unique morphological characteristics that make them identifiable even in advanced states of decomposition. For example, carangids can be identified by caudal scutes, balistids (and monacanthids) by location and number of dorsal spines, and tetraodontids by their unusual beak (Hoese and Moore 1998). This greater conspicuousness, even as most scales, fin rays, and other morphological characters have been digested, may have potentially inflated the importance of these families in the diet. Depending on size-class, anywhere from 15% to 47% of prey fish were not identifiable beyond the superclass Osteichthyes. Similar to parasite studies, continued research into the feeding habits in the region would be greatly enhanced by the inclusion of DNA-based identification (i.e., barcoding), which has proven useful in understanding marine fish diets by successfully identifying prey fish in advanced states of digestion (Valdez-Moreno et al. 2012; Cote et al. 2013).

Dolphinfish are an important fisheries species with a high dependence on pelagic resources throughout ontogeny. The primary components of their diet in the western Gulf of Mexico included fish from the families Balistidae, Monacanthidae, and Carangidae. Some of these prey items are likely fishery species including Gray Triggerfish *Balistes capriscus* and Greater

TABLE 4. Results from a two-way, crossed similarity percentage (SIMPER) analyses for significant effects by size-class on Dolphinfish dietary data. Average abundances are multiplied by 1×10^5 ; sample sizes for total length bins were 25–49 cm (25; $n = 44$), 50–74 cm (50; $n = 199$), 75–99 cm (75; $n = 70$), 100–124 cm (100; $n = 23$), and 125–149 cm (125; $n = 21$).

Taxon	Abundance	Average dissimilarity \pm SD	Contribution (%)	Cumulative contribution (%)
25 versus 50 cm; $t = 1.4908$, $P = 0.014$				
Average dissimilarity = 87.99	25	50		
Carangidae	0.97	0.72	18.02 ± 0.80	20.48
Brachyura	1.28	0.46	17.76 ± 0.88	20.19
Balistidae	0.32	0.24	12.84 ± 0.56	14.59
25 versus 75 cm; $t = 1.7774$, $P = 0.002$				
Average dissimilarity = 88.91	25	75		
Brachyura	1.28	0.41	20.31 ± 0.93	22.84
Carangidae	0.97	0.63	18.22 ± 0.83	20.49
Balistidae	0.32	0.19	10.64 ± 0.50	11.96
25 versus 100 cm; $t = 1.8932$, $P = 0.001$				
Average dissimilarity = 97.25	25	100		
Brachyura	1.28	0.06	16.79 ± 0.82	17.26
Carangidae	0.97	0.14	14.04 ± 0.81	14.44
Balistidae	0.32	0.32	12.70 ± 0.58	13.05
Teuthida	0.00	0.49	9.51 ± 0.53	9.77
25 versus 125 cm; $t = 2.2363$, $P = 0.001$				
Average dissimilarity = 95.35	25	125		
Brachyura	1.28	0.08	15.27 ± 0.86	16.02
Carangidae	0.97	0.17	12.27 ± 0.87	12.86
Monacanthidae	0.32	0.52	9.82 ± 0.86	10.30
Tetraodontidae	0.00	0.61	9.24 ± 0.74	9.69
Portunidae	0.11	0.46	8.50 ± 0.72	8.91
50 versus 75 cm; $t = 1.5172$, $P = 0.013$				
Average dissimilarity = 86.99	50	75		
Carangidae	0.72	0.63	21.52 ± 0.84	24.74
Brachyura	0.46	0.41	15.2 ± 0.71	17.47
Monacanthidae	0.25	0.14	9.33 ± 0.48	10.72
50 versus 100 cm; $t = 1.922$, $P = 0.001$				
Average dissimilarity = 92.33	50	100		
Carangidae	0.72	0.14	14.28 ± 0.73	15.47
Teuthida	0.10	0.49	11.86 ± 0.58	12.85
Monacanthidae	0.25	0.32	10.80 ± 0.59	11.70
Balistidae	0.24	0.32	9.28 ± 0.46	10.05
50 versus 125 cm; $t = 2.2007$, $P = 0.001$				
Average dissimilarity = 89.84	50	125		
Tetraodontidae	0.24	0.61	14.08 ± 0.94	15.67
Monacanthidae	0.25	0.52	13.17 ± 1.00	14.66
Carangidae	0.72	0.17	12.20 ± 0.81	13.58
Portunidae	0.06	0.46	8.04 ± 0.64	8.95
75 versus 100 cm; $t = 1.7372$, $P = 0.001$				
Average dissimilarity = 92.12	75	100		
Carangidae	0.63	0.14	14.68 ± 0.74	15.93
Teuthida	0.14	0.49	13.91 ± 0.65	15.10
Balistidae	0.19	0.32	11.34 ± 0.52	12.30
Tetraodontidae	0.19	0.23	9.91 ± 0.51	10.75
75 versus 125 cm; $t = 2.0404$, $P = 0.001$				
Average dissimilarity = 91.53	75	125		
Tetraodontidae	0.19	0.61	13.81 ± 0.92	15.08
Carangidae	0.63	0.17	12.08 ± 0.82	13.20
Monacanthidae	0.14	0.52	11.73 ± 0.88	12.81
Portunidae	0.03	0.46	9.92 ± 0.73	10.84

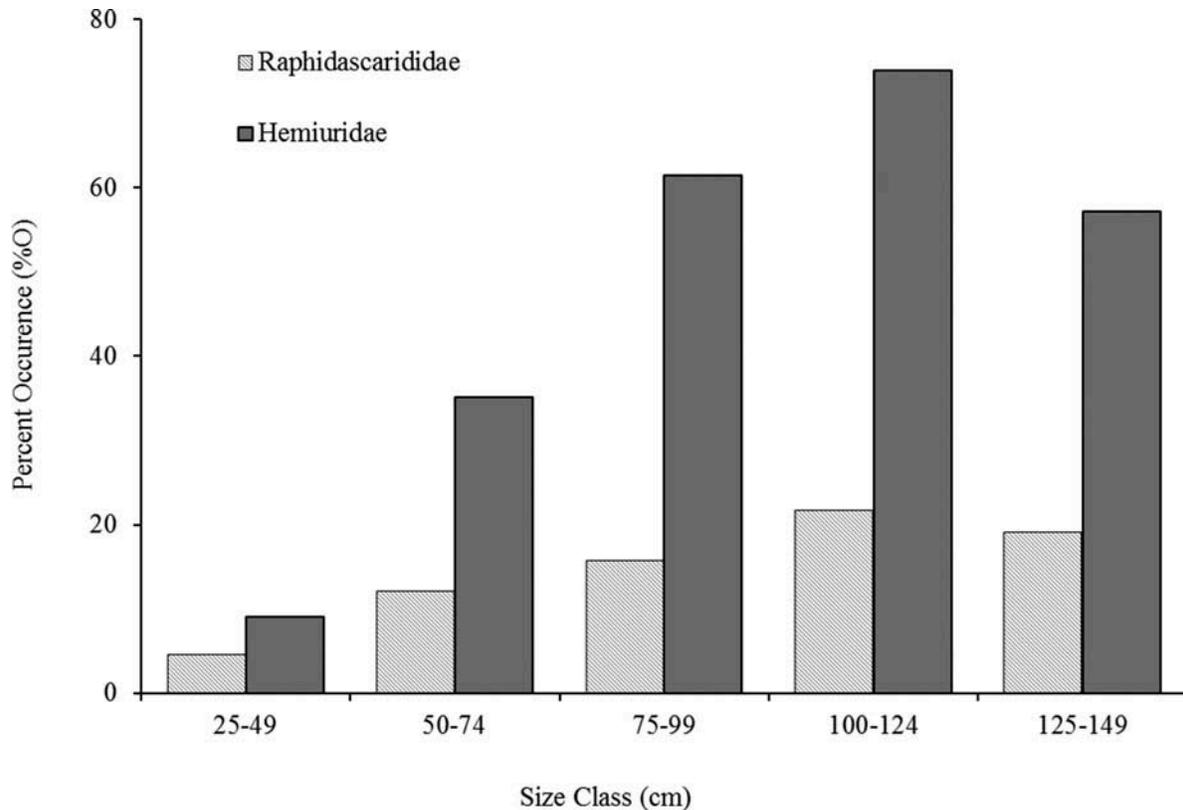


FIGURE 4. Percent occurrence (%O) by size-class (cm) of gastric parasites (families Raphidascarididae and Hemiuridae) from Dolphinfish collected in the western Gulf of Mexico; size-classes were 25–49 cm ($n = 25$), 50–74 cm ($n = 50$), 75–99 cm ($n = 75$), 100–124 cm ($n = 100$), and 125–149 cm ($n = 125$).

Amberjack *Seriola dumerili*. These species are known to settle out of the sargassum community and onto reefs in the Gulf of Mexico (Wells and Rooker 2004a; Simmons and Szedlmayer 2011; Ajemian et al. 2015), thus demonstrating the potential for pelagic–benthic habitat coupling via Dolphinfish predation. Though only one stomach was found to contain Kemp’s Ridley sea turtles, this does suggest that Dolphinfish are potential chelonian predators, which must be considered in sea turtle restoration and conservation efforts. Given the highly mobile nature and the estimated age of fish examined in this study, the timing of collection suggests potential exposure to waterborne contaminants from the Deepwater Horizon oil spill occurs during critical life stages (Rooker et al. 2013; Young 2014). As such, it is important to understand the feeding ecology specific to this region as the ecosystem moves towards recovery. Overall, the diet of Dolphinfish reveals interactions with other managed and protected pelagic species, and these data should help managers face the challenges to sustainable management of these highly migratory pelagic species in the western Gulf of Mexico.

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