

# Diet of Wahoo, *Acanthocybium solandri*, from the Northcentral Gulf of Mexico

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## ABSTRACT

Stomach contents analysis was used to quantitatively describe the diet of wahoo, *Acanthocybium solandri*, from the northcentral Gulf of Mexico. Stomachs were collected opportunistically from wahoo ( $n = 321$ ) that were weighed (TW, kg) and measured (FL, mm) at fishing tournaments during 1997 - 2007. Stomachs were frozen and later thawed for removal and preservation (95% ethanol) of contents to facilitate their examination and identification. Empty stomachs ( $n = 71$ ) comprised 22% of the total collection. Unfortunately, the preserved, un-examined contents from 123 stomachs collected prior to Hurricane Katrina (August 2005) were destroyed during the hurricane. Consequently, assessments of wahoo stomach contents reported here were based on the contents of the 65 'pre-Katrina' stomachs, in addition to the contents of 62 stomachs collected 'post-Katrina' during 2006 and 2007, for a total of 127 stomachs. Wahoo with prey in their stomachs ranged 859 - 1,773 mm FL and 4.4 - 50.4 kg TW and were sexed as: 31 males, 91 females and 5 sex unknown. Stomach contents reported in this study were identified to the lowest taxon possible (depending on the stage of digestion) and analyzed for %N, %W, %F, IRI y %IRI. Stomachs contained pelagic/epipelagic fishes and squid, including evidence of species associated with pelagic *Sargassum*. Prey (309 identified items) belonged to 27 taxa and ranged in stomachs from only one prey in 74 stomachs (58% of total stomachs) to 9 prey in a single stomach. Dominant fish families in the diet were Carangidae, Coryphaenidae, Scombridae and Exocoetidae. A moderate ontogenetic shift in the diet was observed among three size classes of wahoo. The diversity of fishes in the diet suggests that wahoo is an opportunistic predator that feeds on a variety of regionally abundant prey.

KEY WORDS: *Acanthocybium solandri*, wahoo, diet, Gulf of Mexico

## Dieta del peto, *Acanthocybium solandri*, en la Región Central del Norte del Golfo de Méjico

Análisis del contenido estomacal fue usado en forma cuantitativa para describir la dieta del peto, *Acanthocybium solandri*, en el norte del Golfo de Méjico. En los torneos de pesca recreacional ( $n = 321$ ) se presentó la oportunidad de coleccionar estómagos de petos capturados en 1997-2007 registrando el peso total (kg) y largo de horquilla (mm.) del pez. Los estómagos fueron congelados y más tarde descongelados para remover y preservar (95% etanol) su contenido, lo que facilitó su examinación e identificación. Los estómagos desocupados ( $n = 71$ ) constituyeron el 22% del total coleccionado. Colecciones de 123 estómagos que habían sido adquiridos y preservados antes de Agosto del 2005 fueron destruidas durante el Huracán Katrina; sin embargo, otras ( $n = 65$ ) colecciones preservadas 'pre-Katrina' fueron salvadas. Estas colecciones y el contenido de 62 estómagos coleccionados durante 2006 y 2007, formaron la base de este estudio ( $n = 127$ ; 32 machos, 103 hembras, 5 sexo indeterminado). Los petos con presas en sus estómagos tenían un largo de horquilla entre 859 - 1,773 mm. y un peso total de 4.5 - 50.5 kg. El contenido estomacal reportado en este estudio fue identificado hasta el más bajo taxón posible (dependiendo del grado de digestión) y fue analizado utilizando el %N, %W, %F, y IRI de los organismos de presas. Los estómagos contienen peces pelágicos/epipelágicos y calamar, incluyendo evidencia de especies asociadas con *Sargassum* pelágico. Las presas (309 identificadas) pertenecen a 27 taxas encontrándose una presa en 74 de los estómagos (58% del total de estómagos) y hasta 9 presas en un solo estomago. Las familias de peces dominantes en la dieta fueron Carangidae, Coryphaenidae, Scombridae, y Exocoetidae. Un moderado cambio ontogénico en la dieta fue observado entre los tres tamaños del peto. La diversidad de peces en la dieta sugiere que el peto es un predador oportunístico que se alimenta de una variedad de presas que son regionalmente abundantes.

PALABRAS CLAVES: *Acanthocybium solandri*, peto, dieta, Golfo de Méjico

## INTRODUCTION

The wahoo, *Acanthocybium solandri*, is a migratory epipelagic fish in the family Scombridae with cosmopolitan distribution in tropical and subtropical seas (Iversen and Yoshida 1957, Collette and Nauen 1983). In the Western Central Atlantic Ocean (WCA) wahoo occur from New Jersey to Columbia, including Bermuda, the Bahamas, Caribbean Sea and Gulf of Mexico (GOM) (Fischer *et al.* 1978, Robins *et al.* 1986). Wahoo is a

highly esteemed food fish throughout its WCA range where it supports valuable commercial and recreational fisheries, particularly in Bermuda (Luckhurst and Trott 2000), the southeastern Caribbean islands where it is an important artisanal pelagic fishery resource (Oxenford *et al.* 2003), and the northcentral GOM (Franks *et al.* 2000) where it is caught year-around and is among the most preferred species targeted by anglers. Wahoo are managed in U.S Atlantic waters through the Dolphin-Wahoo Fishery

Management Plan (SAFMC 2003). The species is unmanaged in the GOM where its landings have increased considerably since the mid-1980s, but show marked inter-annual variation (SAFMC 2003).

Life history information on wahoo from the WCA is scant, and its ecology in the region is not well known. The paucity of published information results, in part, from difficulties in obtaining adequate samples of this species due to its offshore, seasonal nature of occurrence. Information on the biology and life history of wahoo in the WCA includes Wollam (1969), Hogarth (1976), Manooch and Hogarth (1983), Luckhurst *et al.* (1997), Brown-Peterson *et al.* (2000), Franks *et al.* (2000), Kishore and Chin (2001), Oxenford *et al.* (2004) and Garber *et al.* (2005). On-going studies of wahoo in the WCA include age, growth and reproduction of wahoo from the Bahamas and the Atlantic coast of Florida (R. McBride and K. Maki, Florida Fish and Wildlife Research Institute); and movements/migratory patterns and genetic structure (J. Baldwin, T. Thiesen, Florida Atlantic University).

Published studies on the diet of wahoo from the WCA consist of Hogarth (1976, North Carolina, USA), Collette and Nauen (1983, Atlantic Ocean), and Manooch and Hogarth (1983, U.S. South Atlantic and Gulf coasts). Luckhurst (Unpublished data, cited in Oxenford *et al.* 2003) provided a summary of wahoo dietary studies conducted in the WCA. Other than Manooch and Hogarth (1983) who examined 95 stomachs from wahoo caught from the GOM (71 of which contained prey), accounts of diet and feeding habits of *A. solandri* from the GOM are lacking. Of those 71 wahoo examined by Manooch and Hogarth (1983), 61 were caught in the northcentral GOM off northwest Florida (56 stomachs) and Louisiana's Mississippi River Delta region (5 stomachs), while the remaining 10 fish were caught off northeast Texas (1) and south Texas (9).

As fisheries science moves toward an ecosystem based approach, it is clear that predator-prey interactions can reveal mechanisms that are important in structuring marine communities. The objective of our study was to describe the diet of *A. solandri* caught from the northcentral GOM off Louisiana, Mississippi, Alabama, and northwest Florida and examine our findings in the context of those reported by Manooch and Hogarth (1983) for wahoo collected from the same 'general region' of the northern GOM several years (1980 - 1981) prior to our study.

During the entire study period (1997 - 2007), opportunistic collections of wahoo stomachs totaled 321, of which 250 (78%) contained prey. Of those 250 stomachs with prey, 188 were collected prior to Hurricane Katrina's landfall on the Mississippi coast in August 2005, but, unfortunately, their contents had not been analyzed. The Gulf Coast Research Laboratory (GCRL) building that housed those collections was destroyed during the hurricane, and only 66 (35%) of the 188 collections were found. Consequently, assessments of wahoo stomach contents

reported here were based on the contents of the 65 'pre-Katrina' stomachs, in addition to the contents of 62 stomachs collected 'post-Katrina' during 2006 and 2007, for a total of 127 stomachs.

## MATERIALS AND METHODS

### Field Procedures

Wahoo examined in this study were caught in the hook-and-line recreational fishery from the northcentral GOM off Louisiana, Mississippi, Alabama and northwest Florida (Figure 1) during 1997 - 2007, with the exception of 2001. The study area was bounded by 85.5° to 88.5° Lat. N, then extending diagonally to 90.5° Lat N; and 27.5° and 29.8° Long. W. Wahoo were examined and stomachs were removed at a variety of big game fishing tournaments held annually across the northcentral GOM during May - November. All wahoo were caught during daylight hours, primarily at petroleum platforms and oceanic frontal zones (i.e., convergent zones, upwellings, temperature discontinuities, etc.) that were occasionally associated with pelagic *Sargassum*. Anglers packed their catch in ice immediately following capture. The date, location and time of catch, fork length (FL, mm), total weight (TW, kg) and sex were recorded for all specimens. Excised stomachs were placed in labeled plastic bags and immediately covered with ice for transport to the laboratory where they were frozen. Stomachs were later thawed for removal and preservation (95% ethanol) of contents prior to laboratory examination.



Figure 1. Map of the study area

### Laboratory Procedures

The contents of each stomach were placed onto a 0.840-mm mesh screen sieve and gently washed with fresh water. Contents were sorted taxonomically, identified to species when possible (depending on the stage of digestion), counted and weighed (wet) to the nearest 0.1 gram (g). Prey too digested for unequivocal identification were

recorded as 'remains' and assigned to the appropriate major prey category. The contents from some stomachs were archived for later reference. Numerous prey were identified with reference to McEachran and Fechhelm (1998), and taxonomic classification followed AFS (2004).

### Diet Analysis

*Cumulative prey curve* — To determine if a sufficient number of stomachs had been collected to adequately describe the diet, the order in which the stomachs were analyzed was randomized 10 times and the mean number of new prey items found consecutively in the stomachs was plotted against the number of stomachs that contained prey (Ferry et al. 1997). An asymptotic stabilization of the curve indicates the minimum number of stomachs required to accurately describe the diet (Cortes 1997).

*Quantitative description* — The following criteria were used to determine the importance of the different prey items consumed by wahoo. Taxonomic composition of the diet was quantified by percent numeric abundance (%N), percent of wet mass (%W), and percent frequency of occurrence (%F) (Hyslop 1980) of prey items, cumulating all data for each prey item. These dietary metrics were combined to assess overall prey importance using the Index of Relative Importance (IRI) (Pinkas 1971), where the importance of an item is directly related to the size of the value:  $IRI = (%N + %W) \times %F$ . IRIs were standardized to 100% by calculating the percentage of the total IRI contributed by each prey type (%IRI) and ranged from 0 (absent from diet) to 100 (the only prey consumed) (Barry et al. 1996, Cortés 1997).

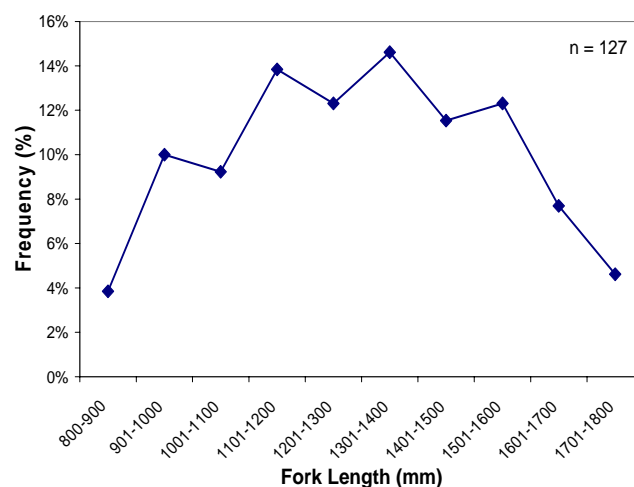
*Ontogenetic shift in diet* — Cluster analysis based on the hierarchical agglomerative method with the group-average linkage procedure was used to compare fourth root transformed mean percent IRI of all food items of individual specimens (exclusive of unidentified fish remains) ontogenetically with the Bray-Curtis similarity coefficient. The cluster analysis based on Bray-Curtis values was computed using PRIMER (version 5.28; PRIMER-E Ltd, Plymouth, UK) (Clarke 1993, Clarke and Warwick 2001). The cluster analysis attempts to create groupings of samples (size classes) based on the variables (prey items,  $n = 27$ ) through a generated similarity matrix. A one-way analysis of similarity (ANOSIM) was performed to test for ontogenetic differences in fourth root transformed mean percent IRI of the raw diet data among size classes. Emphasis was placed on comparing the R-stat values (GLOBAL R) in the output of the ANOSIM analysis. When R-stat values in pair wise comparisons between diets are close to 1 the compositions are very different, whereas when they are close to 0, the compositions are very similar.

*Dietary overlap: locations of capture* — Due to the unfortunate loss of collections resulting from Hurricane Katrina, only 45 collections with specific wahoo catch locations were available for statistical comparison of stomach contents between wahoo caught at deep water petroleum platforms/rigs (21 wahoo) vs. oceanic frontal zones (24 wahoo). Frontal zones include features such as *Sargassum* windrows, temperature discontinuities, and convergent zones, some of which were associated with distinctive bottom features (e.g., relic reefs, salt domes canyons walls). Horn's index of overlap ( $R_o$ , Horn 1966) was used to determine dietary overlap between the two groups. The index ranges 0.0 (no overlap) to 1.0 (complete overlap), and a value of 0.60 indicates a high degree of overlap (Krebs 1989). The Shannon-Wiener Diversity index was used to examine differences in species diversity between the two groups.

Empty stomachs were excluded from computations. *Sargassum* was found in a few stomachs and was most likely ingested incidentally during feeding. *Sargassum*, the giant digenean trematode (*Hirudinella ventricosa*), and stomach contents definitively identified as bait were not used in the description of the diet.

### RESULTS

Stomachs were removed from wahoo that ranged 859 - 1,773 mm FL and 4.4 - 50.5 kg TW. Male wahoo ( $n = 31$ ) ranged 859 - 1,560 mm FL and 4.4 - 24.3 kg TW, and females ( $n = 91$ ) ranged 886 - 1,773 mm FL and 4.6 - 50.4 kg TW. Wahoo with unknown sex ( $n = 5$ ) ranged 1,180 - 1,560 mm FL and 9.4 - 19.5 kg TW. The sex ratio for the 122 sexed fish was 3:1 (F:M). Cumulative prey curves for the data appeared to approach an asymptote, indicating the sample size was probably sufficient to adequately describe the diet of *A. solandri* (Figure 2).



**Figure 2.** Randomized cumulative prey curve for *A. solandri*. Means  $\pm$  1 SE are plotted.

**Description of the diet**

Analysis of stomach contents led to the identification of 309 prey items belonging to 27 taxa. Occurrence of prey in stomachs ranged from only one prey taxa in 74 stomachs (58% of total stomachs) to 10 prey taxa in a single stomach. Inclusive of unidentified prey, 74 (58%) stom-

achs contained one prey taxa, 31 contained 2 taxa, 18 contained 3 taxa, and 4 contained 4 taxa. On all accounts, fish (Class Osteichthyes) were the most important prey of *A. solandri* examined in this study (Table 1).

**Table 1.** Diet composition of 127 *A. solandri*, from the northcentral Gulf of Mexico, expressed as frequency of occurrence (%O), percent number (%N), percent weight (%W), Index of Relative Importance (IRI), and percent Index of Relative Importance (%IRI). T = <0.01.

Prey Taxa	%O	%N	%W	IRI	%IRI
<b>Class Crustacea</b>					
Portunidae					
<i>Portunus sp.</i>	0.8	0.3	T	0.3	T
<b>Class Cephalopoda</b>					
Unidentified squid	13.4	6.5	T	87.2	1.4
<b>Class Osteichthyes</b>					
Scopelarchidae					
<i>Scopelarchus sp.</i>	0.8	0.3	T	0.2	T
Hemiramphidae					
<i>Hemiramphus balao</i>	0.8	0.3	0.3	0.5	T
Exocoetidae					
<i>Cheilopogon sp.</i>	3.9	1.6	1.4	11.9	0.2
Unidentified exocoetid	15.0	9.4	2.0	169.8	2.7
Priacanthidae					
<i>Priacanthus arenatus</i>	0.8	0.3	T	0.3	T
Echeneidae					
Unidentified echeneid	0.8	0.3	0.1	0.4	T
Rachycentridae					
<i>Rachycentron canadum</i>	0.8	0.3	0.7	0.8	T
Coryphaenidae					
<i>Coryphaena hippurus</i>	11.0	5.5	13.4	208.1	3.3
Carangidae					
<i>Caranx sp.</i>	0.8	1.3	T	0.3	T
<i>Caranx crysos</i>	17.3	8.7	30.7	683.5	11.0
<i>Selene vomer</i>	1.6	0.6	T	1.0	T
Ephippidae					
<i>Chaetodipterus faber</i>	0.8	0.3	1.4	1.3	T
Gemplyidae					
<i>Gempylus serpens</i>	0.8	0.3	0.1	0.3	T
Unidentified gempylid	0.8	0.3	T	0.3	T
Trichiuridae					
<i>Trichiurus lepturus</i>	4.7	1.9	2.2	19.4	0.3
Scombridae					
<i>Auxis sp.</i>	6.3	5.8	2.7	53.8	0.9
<i>Thunnus sp.</i>	2.4	1.0	T	2.4	T
<i>Scomberomorus sp.</i>	0.8	0.3	T	0.3	T
<i>Acanthocybium solandri</i>	0.8	0.3	0.2	0.4	T
Unidentified scombrid	7.9	3.2	16.9	158.9	2.6
Centrolophidae					
<i>Hyperoglyphe sp.</i>	0.8	0.3	T	0.3	T
Balistidae					
<i>Xanthichthys ringens</i>	0.8	0.3	T	0.3	T
Diodontidae					
Unidentified diodontid	4.7	3.6	0.3	18.2	0.1
Tetraodontidae					
<i>Sphoeroides spengleri</i>	0.8	0.3	T	0.3	T
Unidentified tetraodontid	0.8	0.3	0.1	0.4	T
Unidentified Osteichthyes	65.4	46.0	27.3	4790.7	77.1

The majority (59%) of individual fish taxa were represented by only one specimen (expressed as a %N value of 0.3, Table 1) and, based on relative importance, contributed little to the diet. Among identifiable fishes, the most important families in the diet based on the combined %IRI values of each family's components, were Carangidae, Coryphaenidae, Scombridae and Exocoetidae (Table 1). Among those families, and in terms of %IRI, *Caranx crysos* (11.1) and *Coryphaena hippurus* (3.4) were the most important identifiable prey in the diet, followed by fish identifiable only as scombrids (most likely tunas, 3.5) and exocoetids (2.9). *Caranx crysos* occurred at the highest %O (17.3) and represented the greatest biomass (30.7 %W) among all prey in the diet (Table 1). The 8.7 %N contribution to the diet by *C. crysos* was exceeded only by unidentified exocoetids (9.4 %N), while the %IRI value of *C. crysos* exceeded three orders of magnitude higher than that of *C. hippurus*.

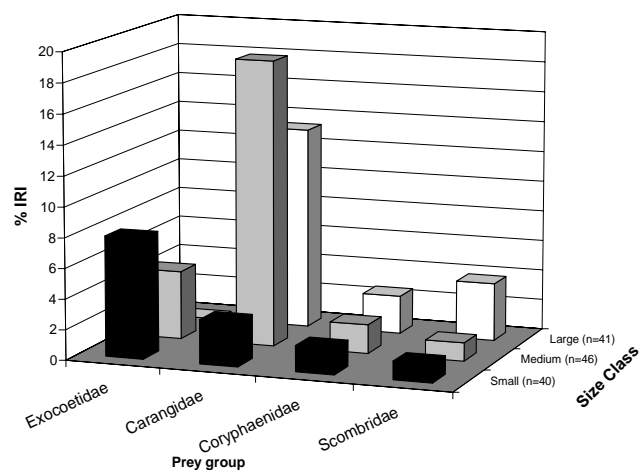
*Auxis* sp., *Trichiurus lepturus*, unidentified diodontids and *Cheilopogon* sp. were occasionally ingested, and *Auxis* sp. ranked third numerically (5.8 %N) and fourth in biomass (2.7 %W) among identifiable fishes. Exocoetids (11 %N) and scombrids (10.6 %N) were the most abundant prey consumed. Due to their advanced state of digestion, numerous fish prey were categorized as unidentifiable Osteichthyes (i.e., fish remains), a category that not only dominated the fish group but, based on all dietary indices, comprised the most significant prey grouping in the overall diet.

Squid (Class Cephalopoda, Order Teuthida), which apparently were digested quickly with only beaks and ocular lenses remaining, occurred in 13.4% of the stomachs and, numerically, contributed 6.5 %N to the diet (Table 1), but, according to %IRI, were of moderate importance in the overall diet. A single specimen of portunid crab, *Portunus* sp., was the only crustacean found among stomach contents

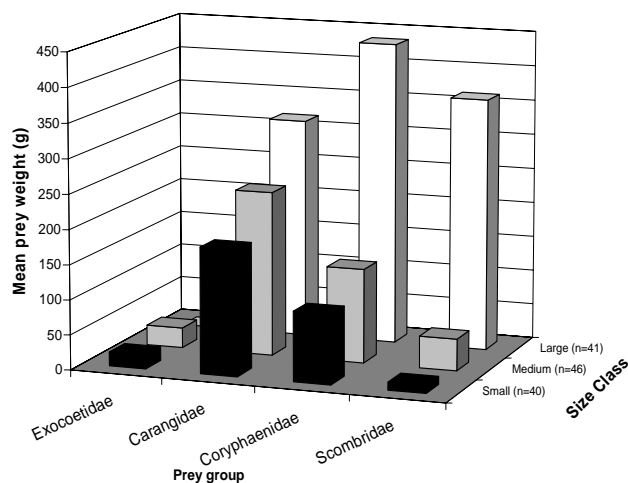
(Table 1). Bait identified in wahoo stomachs consisted of *C. crysos*, *C. hippurus*, *Scomberomorus maculatus* and exocoetids.

### Ontogenetic Shift

Cluster analysis allowed for the identification of three size groups of wahoo that were separated along a size gradient (small, 849 – 1,160; medium, 1,161 – 1,460; and large, 1,461 – 1,773) (Figure 3a). ANOSIM revealed a marginally significant ontogenetic shift in the entire diet among the three size classes (Global R = 0.347,  $p = 0.089$ ). Species diversity decreased with increased size, suggesting perhaps that wahoo are strictly opportunistic feeders when small and become somewhat more specialized when larger (Shannon-Wiener index (Krebs 1989)): small size class,  $H' = 3.368$ ; medium size class,  $H' = 2.932$ ; large size class,  $H' = 2.817$ ). Exclusive of fish remains and based on %IRI, primary prey of each size class of wahoo were: small class (exocoetids and carangids), medium class (*C. crysos*), and large class (*C. crysos*, *C. hippurus* and scombrids) (Figure 3a), suggesting perhaps that small wahoo fed on smaller, easier to catch flying fishes and jacks, while larger wahoo (presumably more mobile and able to capture larger, faster prey) fed largely on *C. crysos*, *C. hippurus* and scombrids. Although we did not measure the length of prey items, the above findings are somewhat mirrored in Figure 3b, where the mean weight of individual prey in families Exocoetidae, Carangidae, Coryphaenidae and Scombridae (Scombridae (i.e., the total weight of prey within each family divided by the number of wahoo within each size class that consumed each prey family) increased with increased wahoo size. The average number of identified prey taxa per size class was 1.93 (small), 1.58 (medium) and 1.41 (large). The mean weight of prey taxa within prey families Exocoetidae, Carangidae, Coryphaenidae and was calculated.



**Figure 3A.** Ontogenetic shift in the four dominant families in the diet of *A. solandri*, expressed as percent Index of Relative Importance (%IRI).



**Figure 3B.** Ontogenetic shift in the four dominant families in the diet of *A. solandri*, expressed as mean prey weight. Size classes are small (860-1,160 mm), medium (1,161-1,460 mm) and large (1,461-1,773 mm)..

#### Dietary Overlap: Locations of Capture

A high dietary overlap was found between fish caught in association with petroleum structures and frontal zone features (Horn index,  $R_o = 0.73$ ). Species diversity of prey items found in the stomachs of fish collected at petroleum structures and frontal zones was similar, with fish from fronts containing a slightly more diverse diet than fish caught at petroleum structures (Shannon-Wiener Diversity index: petroleum structures,  $H' = 2.654$ ; frontal zones,  $H' = 2.681$ ). Both groups consumed 11 prey taxa, seven of which were common to each.

#### DISCUSSION

Prey identified in this study showed that wahoo from northcentral GOM waters were fundamentally piscivorous predators that fed primarily on members of the pelagic and epipelagic fish community, findings generally in accordance with those reported by Manooch and Hogarth (1983) and Oxenford *et al.* (2003). Distribution of prey groups according to their %F in stomachs and the %W or %N they represent is one method to determine aspects of the feeding strategy of wahoo, i.e., is wahoo a specialist or a generalist feeder. The diversity of fishes in the diet we report suggests that wahoo are opportunistic predator that feeds on a variety of regionally abundant prey. Most fishes consumed by wahoo were infrequently encountered and represented by few specimens.

Available studies on the diet of wahoo from the Pacific Ocean, including Iversen and Yoshida (1957) and Kramer (1984), reported squids, pelagic fishes, a few demersal fishes, and to a lesser extent crabs, as prey. Bochard and Techer (2004) found the diet of wahoo caught in association with floating objects (not FADs) in the Indian Ocean

consisted of numerous families of pelagic fishes along with lesser representation by cephalopods and crustaceans. Squid was reported as an important prey for wahoo from the WCA (Collette and Nauen 1983) and the U.S. southeastern Atlantic and northern Gulf coast (Manooch and Hogarth 1983). We found that squid occurred in stomachs with a frequency (13.4 %) similar to that reported by Manooch and Hogarth (1983), albeit the %IRI value of squid in our study was quite low (<0.1%). We also found a single crustacean prey item, a portunid crab (*Portunus* sp.), in the stomach of a 940 mm FL, 4.5 kg TW wahoo that also contained two flying fishes and unidentifiable fish remains. The crab might have been ingested incidentally. Manooch and Hogarth (1983) reported no crustaceans in the diet of wahoo from the northern GOM.

The high percentages of unidentified prey items in this study are linked to advanced digestion state and/or lack of a specific physical structure that would help in the identification of the prey. Fortunately, the head and jaws of tetraodontids and gempylids, the jaws and modified scales (spines) of diodontids, the dorsal spine of balistids and the beaks of squids facilitated identification of those prey, even when in relatively advanced state of digestion. Even though the importance of some prey in the diet, as well as prey diversity, were likely underestimated in this study, our findings indicate that wahoo from the northcentral GOM consume a variety of fish families.

In contrast to Manooch and Hogarth (1983) who found pelagic *Sargassum* in only one stomach, we encountered *Sargassum* in 8% (n = 11) of the wahoo stomachs that contained prey. Pelagic *Sargassum*, recently designated as essential fish habitat (EFH) for wahoo (SAFMC 2003), accumulates in large mats and along oceanic frontal

boundaries in the northern GOM (Comyns *et al.* 2002). Unlike some pelagic fishes that primarily feed at or near the surface of the water, wahoo apparently do not readily feed at the surface (Manooch and Hogarth 1983). Although not included among stomach contents reported in this study, Franks and Russell (In press) found two specimens of *Cerataspsis monstrosa* (the first record of this species from the GOM), a large, larval oceanic penaeid crustacean, from the esophagus (not the stomach) of a wahoo (1020 mm FL, 13.4 kg TW, female) examined during this study. The wahoo was caught on surface fishing gear towed adjacent to a *Sargassum* driftline where it might have incidentally engulfed the larvae, or the larvae might have been regurgitated from a fish consumed by the wahoo.

Our sample consisted of wahoo caught exclusively with hook-and-line gear during the daytime, and we presume the fish were in an active feeding phase at the time of capture. Considering that the majority of prey found in stomachs were in moderate-to-advanced states of digestion, it can be assumed that the wahoo we examined fed during the previous evening and/or early morning. General observations of low-to-moderate degrees of stomach fullness could mean that wahoo eat small amounts of prey (at the same time) or that the digestion process is rapid enough to quickly eliminate large amounts of ingested foods. Demir (1963) found that another scombrid, *Sarda sarda*, fed diurnally with feeding activity much more vigorous in the early morning and towards the evening. With a relatively low percentage of empty stomachs (22%) recorded for the total sample of wahoo sampled in this study ( $n = 321$ ; see Introduction) and the relatively small amount of food typically observed in stomachs, it also can be assumed that the wahoo digestive process is rapid. Of course, empty stomachs also suggest lack of feeding or regurgitation during capture which would result in underestimation of diet composition. Conversely, some prey items may be overestimated due to slow digestion.

Infrequency of baits in stomachs might be explained by the fact that most wahoo were reportedly caught on artificial lures. For those fish not caught on artificial lures, perhaps the bait was not 'hooked' well and was easily removed when the fish attempted to swallow it, or perhaps bait swallowed by fish was regurgitated during the 'fight'.

Small, whole prey (< 10 mm TL) were conspicuously absent from the diet, a finding also reported by Manooch and Hogarth (1983) who observed that wahoo either swallow their prey whole or bite larger prey into smaller pieces and further attributed the lack of small prey in the wahoo diet to the fact that wahoo possess no gill rakers. Allain (2003) reported that wahoo do not swallow prey smaller than 10 mm TL. The greatest length (TL) and biomass (TW) recorded for an identifiable, minimally digested prey in our study were ~400 mm TL (*Trichiurus lepturus*) and 886.7 g (*Carnax crysos*), respectively, while the smallest (TW), identifiable, minimally digested prey

items were *Selene vomer* (0.5 g) and *Priacanthus arenatus* (0.6 g). We believe that the wide size range of wahoo examined in our study eliminated any bias linked to the presence of small prey vs. size of wahoo sampled.

Manooch and Hogarth (1983) observed that wahoo most likely do not feed readily at the surface but exhibit a preference for relatively large, near-surface fishes and squids, however, we report flying fishes (surface zone inhabitants) as part of the diet we describe. Manooch and Hogarth did not find flying fish in their GOM study. Furthermore, wahoo in our study were caught by anglers typically fishing with artificial lures trolled at varying speeds at or near the surface (top meter) of the water (Pers. comm., dock-side angler interviews), which demonstrates that wahoo will swim to the surface to 'attack' their prey. The fact that prey items in our study are considered pelagic and/or epipelagic presupposes that wahoo do not venture deep into the water column to feed. *Gympylus serpens* typically inhabits the mesopelagic zone, but vertically migrates to surface waters to feed as night time approaches. Thus the specimens of Gempylidae, as well as the squids, which also may undergo diel vertical migrations, found in this study may have been consumed by wahoo in late evening hours. Although we did not record the length of most prey items, the majority were considered juveniles of fishes that spend all or part of their life in the surface/near-surface realm, often associating with floating objects.

Since species diversity decreased with increased wahoo size, there was evidence that wahoo are opportunistic feeders when small and perhaps become somewhat specialized when larger. The average number of identified prey taxa per individual wahoo was small (< 2). Based on assessments of the diet of three size classes of wahoo ("small, medium and large"), we found evidence of a marginally significant size-related shift among the groups. Although these groups focused on similar fish prey (families), a change in the relative importance (%) of the prey in the stomachs of each size class was observed. A first change in the feeding habits was recorded from the first to the second size group, due to a decrease in the predation on carangids and exocoetids in the small group and an increase in carangids (primarily *C. crysos*) among the medium size wahoo. A second shift was observed in the third group which fed somewhat less on carangids that found for the medium size group, as well as increased predation on *C. hippurus* and scombrids. Several authors have demonstrated that, when these shifts occur, they almost always involve changes to larger prey (Keast and Webb 1966, Nielson 1980). We did not conduct an assessment of predator/prey size-relationships, primarily because most prey were in advanced stages of digested, as well as the apparent ability of wahoo to use their razor sharp teeth to bite even large prey into consumable portions. However, our observations of stomach contents suggest that small wahoo fed on small, easier to catch flying fishes and jacks, while the larger, more mobile

wahoo captured larger *C. crysos*, *C. hippurus* and combrids (primarily tunas), observations reinforced by the increase in mean weight of individual prey in important prey (families) with increased wahoo size. The behavior of large predators to feed on large prey is in accordance with the traditional optimal foraging theory of maximizing the net rate of energy return in prey selection (Stephens and Krebs (1986). Increase in prey size success can be related to a variety of factors, including increased sustained speed and burst swimming speeds and better visual acuity (Blaxter 1986, Campo *et al.* 2006). Of course, as suggested by Campo (2006), predator-prey size relationships may be only one of the mechanisms for regulating the observed trophic dynamics. Sih and Moore (1990) and Campo (2006), suggested that prey behavior may have as great a role as predator choice in determining predator diets, and a variety of prey behaviors may influence the catch success and /or the encounter probability of the predator (Persson and Diehl 1990), and determine its diet (Campo 2006).

Wahoo examined in this study were caught during spring – fall, which includes the wahoo spawning season (May-August) (Brown-Peterson *et al.* 2000), and although we collected stomachs from wahoo caught in the northcentral GOM during winter, all of those collections were lost during Hurricane Katrina and were not available for seasonal dietary comparisons.

This study represents an account of the diet of wahoo caught from an area of the northern GOM similar to that from which wahoo were caught during the Manooch and Hogarth (1983) study, which incidentally was conducted during the same seasons (summer and fall) encompassed by our study but was somewhat smaller in scope and, importantly, was carried out more than a quarter century prior to the termination of our study. Manooch and Hogarth (1983) did not provide the size range of wahoo they sampled. Similarities among the diets are moderate and include the dominance by fishes, however, the actual prey composition varies substantially. The only fish identifiable to species level reported by both studies was *Coryphaena hippurus*, a rare component of the diet (1.4 % F) reported by Manooch and Hogarth (1983) but the second most important identifiable prey species in our study based on %IRI. Both studies found families Carangidae and Scombridae to represent a principal portion of the diet, however we report identifiable carangids as *C. crysos*, *Caranx* sp. and *Selene vomer*, and identifiable scombrids as *Acanthocybium solandri*, *Auxis* sp., *Scomberomorus* sp. and *Thunnus* sp., whereas Manooch and Hogarth (1983) reported identifiable carangids and scombrids as *Decapterus punctatus* and *Caranx* sp., and *Euthynnus alletteratus*, respectively. To our knowledge, the single wahoo prey specimen (weight of remains, 40.1 g; length of head, 58 mm) few report from the stomach of a 1,050 mm FL fish, represents the first account of cannibalism for *A. solandri*.

Other fish families common to our study and that by Manooch and Hogarth (1983) are Echeneidae, Diodontidae and Tetraodontidae. Not found in our study but reported by Manooch and Hogarth (1983) were *Sardinella aurita* (Clupeidae), *Peprilus* sp. (Stromateidae), *Balistes capricus* (Balistidae) and *Diodon hystrix* (Diodontidae), all of which were minor components of the diet they described. Other obvious differences between the studies include identifiable fishes we report that were not found by Manooch and Hogarth (1983), i.e., *Cheilopogon* sp. (Exocoetidae), *Hemiramphus balao* (Hemiramphidae), *Chaetodipterus faber* (Ephippidae), *Hyperglyphe* sp. (Centrolophidae), *Rachycentron canadum* (Rachycentridae), *Scopelarchius* sp. (Scopelarchidae), *Priacanthus arenatus* (Priacanthidae), *Gempylus serpens* (Gempylidae), *Trichiurus lepturus* (Trichiuridae), *Xanthichthys ringens* (Balistidae), and *Sphoeroides spengler* (Tetraodontidae) (Table 1). Other than perhaps a trophic shift related to the occurrence or abundance of prey available to wahoo over the passage of time since the Manooch and Hogarth (1983) study, or perhaps the small sample size of each study, we cannot account for variations between the diets. Importantly, unidentifiable fish remains comprised the major portion of the diet in both studies. Neither we nor Manooch and Hogarth (1983) compared diets between male and female wahoo in our samples.

The high dietary overlap between wahoo caught at deep water petroleum structures (platforms/rigs) vs. wahoo caught at oceanic frontal zone features was not fully anticipated, due in part to the vast increase in the number of deep water petroleum structures since the Manooch and Hogarth (1983) study period and the unique forage base associated with those structures. Deep water petroleum structures are more than merely passive attractors for large pelagic fishes, including wahoo (Franks 1999), and the behavioral mechanism for the association must be strong. However, highly mobile predators such as wahoo may range widely within their feedings grounds within a short period of time, and prey found in their stomachs might not necessarily have been consumed at the location of catch. Although the sample size used in the 'habitat' comparisons was small, it is apparent that some wahoo prey occurred at both 'habitats'.

As reported in other wahoo feeding studies, the giant intestinal digenetic trematode *Hirudinella ventricosa* (Digenea: Hirudinellidae) was also observed in stomachs we examined. This tenacious fluke was found in 98% of the stomachs examined, and their numbers ranged from two to eleven individuals, with the vast majority of stomachs containing two individuals. This parasite is a common resident in the stomach of other pelagic fishes such as *Coryphaena hippurus* and various scombrids.

In summary, our study confirms that the wahoo is a pelagic carnivore that feeds on a variety of pelagic and epipelagic fishes, as well as squid. Determining trophic interactions between fishes is critical to a better under-



standing (and modeling) of the GOM pelagic ecosystem dynamic, and knowledge of the predatory interactions of wahoo can perhaps be used as a source of information for management of the GOM pelagic ecosystem. It is most unfortunate that 65% of the stomach collections taken prior to Hurricane Katrina were lost during that storm, as analysis of those contents would undoubtedly have provided for a greater assessment of the diet and feeding behavior of wahoo from the region. Nevertheless, our findings expand on previous information presented by Manooch and Hogarth (1983) and contribute to a better understanding of the diet and trophic ecology of wahoo in the GOM.

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