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NOVA SOUTHEASTERN UNIVERSITY OCEANOGRAPHIC CENTER

Trophic Dynamics and Feeding Ecology of the Southeast Florida
Coastal Pelagic Fish Community

By

Travis Allan Moore

Submitted to the faculty of
Nova Southeastern University Oceanographic Center
in partial fulfillment of the requirements for the degree of
Master of Science with a specialty in:

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Abstract

The combined methods of stomach content analysis and stable ^{15}N and ^{13}C isotope biochemistry analysis were used to investigate the trophic dynamics and feeding ecology of coastal pelagic fishes in the waters off southeastern Florida, USA. The coastal pelagic fish complex includes blackfin tuna *Thunnus atlanticus*, dolphinfish *Coryphaena hippurus*, king mackerel *Scomberomorus cavalla*, little tunny *Euthynnus alletteratus*, skipjack tuna *Katsuwonus pelamis*, and wahoo *Acanthocybium solandri*. These coastal teleosts, particularly the tunas and wahoo, are primarily targeted by recreational anglers. However, there is a shortage of available trophic and diet composition data concerning these fishes of the coastal pelagic ecosystem. Stomach and muscle tissue samples were collected from the species of various lengths over a three-year period from March 2010 and March 2013. Across all six species, teleost fishes dominated the prey with an average 64.5% by occurrence, 63.7% by number, and 89.9% by weight. There were two dominant prey families: Clupeidae and Carangidae. Dolphinfish showed the lowest diet overlap among the six species, due to the highly diverse diet. The highest diet overlap occurred between king mackerel and little tunny. The mean $\delta^{15}\text{N}$ ranged from 8.21 ‰ (wahoo) to 13.18 ‰ (king mackerel), and the mean $\delta^{13}\text{C}$ ranged from -18.41 ‰ (king mackerel) to -16.70 ‰ (dolphinfish). Blackfin tuna exhibited the largest $\delta^{15}\text{N}$ range (7.22 to 13.21 ‰), as well as the largest $\delta^{13}\text{C}$ range (-19.13 to -12.99 ‰). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in the muscle tissue showed evidence of shifts to higher trophic levels with an increase in fish size and the formation of distinct trophic groups among the coastal pelagic predators. The $\delta^{13}\text{C}$ also suggested an inshore-offshore spatial relationship among the coastal pelagic fish. The trophic dynamics and feeding ecology data generated by this study will provide valuable baseline data for the coastal pelagic complex and future ecosystem studies.

Keywords: Coastal pelagic, Stomach content analysis, Stable isotopes, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, Ecosystem, Trophic dynamics, Food web, Feeding ecology.

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Introduction

This research study was focused primarily on medium to large size teleost species that inhabit the mid-range coastal pelagic waters associated with the continental shelf, to the pelagic waters associated with the shelf edge and offshore ecosystem. The target fish species for this research study included blackfin tuna *Thunnus atlanticus*, dolphinfish *Coryphaena hippurus*, king mackerel *Scomberomorus cavalla*, little tunny *Euthynnus alletteratus*, skipjack tuna *Katsuwonus pelamis*, and wahoo *Acanthocybium solandri*. These fish species support a vibrant sport fishery in southeast Florida and, with fisheries management moving to ecosystem based management, the need to evaluate the trophic and feeding ecology of multiple species is upon us. To better evaluate their trophic dynamics and feeding ecology, the methods of stomach content analysis and stable isotope biochemistry were combined for the same specimens. Morphometric data and biological samples (stomach, gonads, muscle tissue, and liver tissue) were collected via fishery-dependent and fishery-independent sampling throughout southeast Florida and the Florida Keys. The objective of this research project was to investigate and achieve a greater understanding of the trophic dynamics and feeding ecology present in the coastal pelagic fish community in the waters off the southeast Florida, USA.

This research provides valuable information on the trophic dynamics and feeding ecology for the coastal pelagic fish complex. Presently, there is a shortage of available trophic and feeding ecology data concerning the fishes of the coastal pelagic complex in the southeast Florida ecosystem. With fishery management organizations starting to take an ecosystem-based approach to fisheries management, describing the trophic dynamics and feeding ecology of the middle-upper predators is a vital component of that approach. The ability to incorporate baseline data concerning the trophic dynamics and feeding ecology of the unique coastal pelagic fish complex would greatly enhance the opportunities to successfully manage and develop sustainable fisheries for the future.

Coastal Pelagic Complex

In the Atlantic Ocean waters off the southeast coast of Florida, there is a “coastal pelagic” habitat where the continental shelf edge is extremely close (*ca.* 18-22 km) to the

coastline. These coastal pelagic waters are host to several species of medium to large size pelagic fish that are characterized by similar patterns of highly migratory behavior and relatively high energetic demands. Collectively, that group of fish species is referred to as the “coastal pelagic fish complex” which includes king mackerel, blackfin tuna, skipjack tuna, little tunny, wahoo, and dolphinfish (mahi). These species are commonly targeted by recreational anglers and, comprising 30% of all reported recreational landings in southeast Florida (NMFS, 2012), support a valuable recreational fishery. With all of these medium- to large-bodied predator species inhabiting the southeast Florida coastal pelagic waters and being targeted by the recreational sector, there is the possibility of competition for resources and exploitation of a species by fishing pressure.

With the condensed distance of the continental shelf, the deeper pelagic waters are in close proximity to the highly productive coastal pelagic waters. The shallower coastal pelagic waters are home to coral reef ecosystems and a great diversity of marine life and potential prey items. As the water depth increases over the shelf, there are multiple areas of upwelling and structure which provide habitat for prey items (bait fish) due to the abundance of nutrients (Mann, 2006). The coastal pelagic water can be characterized as an ecotone between the greenish-blue inshore waters to the blue pelagic waters of the open ocean, and it is home to a multitude of ecologically similar fish species.

Blackfin Tuna

Blackfin tuna *Thunnus atlanticus* (Lesson, 1831) is a member of the family Scombridae, which includes the mackerels and tunas. Similar to all members of the genus *Thunnus*, this species has a fusiform body shape which facilitates fast movement through the water, as well as the presence of a swim bladder (Altringham, 2001). Blackfin are a small, epipelagic, oceanic tuna species found only in the warm waters of the western Atlantic Ocean. The species has a geographic distribution from Martha’s Vineyard, Massachusetts south to Rio de Janeiro, Brazil (Collette, 2002). They are abundant in tropical areas with water temperature as the limiting factor influencing the distribution of the species; blackfin tuna only occur in waters at least 20° C or greater (Collette, 2002).

They are considered one of the small tunas, with a common size of 72 cm fork length (FL) and reaching a maximum size of 100 cm FL. The length at first maturity is 49.5 cm FL. The blackfin tuna spawning grounds are believed to be well offshore in pelagic waters of the Florida Current, Gulf of Mexico and Caribbean Sea, as well as coastal waters of northern Brazil (Schaefer, 2001; Collette, 2002). The spawning season off Florida extends from April to November with a peak in May. In the Gulf of Mexico, the spawning season only runs from June to September (Collette, 2002). Like all tunas, blackfin tuna are oviparous broadcast spawners, releasing sperm and eggs into the water column where fertilization occurs (Schaefer, 2001).

Blackfin tuna exhibit a strong schooling behavior, frequently forming large schools often mixed with skipjack tuna. Along with the schooling behavior, blackfin are also migratory in nature. The largest directed commercial fishery for blackfin tuna is located off the southeastern coast of Cuba (Collette, 2002). The Cuban blackfin tuna fishery is part of a mixed fishery that is also directed at skipjack tuna. The two tuna species are primarily landed using live baits and pole gear. For the Cuban fishery, there are no data on catch rates and sizes since the catches are not separated by species. The Lesser Antilles, Haiti, and Dominican Republic are also reported to have a small commercial fishery along with a sport fishery for blackfin tuna (ICCAT, 2006). The largest interest to fisheries for blackfin tuna is the recreational sport fishery. There is a highly valuable recreational fishery for this species in Florida and the Bahamas. In the recreational fishery, the main gear type used to target blackfin is rod-and-reel, where the trolling method is employed. Blackfin are highly regarded for their fighting ability, which explains its popularity among recreational fishermen. The meat is highly prized when fresh, although there is very limited commercial interest for it in the United States.

In the U.S., the management of blackfin tuna is conducted through state level agencies. Currently, blackfin tuna is not managed under any U.S. regional or federal organization, even though the biology and highly migratory behavior of the species would suggest a need to be included under federal management plans. Any incidental landings of blackfin tuna by the U.S. commercial longline fleet are reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT) via the Highly Migratory Species Division (HMS) of the National Marine Fisheries Service

(NMFS). With fisheries management moving towards ecosystem-based management approaches, there is an increased need for data regarding ecologically and economically important fish species.

Dolphinfish

Common dolphinfish *Coryphaena hippurus* (Linnaeus, 1758) is the largest member of the family Coryphaenidae, which only has one genus and two species – *C. hippurus* (common dolphinfish) and *C. equiselis* (pompano dolphinfish). The common dolphinfish¹ – often called and labeled “mahi mahi” by the markets and general public – is an epipelagic species with a geographic distribution worldwide in the tropical and subtropical waters with temperatures warmer than 20° C. Dolphinfish typically inhabit offshore waters as well as coastal, near shore waters over the continental shelf at a depth range of 0 to 85 m (Oxenford, 1999).

Dolphinfish are characterized by a compressed and elongated, fusiform body shape, with the greatest body depth in adults being less than 25% of the standard length (Collette, 2002). They have a single dorsal fin that extends the length of the body. Dolphinfish have a maximum length of 200 cm FL but are commonly found up to 100 cm FL in the Straits of Florida. The length of first maturity for dolphinfish is 48 to 65 cm (males) and 46 to 56 cm (females) fork length (Schwenke, 2008). Spawning occurs primarily from January through July with multiple peaks throughout the season. In the Florida area, spawning intensity peaks from January through March (Schwenke, 2008).

Dolphinfish do exhibit schooling behavior. Small dolphinfish tend to school and travel in groups ranging from a few fish to more than 50 individuals. The larger dolphinfish do not exhibit such a strong schooling behavior, instead traveling in pairs or alone. Schools of dolphinfish are commonly associated with and found around floating objects and large *Sargassum* sp. macroalgae mats (Collette, 2002). Dolphinfish are considered to be highly migratory and are only seasonally abundant over their range (Oxenford, 1999).

¹ For the purposes of this thesis, the names “common dolphinfish” and “dolphinfish” will be used synonymously.

In the United States, there is a strong fisheries interest in dolphinfish from both commercial and recreational sectors. The directed commercial fishery for dolphinfish uses modified pelagic longline gear to target the species at the surface. Dolphinfish is an extremely popular sportfish among recreational anglers. They are commonly targeted using the trolling method, artificial baits, and cut-up fish baits around *Sargassum* sp. mats and other floating objects. The dolphinfish is highly prized by recreational anglers for its fighting ability and meat quality. In Florida, dolphinfish are managed by the South Atlantic Fishery Management Council (SAFMC) and Gulf of Mexico Fishery Management Council (GMFMC) under the “Dolphinfish/Wahoo Fishery Management Plan” (SAFMC, 2003). Since dolphinfish are important to both commercial and recreational fisheries, similar to wahoo, the Federal Management Plan (FMP) establishes allocations between fishery sectors (SAFMC, 2003).

King Mackerel

King mackerel *Scomberomorus cavalla* (Cuvier, 1829) is a member of the family Scombridae and the largest, by physical size, member of the mackerel genus *Scomberomorus*. King mackerel is a subtropical species often found in epipelagic waters associated with coastal areas and outer reefs (Collette, 2002). The species has a geographic distribution from Massachusetts south to Brazil, including the Gulf of Mexico. There are three acknowledged stocks for king mackerel in the western Atlantic Ocean: the North Atlantic, Gulf of Mexico, and Brazilian stocks (ICCAT, 2006). There is also a small resident population in the South Florida waters, which is a mixture of the Atlantic and Gulf of Mexico stocks. The species exhibits a coastal migratory behavior and can migrate long distances along the U.S. East Coast dependent upon the warm water conditions (ICCAT, 2006). They also exhibit a schooling behavior, oftentimes in large schools of similar-sized conspecifics (Collette, 2002).

King mackerel is the largest mackerel species with a maximum reported size of 173 cm fork length (FL) and an average size range between 50 and 90 cm FL. The Florida population of king mackerel reaches first maturity at a fork length of 73 cm for males and 84 cm for females. King mackerel spawning occurs from May through September in the waters over the middle and outer continental shelf (Finucane, 1986).

The spawning season has two peaks, one in late May and the second in early August. They are broadcast spawners, with the sperm and eggs released continuously during the spawning season, and fertilization takes place in the water column. King mackerel larvae are found in water temperatures ranging 26° to 31° C, and can grow at rates from 0.54 mm to 1.33 mm per day (Finucane, 1986).

King mackerel has shown to be one of the most valuable commercial and recreational fish in the South Atlantic Ocean and Gulf of Mexico (Manooch, 1979; ICCAT, 2006). The primary gear type used to land king mackerel is rod-and-reel using either live baiting or trolling techniques. King mackerel is included in the Coastal Migratory Pelagics Fishery Management Plan (FMP), which is jointly managed by the SAFMC and the GMFMC. The Coastal Migratory Pelagics FMP group also includes Spanish mackerel *Scomberomorus maculatus*, cero *S. regalis*, cobia *Rachycentron canadum*, and little tunny *Euthynnus alletteratus*.

Little Tunny

Little tunny *Euthynnus alletteratus* (Rafinesque, 1810) is a member of the family Scombridae. The little tunny, also colloquially called “false albacore,” is a small epipelagic species found worldwide in the tropical and sub-tropical, neritic, coastal waters, between 56° N and 30° S in the Atlantic Ocean, Gulf of Mexico, Caribbean Sea, Mediterranean Sea, and Black Sea. They typically inhabit the surface pelagic waters in the neritic zone over the continental shelf and extend out from the continental shelf edge to the open ocean pelagic waters. Little tunny have a warm water temperature preference ranging from 24° to 30° C (Collette, 2002).

The little tunny species is one of the smallest tunas. It has a fusiform shape that is compact and streamlined with a robust body made for powerful swimming and to facilitate bursts of speed (Altringham, 2001). Little tunny typically exhibits a blue-green or metallic blue coloration with dark wavy stripes – referred to as “mackereling” – on the dorsal side above the lateral line. The distinctive mackereling coloration never extends farther than the middle of the first dorsal fin. The ventral side is a bright white color with 3 to 7 dark spots located around the pelvic and pectoral fins. Even with differences in color pattern and size, the little tunny is commonly mistaken for Atlantic bonito *Sarda*

sarda, and the two species are often collectively termed “bonito” in South Florida fisheries. The swim bladder is absent in the little tunny species, and they must stay moving to stay afloat. Adult little tunny have an average size of 85 cm FL, with an average maximum size of 90 cm FL in the Atlantic Ocean and 100 cm FL in the Mediterranean. The maximum recorded size for the species is 120 cm FL. The species is believed to live to an age of 10 years. The length at first maturity varies by sex. For females, length of maturity is 27 to 37 cm FL, while males reach maturity at approximately 40 cm FL. The spawning season for little tunny in the Atlantic Ocean runs from April through November with the most intense spawning activities occurring between July and August; in the Mediterranean Sea, the spawning season runs from May through September. The species is oviparous with spawning typically taking place offshore in water that is at least 25° C (Collette, 2002).

The little tunny is a schooling species, with schools primarily based on the size of fish and not necessarily by species. Little tunny juveniles that have not reached maturity tend to form compact schools offshore. The larger, mature little tunny school both offshore and in near shore waters, with the larger groups offshore and the smaller groups near shore. They often co-school with other members of the family Scombridae, such as Atlantic bonito and blackfin tuna. Little tunny do exhibit a migratory behavior; however, they are not believed to be as highly migratory as other tunas (Collette, 2002).

In the United States, the primary area of interest to fisheries for the little tunny is in the recreational sector. With the little tunny’s abundance in the coastal pelagic and inshore waters, they are a common sportfish caught on light tackle by recreational anglers. They are also highly regarded by the recreational community as strip or whole bait for billfish and swordfish. The little tunny is managed domestically by the SAFMC and the GMFMC, however it excluded in any management plan (SAFMC, 2011).

Skipjack Tuna

Skipjack tuna *Katsuwonus pelamis* (Linnaeus, 1758) is also a member of the family Scombridae. Skipjack are an epipelagic, oceanic species with a circumglobal distribution in tropical waters with a temperature range from 14.7° to 30° C, but are absent from the Mediterranean Sea and the Black Sea. In the western Atlantic Ocean,

skipjack are found throughout sub-tropical and tropical waters from Cape Cod, Massachusetts to Argentina (Collette, 2002).

Similar to the tunas from the genus *Thunnus*, the skipjack tuna has a fusiform, rounded, and elongated body that facilitates fast movement through the water. However, the swim bladder is absent in this species. Skipjack tunas have a distinctive coloration pattern of four to six longitudinal dark purplish/blue bands running along the silvery ventral side of the body. They commonly reach a size of 80 cm FL and can grow to a maximum size of 100 cm FL. Fork length at first maturity for skipjack is achieved at approximately 45 cm. Skipjack are believed to have a life span of 8 to 10 years (Collette, 2002). Skipjack are oviparous, spawning year round in warm equatorial waters. In sub-tropical waters, spawning occurs from the spring to early fall, and as the distance from the equator increases, the spawning season becomes shorter (Schaefer, 2001).

Skipjack exhibit a strong schooling behavior, especially in surface waters, oftentimes jumping or breaching the surface during high levels of activity. The schooling behavior is commonly associated with drifting objects, *Sargassum* sp. patches (large lines of these patches along oceanic fronts are referred to by anglers as “weedlines”), FADs (fish aggregating devices), sharks, whales, and other large tuna species. The most common other tuna species that skipjack are associated with is blackfin (Collette, 2002).

The worldwide geographic distribution, fast growth rates, and predictable schooling behavior makes skipjack tuna a commonly targeted species by both the commercial and recreational fishing sectors. Skipjack tuna make up 60% of the commercial tuna landings worldwide (Collette, 2001). The majority of landed skipjack are marketed as canned “chunk light” tuna. In the United States, the skipjack tuna is managed by the NMFS Highly Migratory Species (HMS) Management Division with guidance from the constituent-based HMS Advisory Panel (NMFS, 1999).

Wahoo

Wahoo *Acanthocybium solandri* (Cuvier, 1831) is also a member of the family Scombridae that includes mackerels and tunas. Wahoo are an offshore, mainly epipelagic species with a worldwide geographic distribution in tropical and sub-tropical waters. In the Atlantic Ocean, wahoo can be found between 35° N and 38° S, and typically prefer

the waters over the continental shelf edge as well as the pelagic open ocean environment (Collette, 2002).

Wahoo is one of the largest non-tuna species within the scombrids. They are characterized by a fusiform body shape that is very elongated and slightly compressed (Collette, 2002). Wahoo have an elongated, powerful jaw that forms a beak-like snout. The head and body shape of the wahoo, along with high endurance, help facilitate extremely fast swimming speeds. Wahoo have recorded swimming speeds up to 60 miles per hour. A distinguishing coloration pattern for wahoo is the presence of 24 to 30 wavy cobalt-blue vertical bars that run along the lateral length of the body and extend below the lateral line. Another distinguishing body characteristic is the complete concealment of the posterior part of the maxilla under the preorbital bone (Collette, 2002). Unlike many of the tunas in the Scombridae family, the swim bladder is present in wahoo and aids in buoyancy control. Wahoo have an average size ranging between 100 and 170 cm FL (Hogarth, 1976). The maximum size for wahoo is 250 cm FL. Wahoo, like other scombrids, show size and weight variations associated with changes in latitude (Collette, 2001). The weight tends to increase with the increased distance north or southwards of the equator, which is correlated to water temperature. The length of first maturity for wahoo ranges from 85 to 105 cm fork length. Spawning is believed to occur primarily over the summer months in the western North Atlantic Ocean (Hogarth, 1976; Jenkins, 2009). In the western Atlantic Ocean, the Caribbean Sea, and waters near Florida, wahoo spawning occurs from May through August with peaks during June and July (Jenkins and McBride, 2009).

Wahoo, unlike other scombrids, do not exhibit a schooling behavior. They are primarily a solitary fish in the pelagic environment. They do occasionally form small, loose aggregations and congregate near drifting objects or *Sargassum* sp. macroalgae. Wahoo do exhibit a highly migratory behavior, occurring in the tropical and subtropical waters (Collette, 2002).

The primary area of interest to fisheries for wahoo is the recreational sector. In the United States, there is a directed commercial fishery for wahoo, where the pelagic longline gear type is used to target the species. However, wahoo are often times encountered and landed in the shark and swordfish pelagic longline fishery. Wahoo are

popular sportfish among recreational anglers. They are commonly targeted using a high speed trolling technique and “light tackle” gear with artificial baits or bait strips. Wahoo are highly prized by recreational anglers for their intense high speed fights when hooked up on a rod and reel. Wahoo is managed by the SAFMC under the “Dolphinfish/Wahoo Fishery Management Plan” (SAFMC, 2003). Since wahoo are important to both commercial fisheries and recreational anglers, the FMP establishes allocations between fishery sectors (SAFMC, 2003).

Diet and Trophic Dynamics

In general, the more biologically productive the environment, such as estuarine or coastal areas, the larger and more complex the food web (Pimm, 1987). To truly understand the coastal pelagic ecosystem and trophic dynamics within it, a quantitative food web and trophic position study must be conducted. Stomach content analysis has traditionally been used to characterize the diet of fishes, and this usually involves the physical removal of the stomach and the subsequent removal and/or examination of the contents contained in the stomach. There are also established lavage techniques for the removal of stomach contents from live fishes; however, those techniques are only performed on individuals that are going to be released and those methods are impractical for many species (Bowen, 1996). Since all of the fish species in the coastal pelagic complex are targeted by recreational anglers are edible and are often used as bait to catch other coastal pelagic species, the live release of these fish is uncommon. Also, if various other biological samples – such as liver, muscle tissue, gonads, and otoliths – are planned to be collected for other projects, the non-lethal lavage and release method is not appropriate.

Regardless, both methods for the removal of the stomach contents can provide quantitative data on the diet of the particular fish species. The stomach content data are generally presented in three indices: frequency of occurrence (%O), composition by number (%N), and composition by weight (%W) (Bowen, 1996). Those indices are used to calculate the “index of relative importance” (IRI) for each fish species (Hyslop, 1980; Cortes, 1997). The multiple data indices can give indications as to what prey items are more important to a particular predator species, as well as the diversity of the diet

(Hyslop, 1980; Hall, 1995). In areas where interspecific and intraspecific competition can occur, stomach content data also allow for the examination of diet overlap.

Stomach content analysis is a method for reconstructing the pelagic food web and illustrating interactions among multiple species within a specific area. However, some problems are associated with the analysis, including varying digestion rates, potential misidentification of stomach contents, and determination of bait items in the stomach versus naturally preyed upon items. Soft bodied organisms (e.g. squid) can be difficult to identify due to faster digestion rates compared to hard or dense bodied items. Problems can also occur as a result of the time lag between removing the stomach and the chemical fixation and preservation process; due to enzymes still present and active in the stomach, partial digestion of the contents can occur before laboratory examination (Bowen, 1996). In addition to the potential error associated with prey identification, the stomach contents contain only a short-term view into the diet (Pinkas, 1971). In general, stomach contents provide data on the most recent or last few prey items ingested by the predator fish before it was caught (Hyslop, 1980).

To overcome some of the inherent problems associated with stomach content analyses, a newer approach was employed that uses stable isotope analysis in combination with stomach content data to examine the dynamics of food webs. Stable isotope analysis is based on the premise that there are several isotopic versions of most elements in nature, varying only in the number of neutrons in the atomic nucleus. Because of this slight difference in atomic mass, the lighter isotope of these elements is used preferentially in metabolic reactions within biological tissues. This difference also results in these “lighter” isotopes being preferentially excreted from the organism, leaving the “heavier” isotopes behind in the tissues. Examining the ratios of these “light” and “heavy” isotopes within the biological tissues and various geographic locations can then provide information on such activities as migrations, transitions between freshwater and saltwater systems, natal origin, diet source and trophic position.

Stable isotope analysis has also emerged as one of the primary means to analyze food web structure. Stable isotopes are useful because they provide time and space integrated insights into trophic dynamics among organisms. For food web studies using stable isotope analyses, including large teleosts in the pelagic environment, the two

common elements carbon (C) and nitrogen (N) are used (Estrada, 2005; Menard, 2007; Layman, 2012). The ratio of carbon isotopes can vary among primary producers, but there is little change with trophic transfers within consumers. Therefore, carbon isotopes can be used to determine the original sources of dietary carbon for a particular organism (DeNiro, 1978; Peterson, 1987). The choice of nitrogen isotopes for a trophic study is due to the stepwise enrichment of nitrogen with trophic transfers among consumers (DeNiro, 1981).

Stable carbon isotopes are used as an indication of carbon source for the predatory fish. The stable isotope composition of the carbon consumed equals the integrated composition of that which is assimilated, respired, and excreted. The enrichment in $\delta^{13}\text{C}$ of a whole animal must, therefore, be balanced with depletion via respired carbon dioxide and/or excreted carbon. The composition of carbon isotopes of an animal reflects the isotopic composition of its diet, with an average of 1 per mil (‰) enrichment in the whole body relative to the diet (DeNiro and Epstein, 1978). Using stable carbon isotopes involves determining the $\delta^{13}\text{C}$ of a predator fishes' diet and then determining the relative contribution of potential diet sources. Since carbon fractionation is limited, typically increasing by 1‰ per trophic level as carbon moves through the food web, $\delta^{13}\text{C}$ has been used in the pelagic environment to differentiate the major source of carbon input for the organism (Peterson and Fry, 1987). For fish, $\delta^{13}\text{C}$ tends to be enriched (less negative) for nearshore species, whereas $\delta^{13}\text{C}$ tend to be depleted (more negative) for offshore (pelagic) species (France, 1995).

Stable nitrogen isotope analysis is also used to infer the diet of predatory fishes. As with carbon, the nitrogen stable isotope makeup of an animal reflects its diet with the $\delta^{15}\text{N}$ increasing in the consumer relative to its prey. The typical increase in $\delta^{15}\text{N}$ per trophic level is 3.0 to 4.0‰ (DeNiro, 1981; DeNiro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002). Due to this relatively large increase per trophic step, $\delta^{15}\text{N}$ is used to estimate the trophic position (DeNiro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002; Estrada, 2005). By evaluating $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ together for each predator fish species, the estimated diet and trophic position can be determined and some insight into the spatial area where members of that species are feeding (near shore, reef edge, or pelagic) can be inferred. The trophic position and primary diet source data obtained from

stable isotope analysis for each species can provide valuable insight into the coastal pelagic food web.

The combination of stomach content and stable isotope analyses provides key components for the evaluation of the trophic dynamics. The stomach content analyses provide data on the short term (i.e., items preyed upon 1 to 3 days prior to capture). The longer term (i.e., 4 to 6 weeks) data on diet and prey assimilation, as well as trophic position, is provided by the stable isotope analyses. The third component to be evaluated with the trophic dynamics of the coastal pelagic community is the stomach content and stable isotope data for the various size classes (i.e., juveniles versus mature and various length classes) of each species. Collecting and analyzing muscle tissue from the fish sampled at various lengths can elucidate the trophic position and food web dynamics for each size class, approximating the different life cycle stages of the particular fish species. The information obtained regarding the trophic dynamics and feeding ecology is invaluable and provides a baseline dataset for the coastal pelagic fish complex.

Materials and Methods

Specimen Collection

The coastal pelagic fishes were sampled through a combination of both fishery-dependent and fishery-independent collection methods that occurred twice a month in the coastal pelagic waters off Broward, Miami-Dade, and Monroe counties in southeast Florida (Fig. 1) from March 2010 to March 2013. The fishery-dependent sampling consisted of dockside sampling from recreational anglers, as well as sample collection at various large, recreational, pelagic fishing tournaments throughout southeast Florida and the Florida Keys.

At each fishing tournament, a sampling station was set up at or near the dock and weigh station. The sampling station location allowed the tournament anglers to weigh in their catch for the tournament and then voluntarily bring their fish to have morphometric data (e.g. fork length, etc.) recorded and biological samples collected. The various biological samples collected from the fish included the stomach, gonads, muscle, liver,



Figure 1. Study sampling area which includes the U.S. waters off of Broward, Miami-Dade, and Monroe counties. The red stars indicate sampling locations (tournament sites, general landing locations, etc.).

blood, and skin mucus. The individual fish was returned to the angler once the samples were collected.

The fishing tournament sampling station served multiple functions. First, it proved to be an efficient and cost-effective technique to simultaneously collect large amounts of data from multiple highly migratory species that have overlapping distributions and potentially overlapping diets. Second, it fostered collaboration between recreational anglers and scientists, and educated the local public on general fishery science. The collaboration with the anglers benefited this particular study by building trust with the recreational community, which resulted in increased opportunities to collect samples from the anglers.

The fishery independent sampling occurred onboard Nova Southeastern University Oceanographic Center (NSU OC) research vessels. An experimental gillnet, consisting of different sized meshes within a single mesh panel, was deployed off a NSU OC research vessel to collect small and large pelagic fishes. A directed rod-and-reel sampling effort also occurred from the NSU OC research vessel while on the water during the gillnet deployments. Sampling via gillnet and rod-and-reel from the NSU OC research vessels allowed for samples to be collected during time periods when fishing tournaments were taking place.

For the majority of all the fish sampled, morphometric and biological data was collected. The morphometric data was recorded on data sheets and included total, fork, and standard length (to the nearest one-tenth centimeter). Fork length (FL) was chosen as the standard measurement for all analyses and comparisons since FL is the measurement type referenced in regulations by management organizations. For the biological samples, stomach contents and muscle samples were used for the trophic dynamics and feeding ecology analysis. Every sample collected from a fish was labeled with a sample ID (e.g., “BLK 025²”) as a reference for the analyses. The three letter species abbreviation was based on NMFS Pelagic Observer Species codes (NMFS, 2010). The liver, blood, and mucus samples were archived and utilized for ongoing projects examining ecotoxins and

² Individual samples were numbered sequentially per year as they come into the lab. For example, “BLK 25” represents the twenty-fifth blackfin tuna sampled during year 1 and “BLK 210” represents the tenth blackfin sampled during year 2.

endocrine-disruption chemicals, while the gonads were used for ongoing reproductive assessments.

Stomach Content Analyses

Once the stomach was removed from the fish in the field, it was labeled with a sample ID and placed on ice in a marine cooler for transport back to the NSU OC Fisheries Research Laboratory. The larger stomachs were inserted individually into cloth bags with an identification tag and were placed in 10% buffered formalin for approximately one month until fixation was complete (Bowen, 1996). The smaller stomachs were placed in glass jars to undergo fixation. The stomachs were then transferred to a 70% isopropyl or ethanol solution for storage prior to the content analysis (Bowen, 1996). Both large and small stomachs were placed in cloth bags and chemically preserved in a sealed 5-gallon bucket.

For the stomach content analysis, the stomach was removed from the ethanol solution and the “full” stomach weight was recorded. The stomach was subsequently opened and all of the content was removed and placed on a dissection tray. A subjective stomach fullness coefficient (0 = empty, 1 = $\frac{1}{4}$ full, 2 = $\frac{1}{2}$ full, 3 = $\frac{3}{4}$ full, and 4 = full) was determined based on a visual assessment of the stomach (Headley, 2009). The “empty” stomach weight was recorded and the contents sorted. The identifiable prey items were identified to the lowest possible taxonomic level, and wet weight and length of each item was recorded. Each prey item was given a value-based digestion rate (e.g., 1 = fresh, 2 = whole or partially digested, 3 = fragmented or advanced digestion, 4 = hard parts only). Any unidentifiable material was recorded and weighed. Identifiable (fishery) bait items, if present, were noted and removed, but not included in the stomach fullness coefficient and analysis indices (Bowen, 1996).

The results of the stomach content analyses were used to calculate the following indices: percent frequency of occurrence, percent composition by number, percent composition by weight, and by the index of relative importance (Hyslop, 1980; Cortes, 1997). The percent frequency by occurrence (%O) quantifies the diet by compiling a total list of prey items found in the stomachs of the predator, and then comparing the presence or absence of a given prey type for that particular predator. The percent

composition by number (%N) is determined by the number of prey items of each prey type, and the number of each prey item type is expressed as a percentage of the total number of prey items found. The percent composition by weight (%W) is the weight of each prey item expressed as a percentage of the total weight of prey items found in an individual stomach (Bowen, 1996). The %W data can suggest and identify to an extent which prey types are more important to the predator fish species' nutrition. The quantitative indices of analysis: %O, %N, and %W were combined and used to calculate the “index of relative importance” (IRI) (Pinkas, 1971).

$$\text{IRI} = (\%N + \%W) * (\%O)$$

Since the %O is a non-additive index, the values for higher taxonomic levels could be greater than 100% (e.g., 112.6 %O of teleost³), which affects the IRI. In order to compare specific prey categories, the IRI was converted to a percentage using the following equation (Cortes, 1997):

$$\%IRI_i = 100 * (\text{IRI} / \sum \text{IRI}_i)$$

To further evaluate the coastal pelagic foodweb, the interspecific relationships among the predators were analyzed. To measure the diet overlap between pairs of predators, two data sets, normalized %O and %W, were used. The prey items were grouped by family taxon. The diet overlap was computed via the Schoener's Index equation:

$$\alpha = 1.0 - 0.5 \times \sum |p_{ij} - p_{ik}|$$

where j and k are the two predator species, p_{ij} is the proportional contribution of the prey taxon i to the total frequency or weight of prey items from predator species j , and p_{ik} is the proportional contribution of prey taxon i to the total frequency or weight of prey items from predator species k . The index varies from 0 (no overlap) to 1 (complete

³ An individual fish can ingest more than one prey item of the same species or family. For example, a stomach contains 3 ballyhoo and 1 squid. The %O of teleost would be greater than 100%.

overlap), with an accepted significance value of $\alpha \geq 0.60$ (Wallace, 1981). In situations where data on prey availability were absent, the Schoener's index was appropriate (Wallace, 1981).

Stable Isotope Analyses

Approximately 30 g of white muscle tissue from each individual sample was collected and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The muscle tissue collected in the field was kept on ice in a cooler during the remainder of that day's field work and transported back to the NSU OC Fisheries Lab where it was stored in a -80°C freezer until processing. During muscle tissue processing, a clean portion of the tissue was cut into small 3-5 mm² pieces, put on drying tin and placed in a 60°C oven to be dehydrated. After a 48 to 72 hour time period, the tissue samples were removed from the oven and pulverized for homogeneity using a Wig-L-Bug amalgamator. Approximately 0.5-0.8 mg of the homogenized tissue was weighed and pelletized in aluminum tins to undergo stable isotope analysis using a mass spectrometer.

The mass spectrometer combusts the individual tissue samples which releases the carbon and nitrogen gases. Magnets inside the mass spectrometer separate the heavier isotopes (C^{13} and N^{15}) from the lighter isotopes (C^{12} and N^{14}) by mass. Duplicate subsamples of each sample were combusted and analyzed for stable isotope ratios using a Costech 4010 elemental analyzer coupled to a Delta V Advantage stable isotope mass spectrometer via a ConFlo IV interface continuous flow mode. Reproducibility was 0.2‰ for both carbon and nitrogen stable isotope ratios. All samples were linearly corrected with a two-point linear correction to acetanilide and urea standards calibrated to a V-PDB (Pee Dee Belemnite) standard. Pee Dee Belemnite is the standard used for $^{13}\text{C}/^{12}\text{C}$, and atmospheric air is used for $^{15}\text{N}/^{14}\text{N}$. The ratio of the heavy to light isotopes (e.g., $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$) for each tissue sample was calculated and represented by the (δ) symbol and expressed in parts per thousand (‰) using the equation:

$$\delta (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$$

Since the fractionation of carbon isotopes is typically < 1‰ increase per trophic level, the $\delta^{13}\text{C}$ was used to indicate dietary assimilation of prey items and spatial reference for a given predator species (DeNiro and Epstein, 1978; Tieszen, 1983; Peterson and Fry, 1987). The $\delta^{15}\text{N}$ was used to estimate the trophic position for species within the food web (DeNiro and Epstein, 1981; Post, 2002; Fry, 2006). The following equation was used to estimate the trophic position of the predator fish species:

$$\text{Trophic position} = \lambda + \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}}{\Delta_n}$$

where λ is the trophic position of the organism used for $\delta^{15}\text{N}_{\text{base}}$, Δ_n is the enrichment of $\delta^{15}\text{N}$ per trophic increase, and $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value for the study species (Post, 2002). The trophic position can be estimated because the $\delta^{15}\text{N}$ of the consumer (predator fish) is typically 3-4‰ enriched relative to its diet.

Muscle tissue from both males and females, all size classes, and the two seasons were analyzed. Several potential prey items such as Penaeidae (shrimp), Exocoetidae (flying fishes), Clupeidae (herrings and shads), and Carangidae (jacks) have already undergone stable isotope analysis in prior studies and their values published (Estrada, 2005; Rooker, 2006).

Data Analysis

The SPSS software package (v 20; IBM, Inc.) was used for the statistical analysis. A multiple comparison one-way ANOVA was used to determine significant difference among the data. A Pearson's r correlation coefficient test was used to determine potential correlations and both linear regression and multiple regression analyses were used to determine strength of relationship and each variable. The research area was sub-divided into five geographic subareas based on the sampling locations. For the comparison of mature versus juvenile, the individuals from each species were classified as either juvenile or mature based on published length-at-maturity metrics. If there was a different length-at-maturity for males and females, then the largest length was used to ensure that only reproductively mature individuals were represented in the "mature" classification.

The determination of landing season (e.g., wet season or dry season) was based on the climate of South Florida, where the presence/absence of a daily cycle of showers and thunderstorms defines the “rainy season”. The start/end date for the rainy and dry seasons was determined by the Miami-South Florida National Weather Service Forecast Office (National Weather Service, 2013).

Results

Specimen Collection

A total of 782 coastal pelagic fish were collected between March 2010 and March 2013, comprising: blackfin tuna (n = 168), dolphinfish (n = 87), king mackerel (n = 212), little tunny (n = 249), skipjack tuna (n = 42), and wahoo (n = 24) (Table 1).

Morphometric data (e.g., fork length, FL) were recorded for > 90% of the individuals sampled (Table 2). The distribution of male and females sampled varied for each species (Table 3; Fig. 2), with the majority of females collected from dolphinfish (63.5%), king mackerel (68.4%), and wahoo (54.6%). A majority of the blackfin tuna, dolphinfish, king mackerel, little tunny, and skipjack tuna sampled were mature individuals. Only wahoo (62.5%) had a higher proportion of juveniles sampled (Table 4; Fig.3). The distribution of samples collected by landing season (Fig. 4) varied for each species and only little tunny (90.4% wet season) and wahoo (70.8% wet season) demonstrated a considerable difference in amount of samples collected per season.

Stomach Content Analysis

In total, 408 stomach samples from the six coastal pelagic species were collected and analyzed during the three year time period. Overall, the majority of stomachs analyzed from the six species (90% blackfin, 93% dolphinfish, 68% king mackerel, 65% little tunny, 94% skipjack, and 100% wahoo) contained prey items (Table 5). A higher percentage of stomachs sampled from blackfin, dolphinfish, king mackerel, little tunny, and skipjack were from mature individuals. Only wahoo had a higher percentage of juveniles sampled (Table 5). A total of 23 prey taxa families were identified from the stomachs of the six predator species. The family Clupeidae (herrings, shads, sardines, and

Table 1. Landing location with the total number of samples collected from each coastal pelagic fish species.

Species	Landing Location				
	Fort Lauderdale	Miami Beach	Islamorada, FL Keys	West Palm Beach	Pompano Beach
BLK	94	37	30	0	7
DOL	11	49	25	1	1
KGM	23	76	13	6	94
LTA	166	21	3	34	25
SKJ	16	11	10	0	5
WAH	1	12	9	1	1

Table 2. Fork length characteristics for the six coastal pelagic predator fish species.

Species	Fork Length (cm)						
	Total N	Valid N	Mean	Minimum	Maximum	Standard Deviation	Standard Error of Mean
BLK	168	151	57.36	34.30	92.00	16.48	1.34
DOL	87	86	77.58	28.40	114.00	17.22	1.86
KGM	212	212	100.34	72.20	210.00	16.53	1.14
LTA	249	236	61.96	25.00	84.00	12.23	.80
SKJ	42	39	56.75	29.00	77.40	11.83	1.89
WAH	24	24	93.28	53.40	132.70	27.17	5.55

Table 3. Percentage of gender (male or female) sampled for each coastal pelagic predator fish species.

Species	Male		Female	
	Total N	Percentage	Total N	Percentage
BLK	107	72.8%	40	27.2%
DOL	31	36.5%	54	63.5%
KGM	66	31.6%	143	68.4%
LTA	148	66.1%	76	33.9%
SKJ	17	50.0%	17	50.0%
WAH	10	45.5%	12	54.5%

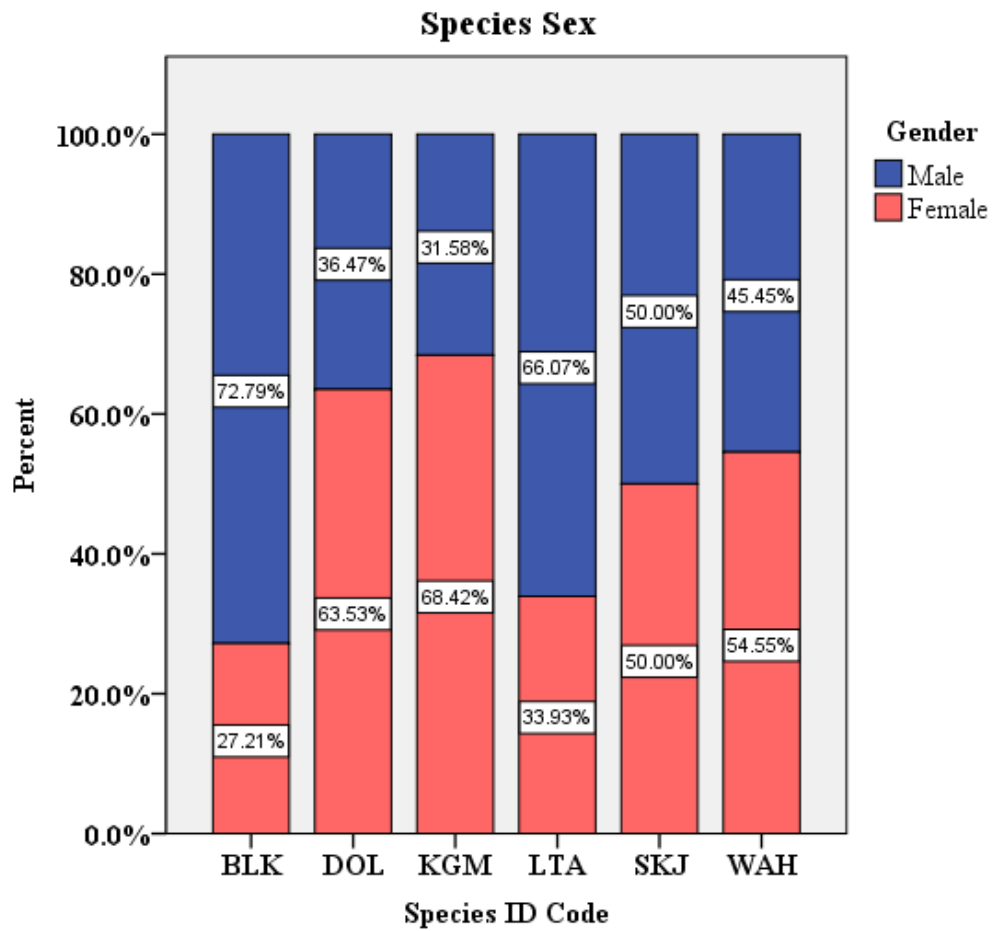


Figure 2. Percentage of gender (male or female) sampled for each coastal pelagic predator fish species.

Table 4. Size-class (Juvenile or Mature) of the samples collected for each coastal pelagic predator fish species, expressed by number and percentage.

Species	Juvenile		Mature	
	<i>N</i>	Percentage	<i>N</i>	Percentage
BLK	59	39.1%	92	60.9%
DOL	13	15.1%	73	84.9%
KGM	9	4.2%	203	95.8%
LTA	13	5.5%	223	94.5%
SKJ	7	17.5%	33	82.5%
WAH	15	62.5%	9	37.5%

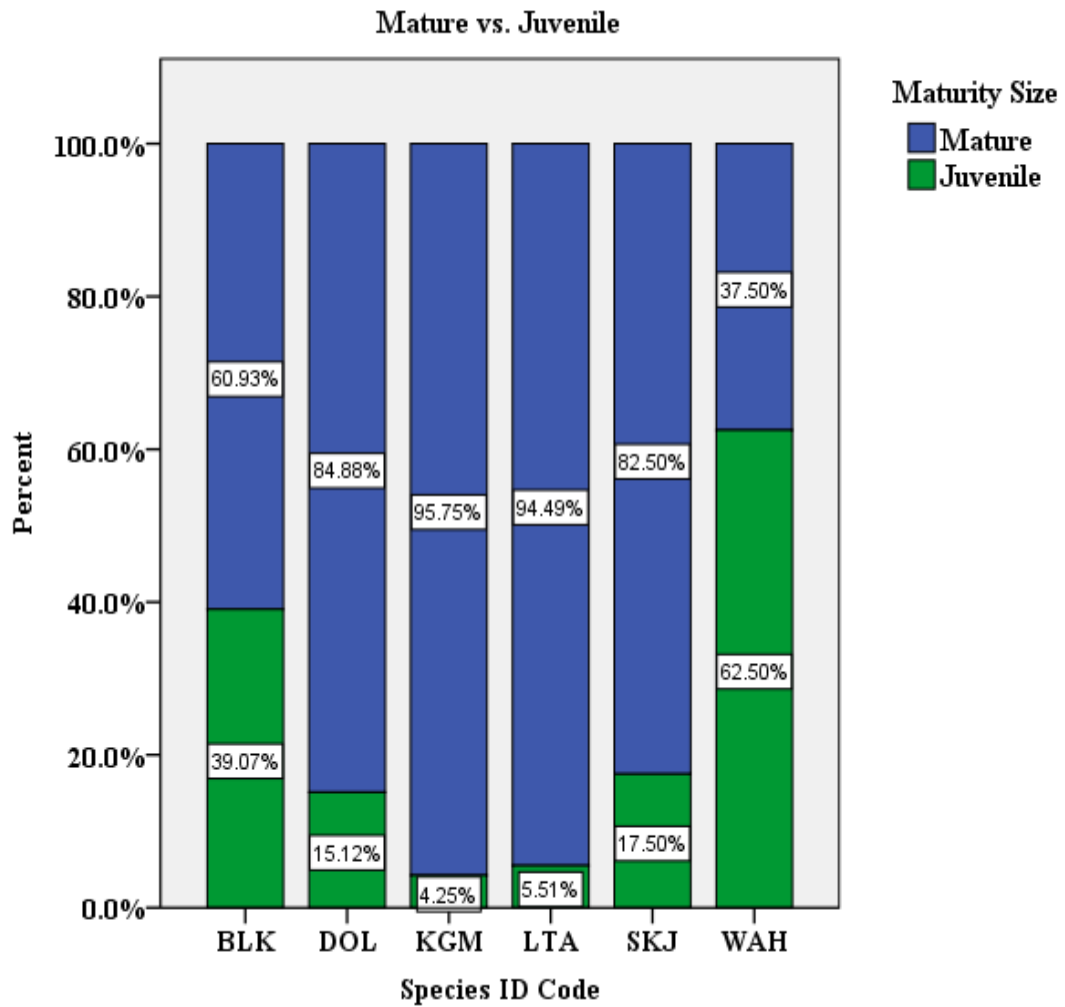


Figure 3. The size-class (Juvenile or Mature) for the samples collected for each coastal pelagic fish species, expressed by percentage.

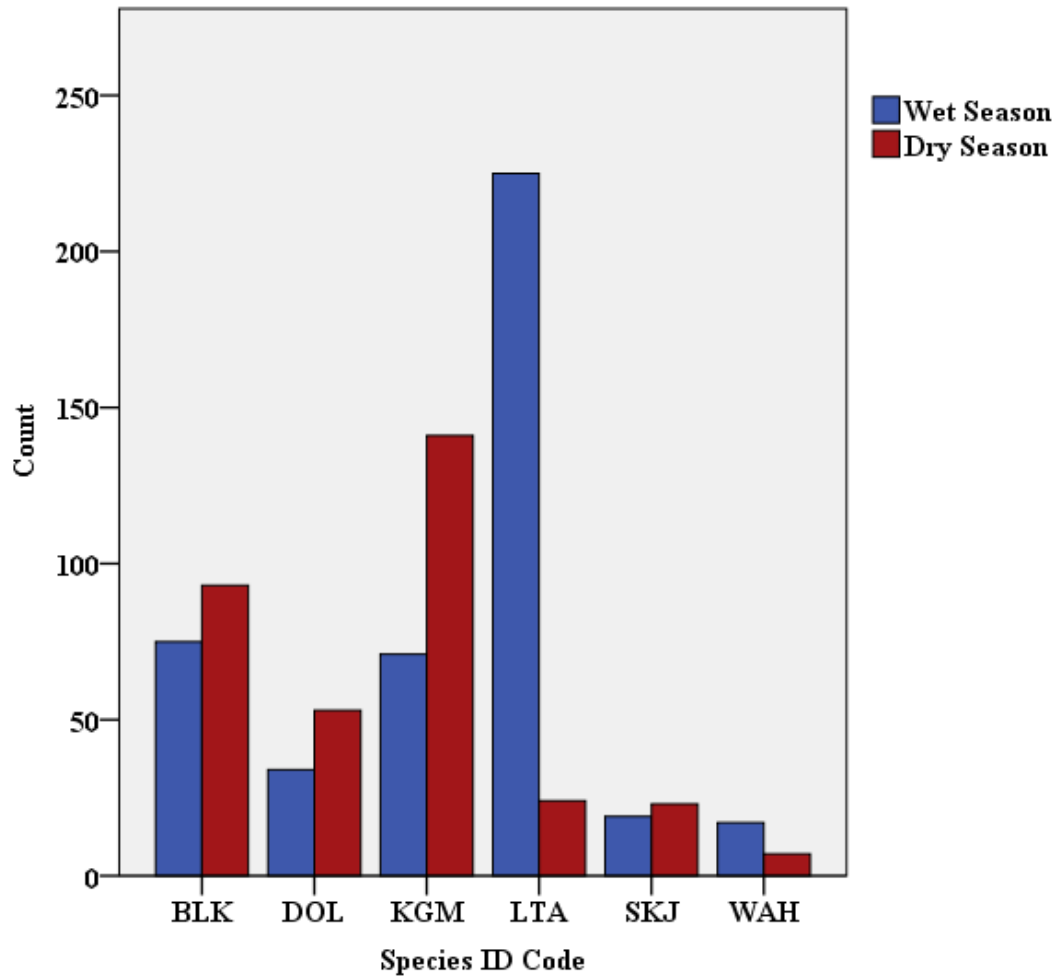


Figure 4. The samples collected from each coastal pelagic fish species, expressed by landing season (wet season or dry season).

Table 5. The number of stomachs collected and number of stomachs used in the analyses containing prey items for each coastal pelagic species.

Species	Mean Fork Length (cm)	Stomach Contents	
		<i>N</i>	<i>N with Prey</i>
BLK	57.36	61	55
DOL	77.58	72	67
KGM	100.34	168	114
LTA	61.96	54	35
SKJ	56.75	33	31
WAH*	93.28	20	20

- * The majority of stomachs collected from juvenile specimens based on the mean FL which is less than the average length at first maturity

menhaden) was the most commonly occurring prey item, being identified in stomachs from all the predator species except wahoo. According to the IRI, teleost (89.21%) was the most important prey items for all six species, followed by crustaceans (5.06%), arthropod (2.85%), and cephalopod (2.69%). A full breakdown of IRI percentages per predator species is presented in Table 6.

The blackfin tuna diet (Table 7; Fig. 5) exhibited moderate diversity, comprising 12 identifiable prey taxa in the 55 non-empty stomachs examined. The prey items found in the stomachs included teleost fishes, crustaceans, cephalopods, arthropods, and plant material. The teleost fishes comprised the largest portion of the diet (%O = 60%, %N = 46.1%, %W = 93.24%) and demonstrated the highest relative importance (%IRI = 90.44%). Among the identifiable teleosts, the families Clupeidae (%O = 17.0%, %N = 13.0%, %W = 38.92%) and Exocoetidae (%O = 6.0%, %N = 5.6%, %W = 26.5%) contributed the most to the diet by occurrence, number, and weight. The unidentifiable teleosts group (%O = 26.0%, %N = 24.2%, %W = 9.4%, %IRI = 38.47%) demonstrated the highest occurrence and number of items; however, the weight was considerably lower compared to other teleost prey items. Clupeids (%IRI = 38.9%) demonstrated the greatest relative importance to the overall diet. Crustacea (%O = 17.0%, %N = 21.4%, %W = 1.2%, %IRI = 12.1%), and in particular the family Penaeidae (%O = 7.0%, %N = 14.9%, %W = 0.7%, %IRI = 4.8%), exhibited the greatest occurrence and number among non-teleosts, as well as the relative importance to the diet. Cephalopods, arthropods, and plant material (%IRI = 2.5% combined) did not show a high relative importance to the diet.

The dolphinfish diet (Table 8; Fig. 6) exhibited the greatest amount of diversity, comprising 17 identifiable prey taxa in 67 non-empty stomachs examined. The prey items found in the stomachs included teleost fishes, crustaceans, cephalopods, and plant material. The teleost fishes comprised the largest contribution to the diet (%O = 77.8%, %N = 89.5%, %W = 98.2%) and demonstrated an overwhelmingly high relative importance (%IRI = 97.3%). The most frequent teleost families were Clupeidae (%O = 11.1%, %N = 10.1%), Exocoetidae (%O = 9.3%, %N = 4.4%), Balistidae (%O = 5.6%, %N = 10.5%), and Carangidae (%O = 5.6%, %N = 2.6%). Within the teleosts, Clupeidae

Table 6. Summary of prey families in the stomach contents of each coastal pelagic predator fish species, expressed as index of relative importance percentage (IRI %). (Continued to following page)

IRI (%)

	Blackfin Tuna	Dolphinfish	King Mackerel	Little Tunny	Skipjack Tuna	Wahoo
Teleostei	89.11	97.29	97.99	88.66	76.13	86.06
Family Synodontidae		0.07				
Family Belonidae		0.42				
Family Exocoetidae	8.08	7.13	0.11		1.46	
Family Hemiramphidae	0.09		0.04	1.81		0.72
Family Clupeidae	37.39	7.25	3.24	45.50	52.80	
Family Engraulidae		0.97				
Family Chaetodontidae		0.06				
Family Corphaenidae		0.03				
Family Sparidae		0.02				
Family Carangidae	3.90	1.83	19.10	18.89		0.13
Family Haemulidae			0.02			
Family Syngnathidae	0.02	0.02				
Family Diodontidae		0.34				
Family Sternoptychinae	0.05					
Family Balistidae	0.28	2.47				0.82
Family Tetraodontidae	0.02	0.18				
Family Monacanthidae		0.45				0.41
Unidentifiable Teleost	39.29	76.07	75.49	22.45	21.87	83.97

Table 6. (Continued) Summary of prey families in the stomach contents of each coastal pelagic predator fish species, expressed as index of relative importance percentage (IRI %).

	IRI (%)					
	Blackfin Tuna	Dolphinfish	King Mackerel	Little Tunny	Skipjack Tuna	Wahoo
Crustacea	6.01	0.02	0.31	0.12	18.86	
Order Decapoda					0.12	
Family Portunidae		0.02				
Family Penaeidae	6.01		0.31	0.12	18.74	
Cephalopoda	1.45	0.18	0.03	1.47	1.70	11.30
Order Teuthida						
Family Loliginidae					1.70	
Family Ommastrephidae	0.13		0.03	1.33		3.32
Unidentifiable Cephalopoda	1.32	0.18		0.14		7.97
Arthropoda	0.44			7.91	0.20	
Order Amphipoda					0.14	
Order Isopoda	0.44				0.06	
Plantae	0.67	2.24	0.07	0.07	0.23	0.09
Family Hydrocharitaceae	0.09	0.22			0.23	0.09
Family Sargassaceae	0.58	2.03	0.07	0.07		
Unidentifiable Material	2.32	0.27	1.61	1.78	2.89	2.56

Table 7. Blackfin tuna *Thunnus atlanticus*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%). (Continued to following page)

	O	%O	N	% N	W (g)	% W	IRI	IRI (%)
Teleotei	59	0.60	99.00	46.05	2224.80	93.24	14941.81	90.44
Order Beloniformes								
Family Exocoetidae	6	0.06	12.00	5.58	633.30	26.54	350.43	8.49
Family Hemiramphidae	1	0.01	1.00	0.47	40.10	1.68	3.90	0.09
Order Clupeiformes								
Family Clupeidae	17	0.17	28.00	13.02	928.60	38.92	1605.45	38.90
Order Gasterosteiformes								
Family Syngnathidae	1	0.01	1.00	0.47	0.50	0.02	0.88	0.02
Order Perciformes								
Family Carangidae	5	0.05	5.00	2.33	391.20	16.40	170.19	4.12
Order Stomiiformes								
Family Sternoptychidae	1	0.01	2.00	0.93	1.70	0.07	1.82	0.04
Order Tetraodontiformes								
Family Balistidae	2	0.02	6.00	2.79	5.00	0.21	10.91	0.26
Family Tetraodontidae	1	0.01	1.00	0.47	0.20	0.01	0.86	0.02
Unidentifiable Teleost	26	0.26	52.00	24.19	224.20	9.40	1587.53	38.47

Table 7. (Continued from previous page)

Blackfin tuna (<i>Thunnus atlanticus</i>) Stomach Content Analysis								
	O	%O	N	% N	W (g)	% W	IRI	IRI (%)
Crustacea	17	0.17	46.00	21.40	27.78	1.16	697.30	12.18
Order Decapoda	10	0.10	35.00	16.28	10.90	0.46	304.29	7.37
Family Penaeidae	7	0.07	32.00	14.88	16.88	0.71	198.43	4.81
Cephalopoda	5	0.05	17.00	7.91	80.58	3.38	102.58	1.43
Family Ommastrephidae	2	0.02	3.00	1.40	0.18	0.01	5.10	0.12
Unidentifiable Cephalopoda	3	0.03	14.00	6.51	80.40	3.37	53.90	1.31
Arthropoda	4	0.04	5.00	2.33	0.90	0.04	17.19	0.42
Order Isopoda	4	0.04	5.00	2.33	0.90	0.04	17.19	
Plantae	6	0.06	6.00	2.79	9.60	0.40	34.83	0.64
Order Alismatales								
Family Hydrocharitaceae	2	0.02	2.00	0.93	0.60	0.03	3.47	0.08
Order Fucales								
Family Sargassaceae	4	0.04	6.00	2.79	9.00	0.38	23.04	0.56
Unidentifiable Material	8	0.08	10.00	4.65	42.40	1.78	93.50	2.27
Total		1.00	215.00	100.00	2386.06	100.00	4126.61	100.00

BLK

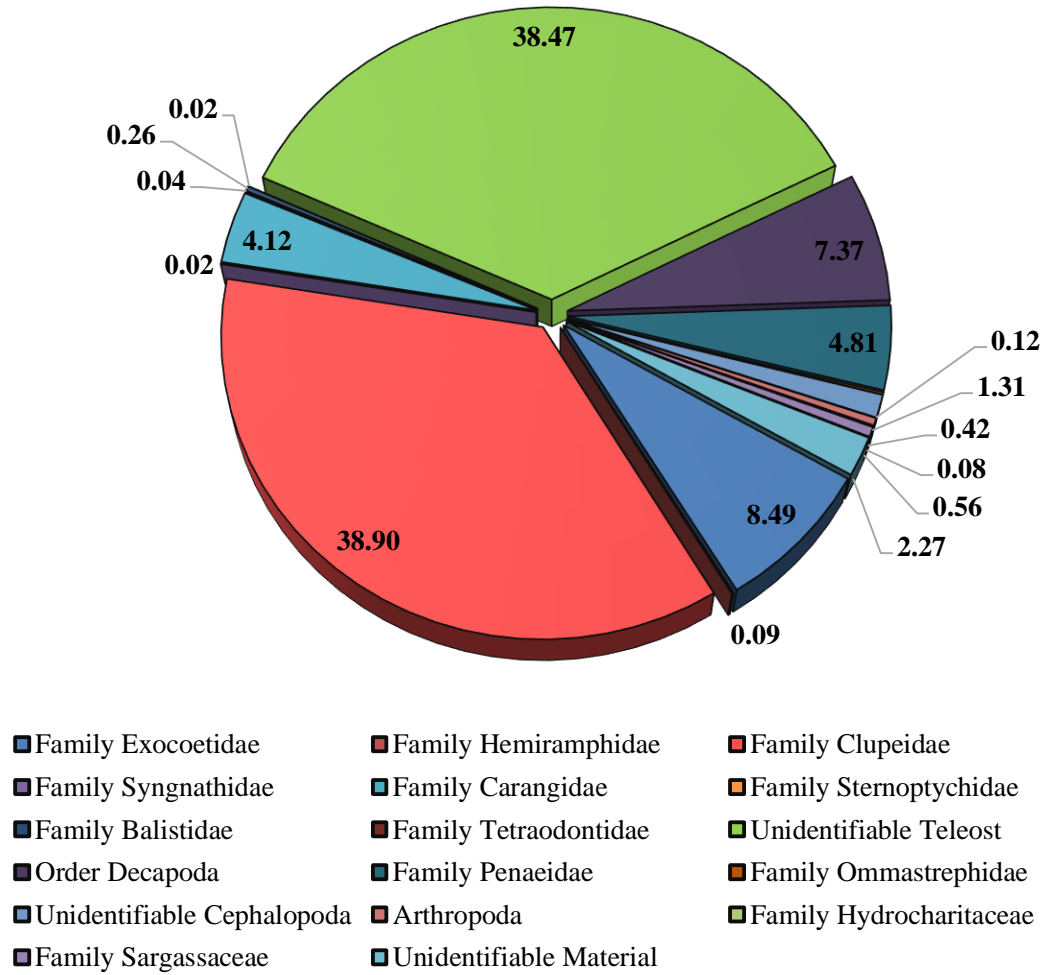


Figure 5. Blackfin tuna *Thunnus atlanticus*, stomach contents by prey taxon, expressed in %IRI.

Table 8. Dolphinfish *Coryphaena hippurus*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%).

	O	%O	N	% N	W (g)	% W	IRI	IRI (%)
Teleotei	84.00	0.778	204.00	89.47	3269.70	98.22	23532.32	97.29
Order Aulopiformes								
Family Synodontidae	1.00	0.009	1.00	0.44	67.40	2.02	3.68	0.07
Order Beloniformes								
Family Belonidae	2.00	0.019	3.00	1.32	191.90	5.76	21.14	0.42
Family Exocoetidae	10.00	0.093	10.00	4.39	652.30	19.60	357.93	7.13
Order Clupeiformes								
Family Clupeidae	12.00	0.111	23.00	10.09	339.90	10.21	363.56	7.25
Family Engraulidae	2.00	0.019	11.00	4.82	383.00	11.51	48.75	0.97
Order Perciformes								
Family Chaetodontidae	1.00	0.009	1.00	0.44	55.50	1.67	3.14	0.06
Family Corphaenidae	1.00	0.009	1.00	0.44	19.40	0.58	1.52	0.03
Family Sparidae	1.00	0.009	1.00	0.44	3.80	0.11	0.83	0.02
Family Carangidae	6.00	0.056	6.00	2.63	252.90	7.60	91.60	1.83
Order Gasterosteiformes								
Family Syngnathidae	1.00	0.009	1.00	0.44	3.30	0.10	0.80	0.02
Order Tetraodontiformes								
Family Diodontidae	3.00	0.028	3.00	1.32	81.40	2.45	16.84	0.34
Family Balistidae	6.00	0.056	24.00	10.53	109.90	3.30	123.83	2.47
Family Tetraodontidae	2.00	0.019	2.00	0.88	70.90	2.13	8.98	0.18
Family Monacanthidae	3.00	0.028	8.00	3.51	49.90	1.50	22.42	0.45
Unidentifiable Teleost	33.00	0.306	109.00	47.81	988.20	29.69	3816.84	76.07

Table 8. (Continued from previous page)

Dolphinfish (<i>Coryphaena hippurus</i>) Stomach Content Analysis								
	O	%O	N	% N	W (g)	% W	IRI	IRI (%)
Crustacea		0.009						0.02
Family Portunidae	1.00	0.009	1.00	0.44	2.30	0.07	0.76	0.02
Cephalopoda		0.028						0.18
Unidentifiable Cephalopoda	3.00	0.028	3.00	1.32	24.30	0.73	9.16	0.18
Plantae	16.00	0.148	16.00	7.02				2.24
Order Alismatales								
Family Hydrocharitaceae	4.00	0.037	4.00	1.75	1.90	0.06	10.81	0.22
Order Fucales								
Family Sargassaceae	12.00	0.111	12.00	5.26	13.90	0.42	101.74	2.03
Unidentifiable Material	4.00	0.037	4.00	1.75	16.70	0.50	13.47	0.27
Total	108.00	1.000	228.00	100.00	3328.80	100.00	5017.80	100.00

DOL

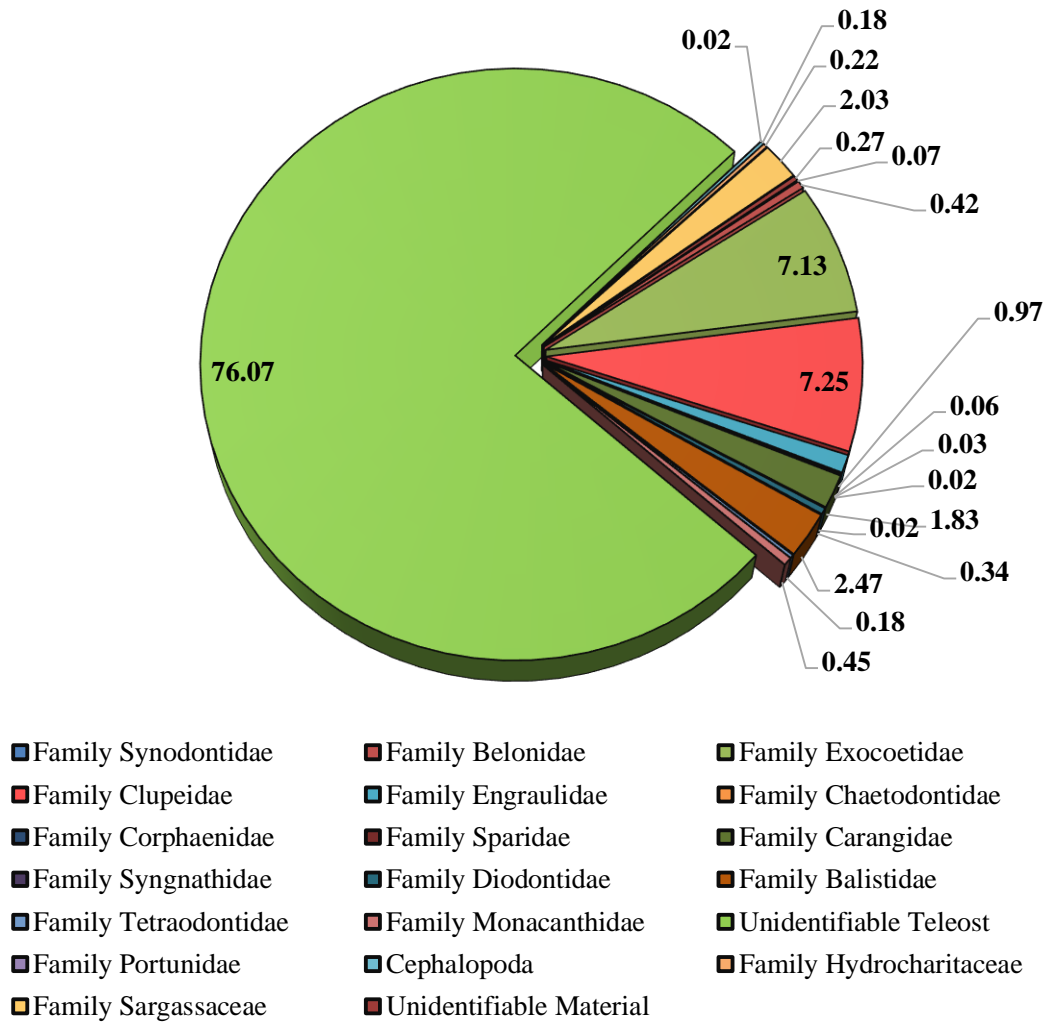


Figure 6. Dolphinfish *Coryphaena hippurus*, stomach contents by prey taxon, expressed in % IRI.

(%IRI = 7.25%) and Exocoetidae (%IRI = 7.13%) exhibited a relative importance to the diet. The unidentifiable teleost group (%IRI = 76.1%) demonstrated the highest relative importance to the overall diet. The family Sargassaceae (%O = 11.1%, %N = 5.3%, %IRI = 2.24%) had the highest non-teleost values for occurrence, number, and relative importance. Classes Crustacea and Cephalopoda (%IRI = 0.2% combined) did not show a significant importance to the diet. The presence of the family Coryphaenidae (%O = 0.01%, %N = 0.44%) within the stomachs potentially suggest a degree of cannibalism on individuals of the same family.

The king mackerel diet (Table 9; Fig. 7) exhibited a limited amount of diversity, comprising 8 identifiable prey taxa in the 114 non-empty stomachs examined. The prey items found in the stomachs include teleost fishes, crustaceans, cephalopods, and plant material. Teleosts comprised the largest portion of the diet (%O = 81.3%, %N = 86.3%, %W = 97.3%) and demonstrated an overwhelming high relative importance (%IRI = 98%). Among the teleosts, the family Carangidae (%O = 18%), %N = 13.7, %W = 50.6%) made up the majority of the diet by occurrence, number and weight. Carangidae (%IRI = 19.1%) also exhibited an important contribution to the diet. The unidentifiable teleost group (IRI% = 75.5%) showed the greatest relative importance to the diet overall. Crustaceans, cephalopods, and plant material (%IRI = 0.41% combined) did not show any significant importance to the diet.

The little tunny diet (Table 10; Fig. 8) exhibited a low amount of diversity, comprising only 7 identifiable prey taxa in the 35 non-empty stomachs examined. The prey items included teleost fishes, crustaceans, cephalopods, arthropods, and plant material. Teleosts comprised the largest portion of the diet (%O = 70%, %N = 48%, %W = 86.6%), and exhibited the highest relative importance (%IRI = 88.7%). The family Clupeidae was the most frequently occurring (%O = 25%), although Carangidae (%N = 19.1%) had a higher number of prey items within the stomachs. Clupeidae (%IRI = 45.5%) showed the most relative importance of all identifiable teleosts, followed by Carangidae (%IRI = 18.9%), to the diet. Arthropoda had a high number of prey items (%N = 44.1%); however, the low occurrence (%O = 0.05%) and weight (%W = 0.11%) illustrated a lack of significance to the diet. Crustaceans, cephalopods, and plant material (%IRI = 1.66% combined) did not show any significant importance to the diet.

Table 9. King mackerel *Scomberomorus cavalla*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%).

	O	%O	N	% N	W(g)	% W	IRI	IRI (%)
Teleotei	104	0.81	151.00	86.29	4615.60	97.27	16745.89	97.99
Order Beloniformes								
Family Exocoetidae	2	0.02	2.00	1.14	140.00	2.95	7.18	0.11
Family Hemiramphidae	1	0.01	2.00	1.14	89.70	1.89	2.66	0.04
Order Clupeiformes								
Family Clupeidae	12	0.09	17.00	9.71	532.10	11.21	220.30	3.24
Order Perciformes								
Family Carangidae	23	0.18	24.00	13.71	2401.00	50.60	1297.60	19.10
Family Haemulidae	1	0.01	1.00	0.57	31.10	0.66	1.08	0.02
Unidentifiable Teleost	65	0.51	105.00	60.00	1421.70	29.96	5129.45	75.49
Crustacea	6	0.05	6.00	3.43	26.90	0.57	21.03	0.31
Order Decapoda								
Family Penaeidae	6	0.05	6.00	3.43	26.90	0.57	21.03	0.31
Cephalopoda	2	0.02	2.00	1.14	0.50	0.01	2.02	0.03
Order Teuthida		0.00						
Family Ommastrephidae	2	0.02	2.00	1.14	0.50	0.01	2.02	0.03
Plantae	3	0.02	3.00	1.71	0.30	0.01	4.53	0.07
Order Fucales								
Family Sargassaceae	3	0.02	3.00	1.71	0.30	0.01	4.53	0.07
Unidentifiable Material	13	0.10	13.00	7.43	101.60	2.14	109.13	1.61
Total		1.00	175.00	100.00	4744.90	100.00	6794.98	100.00

KGM

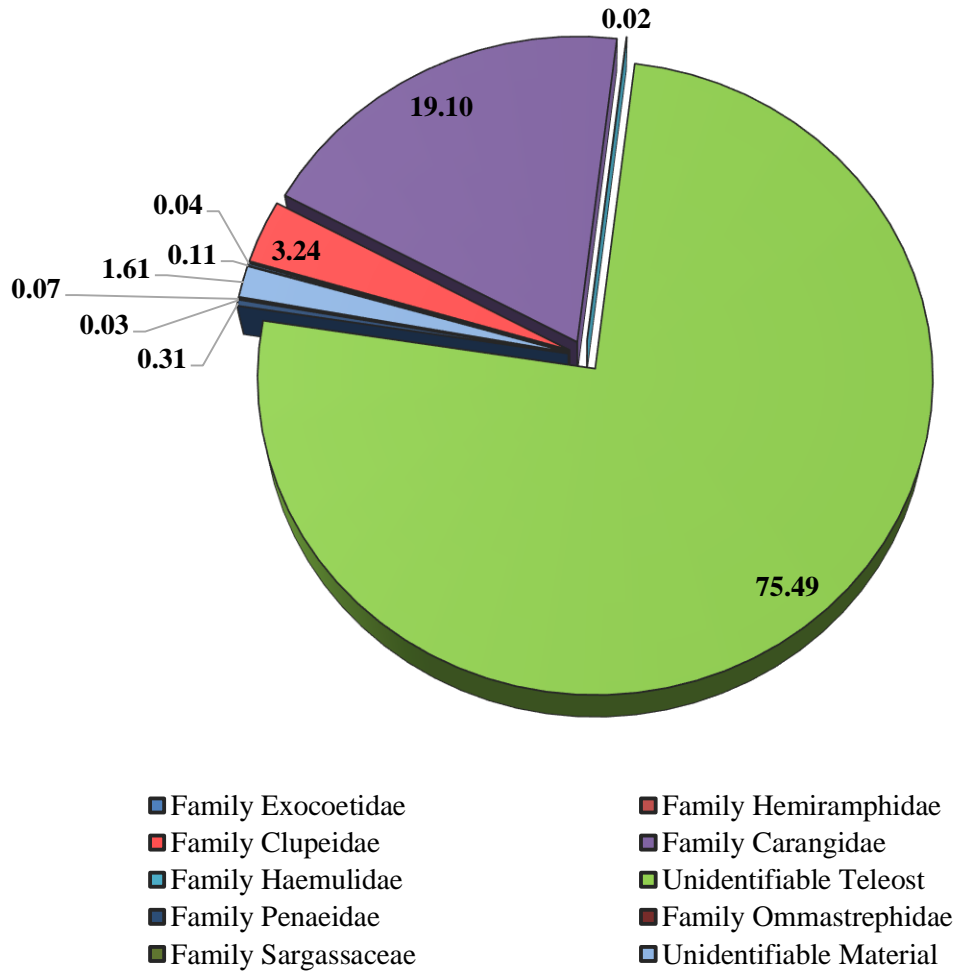


Figure 7. King mackerel *Scomberomorus cavalla*, stomach contents by prey taxon, expressed in %IRI.

Table 10. Little tunny *Euthynnus alletteratus*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%).

	O	%O	N	% N	W(g)	% W	IRI	IRI (%)
Teleotei	28	0.700	73.00	48.03	1236.30	86.64	10773.49	88.66
Order Beloniformes								
Family Hemiramphidae	2	0.050	2.00	1.32	125.90	8.82	57.94	1.81
Order Clupeiformes								
Family Clupeidae	10	0.250	24.00	15.79	500.20	35.06	1452.70	45.50
Order Perciformes								
Family Carangidae	4	0.100	29.00	19.08	480.80	33.70	603.14	18.89
Unidentifiable Teleost	12	0.300	18.00	11.84	129.40	9.07	716.94	22.45
Cephalopoda	2	0.050	6.00	3.95	178.00	12.47	93.84	1.47
Order Teuthida								
Family Ommastrephidae	1	0.025	4.00	2.63	175.20	12.28	42.60	1.33
Unidentifiable Cephalopoda	1	0.025	2.00	1.32	2.80	0.20	4.32	0.14
Arthropoda	2	0.050	67.00	44.08	1.60	0.11	252.52	7.91
Order Isopoda	1	0.025	1.00	0.66	0.10	0.01	1.90	
Crustacea	1	0.050	66.00	43.42	1.50	0.11	124.36	0.12
Order Decapoda	1	0.025	66.00	43.42	1.50	0.11	124.36	
Family Penaeidae (shrimp)	1	0.025	2.00	1.32	0.20	0.01	3.80	0.12
Plantae	1	0.025	1.00	0.66	1.30	0.09	2.14	0.07
Order Fucales								
Family Sargassaceae	1	0.025	1.00	0.66	1.30	0.09	2.14	0.07
Unidentifiable Material	5	0.125	5.00	3.29	9.70	0.68	56.70	1.78
Total		1.000	152.00	100.00	1426.90	100.00	3192.80	100.00

LTA

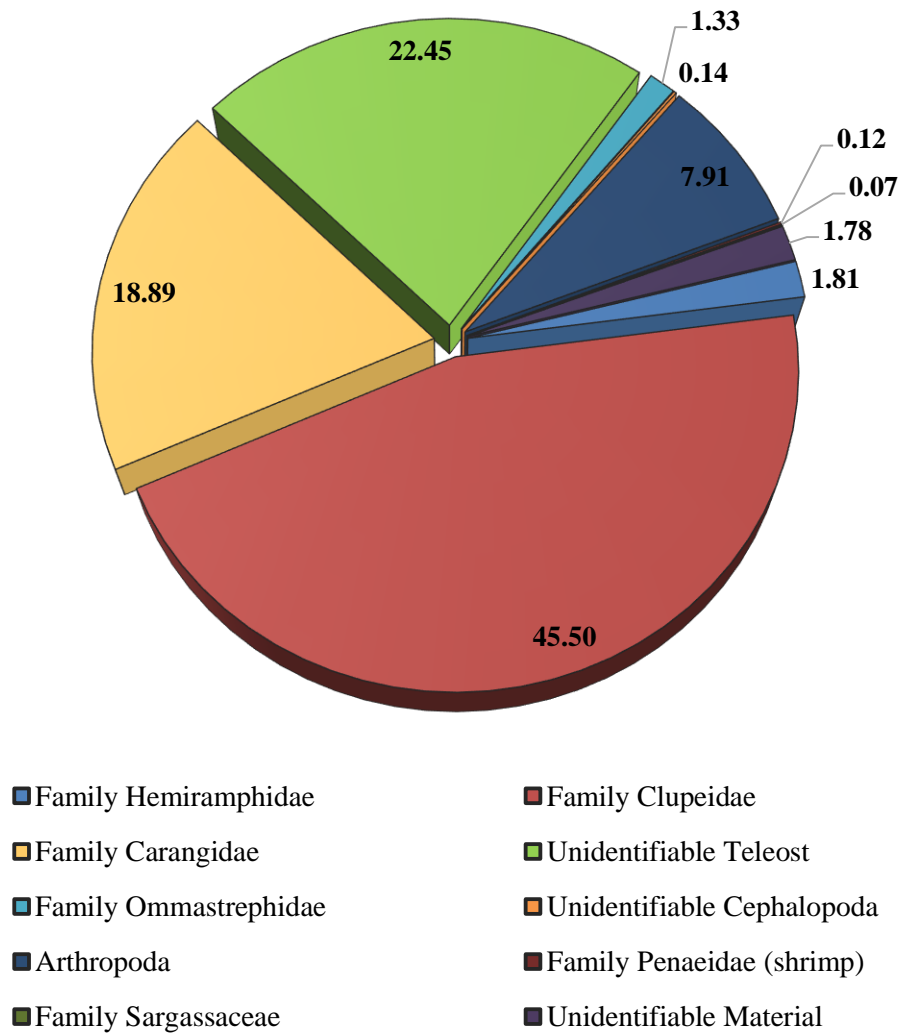


Figure 8. Little tunny *Euthynnus alletteratus*, stomach contents by prey taxon, expressed in %IRI.

The skipjack tuna diet (Table 11; Fig. 9) exhibited a low diet diversity, with only 7 identifiable prey taxa in the 31 non-empty stomachs examined. The prey items included teleost fishes, crustaceans, cephalopods, arthropods, and plant material. Teleosts comprised the large majority of the diet (%O = 42%, %N = 62.5%, %W = 85.2%), and exhibited the highest importance (%IRI = 76.1%). The most frequent and largest weight percentage family of teleosts was Clupeidae (%O = 19.4%, %N = 40%, %W = 53.6%). Penaeidae had a relatively high occurrence (%O = 19.4%, %N = 29.2%), although the weight (%W = 4%) was low when compared to other frequently occurring prey items. The families Clupeidae (%IRI = 52.8%) and Penaeidae (%IRI = 18.7%) were determined to have an importance within the diet. The unidentifiable teleosts group (%O = 19.4%, %N = 20.8%, %W = 17.9%) had a significant contribution in the diet, and relative importance (%IRI = 21.9%). Cephalopods, arthropods, and plant material (%IRI = 2.13% combined) did not demonstrate a relative importance to the diet.

The wahoo diet (Table 12; Fig. 10) exhibited the lowest diversity, with only 6 identifiable prey taxa in the 20 non-empty stomachs examined. The prey items included teleost fishes, cephalopods, and plant material. Teleost fishes comprised the majority of the diet (%O = 56.3%, %N = 50%, %W = 78.8%) and demonstrated the highest importance (%IRI = 86.1%). Among the teleosts, Balistidae (%O = 6.3%, %N = 3.9%, %W = 2.4%) and Monacanthidae (%O = 6.3%, %N = 2.6%, %W = 0.56%) had the highest frequency occurring and by number percentage of prey item families. The family Hemiramphidae had the largest contribution by weight (%W = 9.73%). Cephalopoda (%O = 28.1%, %N = 20.5%, %W = 16.6%) was the most frequently occurring and had the largest contribution to the diet of all non-teleosts. The %IRI showed that Cephalopoda (11.3%), including Ommastrephid squids (3.3%), had a relatively moderate importance in the diet. Teleosts had the highest %IRI (86.1%), although none of the individually identifiable prey taxa were significant. The unidentifiable teleosts group (%IRI = 84%) showed the most importance to the overall diet. Plant material (Hydrocharitaceae) did not account for an important contribution to the diet.

The Schoener's Index utilized the normalized %O values to calculate the values for diet overlap among the six predator species, and a metric was used to compare the species to each other (Table 13). The diet overlap values varied ($\alpha = 0.558$ to $\alpha = 0.888$)

Table 11. Skipjack tuna *Katsuwonus pelamis*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%).

	O	%O	N	% N	W(g)	% W	IRI	IRI (%)
Teleotei	13	0.419	105.00	62.50	1286.00	85.15	6191.95	76.13
Order Beloniformes								
Family Exocoetidae	1	0.032	3.00	1.79	207.00	13.71	49.98	1.46
Order Clupeiformes								
Family Clupeidae	6	0.194	67.00	39.88	809.00	53.57	1808.71	52.80
Unidentifiable Teleost	6	0.194	35.00	20.83	270.00	17.88	749.26	21.87
Crustacea	7	0.226	50.00	29.76	70.10	4.64	776.86	18.86
Order Decapoda	1	0.032	1.00	0.60	10.50	0.70	4.16	0.12
Family Penaeidae	6	0.194	49.00	29.17	60.40	4.00	641.93	18.74
Cephalopoda	2	0.065	4.00	2.38	100.40	6.65	58.25	1.70
Order Teuthida	2	0.065	4.00	2.38	100.40	6.65	58.25	1.70
Family Loliginidae	2	0.065	4.00	2.38	100.40	6.65	58.25	1.70
Arthropoda	2	0.065	2.00	1.19	5.00	0.33	7.68	0.20
Order Amphipoda	1	0.032	2.00	1.19	4.90	0.32	4.89	0.14
Order Isopoda	1	0.032	1.00	0.60	0.10	0.01	1.94	0.06
Plantae	2	0.065	2.00	1.19	0.40	0.03	7.87	0.23
Order Alismatales	2	0.065	2.00	1.19	0.40	0.03	7.87	0.23
Family Hydrocharitaceae	2	0.065	2.00	1.19	0.40	0.03	7.85	0.23
Unidentifiable Material	5	0.161	5.00	2.98	47.60	3.15	98.84	2.89
Total		1.000	168.00	100.00	1510.20	100.00	3425.81	100.00

SKJ

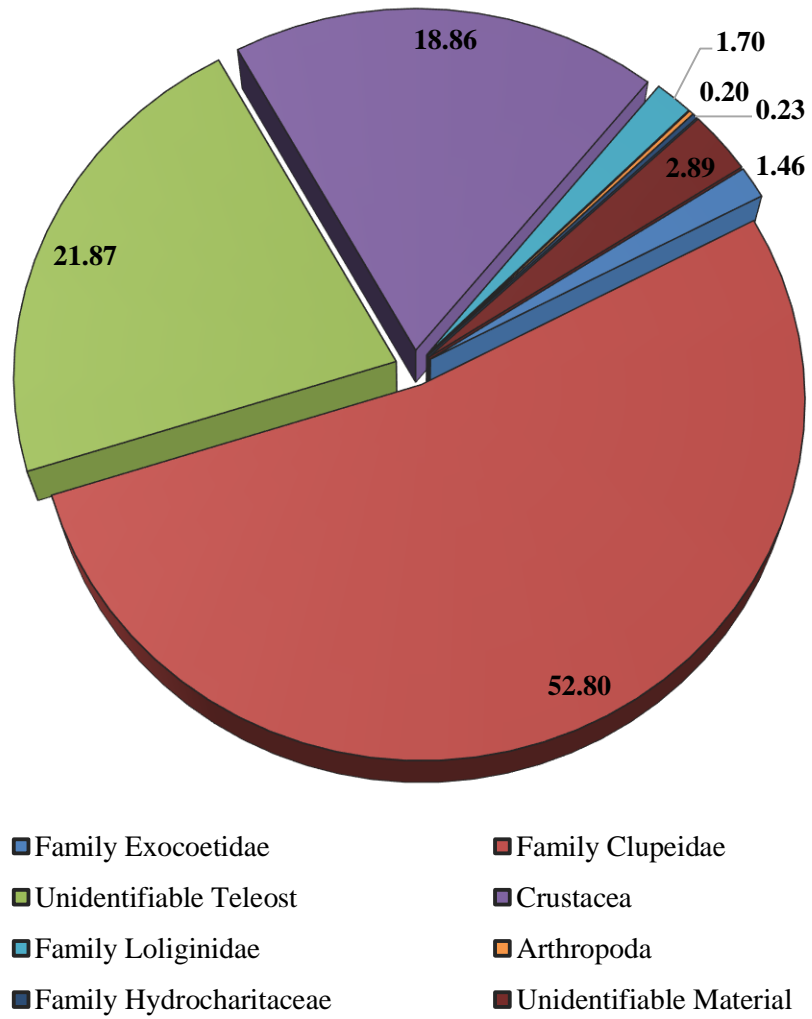


Figure 9. Skipjack tuna *Katsuwonus pelamis*, stomach contents by prey taxon, expressed in %IRI.

Table 12. Wahoo *Acanthocybium solandri*, summary of stomach content analyses, expressed as percentages based on frequency of occurrence (%O), by number (%N), by weight (%W), and index of relative importance (IRI%).

	O	%O	N	% N	W(g)	% W	IRI	IRI (%)
Teleotei	18.00	0.56	39.00	50.00	293.20	78.82	11593.55	86.06
Order Beloniformes								
Family Hemiramphidae	1.00	0.03	1.00	1.28	36.20	9.73	55.07	0.72
Order Perciformes								
Family Carangidae	1.00	0.03	1.00	1.28	2.60	0.70	9.90	0.13
Order Tetraodontiformes								
Family Balistidae	2.00	0.06	3.00	3.85	8.90	2.39	62.39	0.82
Family Monacanthidae	2.00	0.06	2.00	2.56	2.10	0.56	31.29	0.41
Unidentifiable Teleost	12.00	0.38	32.00	41.03	243.40	65.43	6387.34	83.97
Cephalopoda	9.00	0.28	16.00	20.51	61.60	16.56	1668.24	11.30
Order Teuthida								
Family Ommastrephidae	3.00	0.09	6.00	7.69	34.10	9.17	252.88	3.32
Unidentifiable Cephalopoda	6.00	0.19	10.00	12.82	27.50	7.39	606.39	7.97
Plantae	1.00	0.03	1.00	1.28	0.10	0.03	6.54	0.09
Order Alismatales								
Family Hydrocharitaceae	1.00	0.03	1.00	1.28	0.10	0.03	6.54	0.09
Unidentifiable Material	4.00	0.13	4.00	5.13	17.10	4.60	194.50	2.56
Total		1.00	78.00	100.00	372.00	100.00	7606.31	100.00

WAH

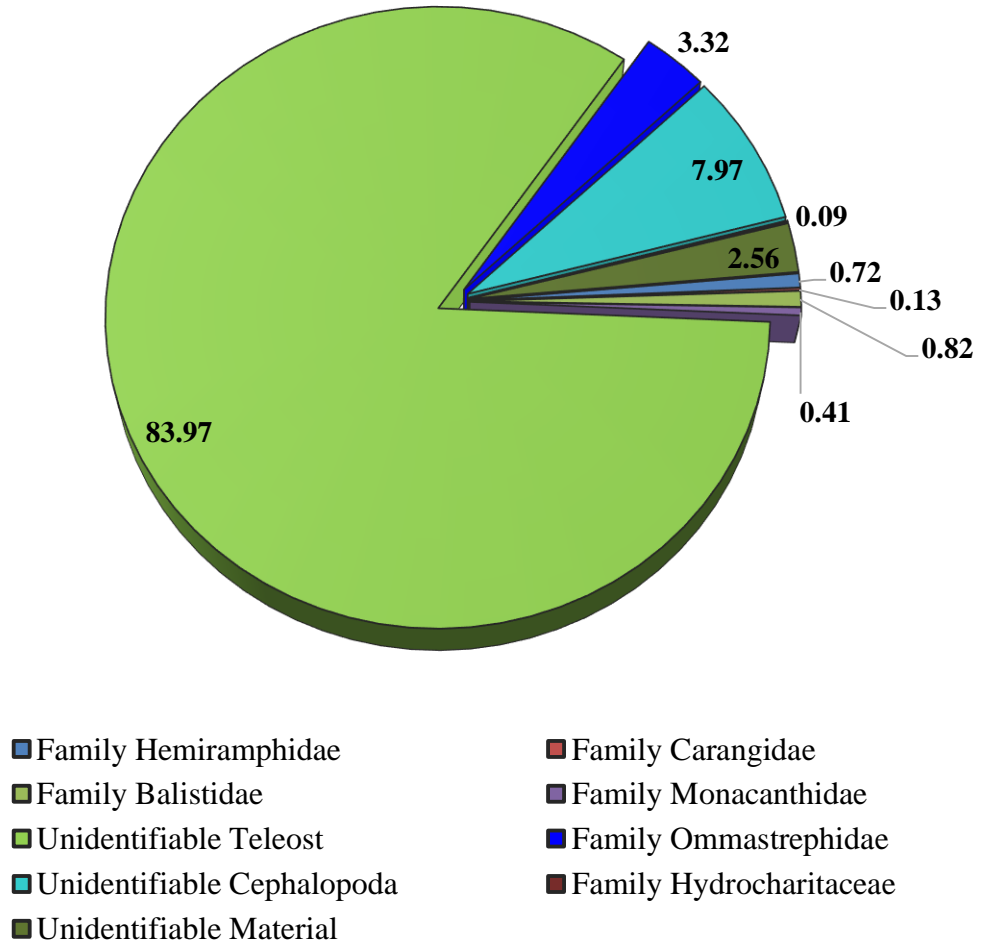


Figure 10. Wahoo *Acanthocybium solandri*, stomach contents by prey taxon, expressed in %IRI.

Table 13. Values of the Schoener's diet overlap index between each coastal pelagic predator fish species. Overlap was measured using the metric normalized percent frequency of occurrence (%O).

Predator	BLK	DOL	KGM	LTA	SKJ	WAH
BLK	1.000	0.686	0.716	0.788	0.858	0.707
DOL	0.686	1.000	0.863	0.799	0.558	0.659
KGM	0.716	0.863	1.000	0.888	0.606	0.704
LTA	0.788	0.799	0.888	1.000	0.719	0.763
SKJ	0.858	0.558	0.606	0.719	1.000	0.640
WAH	0.707	0.659	0.704	0.763	0.640	1.000

between pairs of predators. The diet overlap between king mackerel and little tunny ($\alpha = 0.888$), between king mackerel and dolphinfish ($\alpha = 0.863$), and between blackfin tuna and skipjack tuna ($\alpha = 0.858$) were the highest of all species evaluated. Conversely, the values between dolphinfish and skipjack tuna ($\alpha = 0.558$), and between skipjack tuna and king mackerel ($\alpha = 0.606$) showed the lowest diet overlap among the species. Significant diet overlap ($\alpha \geq 0.60$) was found between all the study species except between dolphinfish and skipjack tuna ($\alpha = 0.558$).

Stable Isotope Analysis

A total of 258 muscle tissue samples from the six coastal pelagic species were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 14; Fig. 11-14). The mean $\delta^{15}\text{N}$ ranged from 8.21 ‰ (wahoo) to 13.18 ‰ (king mackerel), and the mean $\delta^{13}\text{C}$ ranged from -18.41 ‰ (king mackerel) to -16.70 ‰ (dolphinfish). Blackfin tuna exhibited the largest $\delta^{15}\text{N}$ range (7.22 to 13.21 ‰), as well as the largest $\delta^{13}\text{C}$ (-20.68 to -16.47 ‰) range.

Considerable variation in the trophic position between the six species was discovered based on the nitrogen and carbon isotopic values from the muscle tissue. A multiple comparison, one-way ANOVA found a significant difference in $\delta^{15}\text{N}$ ($n = 259$, $df = 5$, $F = 88.642$, $p < 0.0005$) and $\delta^{13}\text{C}$ ($n = 259$, $df = 5$, $F = 28.216$, $p < 0.0005$) among all six species. A further examination of the stable nitrogen and carbon isotopic values was conducted to determine if any of the species could be grouped together in trophic guilds. A combined mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plot for all the species (Fig. 14) illustrated three distinct groupings.

To evaluate the relationship between fish size and trophic position, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were tested against various aspects related to size and environmental conditions. A Pearson's r correlation coefficient test indicated a significant positive correlation between fork length and $\delta^{15}\text{N}$ for blackfin tuna ($n = 75$, $r = .896$, $p < 0.0001$), king mackerel ($n = 53$, $r = .367$, $p < 0.0001$), little tunny ($n = 36$, $r = .462$, $p < .005$), skipjack ($n = 27$, $r = .600$, $p < 0.001$), and wahoo ($n = 22$, $r = .934$, $p < 0.0001$). However, dolphinfish was the only species with a negative correlation ($n = 46$, $r = -.369$, $p < 0.0001$). A linear regression analysis further confirmed the relationship between fork length and $\delta^{15}\text{N}$ (both

Table 14. Isotope values for $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) for the 6 coastal pelagic predator fish species sampled off the southeastern Florida coast between 2010 and 2013.

Species ID Code	<i>N</i>	Fork Length (cm)				$\delta^{15}\text{N}$ ‰				$\delta^{13}\text{C}$ ‰			
		Mean	Min.	Max.	SE	Mean	Min.	Max.	SE	Mean	Min.	Max.	SE
BLK	75	63.30	34.30	92.00	2.04	10.05	7.22	13.21	.19	-18.08	-20.68	-16.47	.13
DOL	45	76.07	51.40	103.20	2.29	9.26	7.58	12.14	.17	-16.70	-19.13	-15.82	.10
KGM	53	99.82	56.00	135.00	2.37	13.18	10.92	15.29	.15	-18.41	-20.39	-16.21	.13
LTA	36	62.33	34.00	82.50	2.29	12.32	9.45	14.89	.19	-17.55	-19.33	-16.43	.12
SKJ	27	57.23	34.00	73.60	1.98	8.68	7.15	12.83	.28	-16.87	-17.99	-16.26	.08
WAH	22	91.81	53.40	132.70	5.87	8.21	6.46	10.32	.25	-16.92	-20.05	-15.81	.21

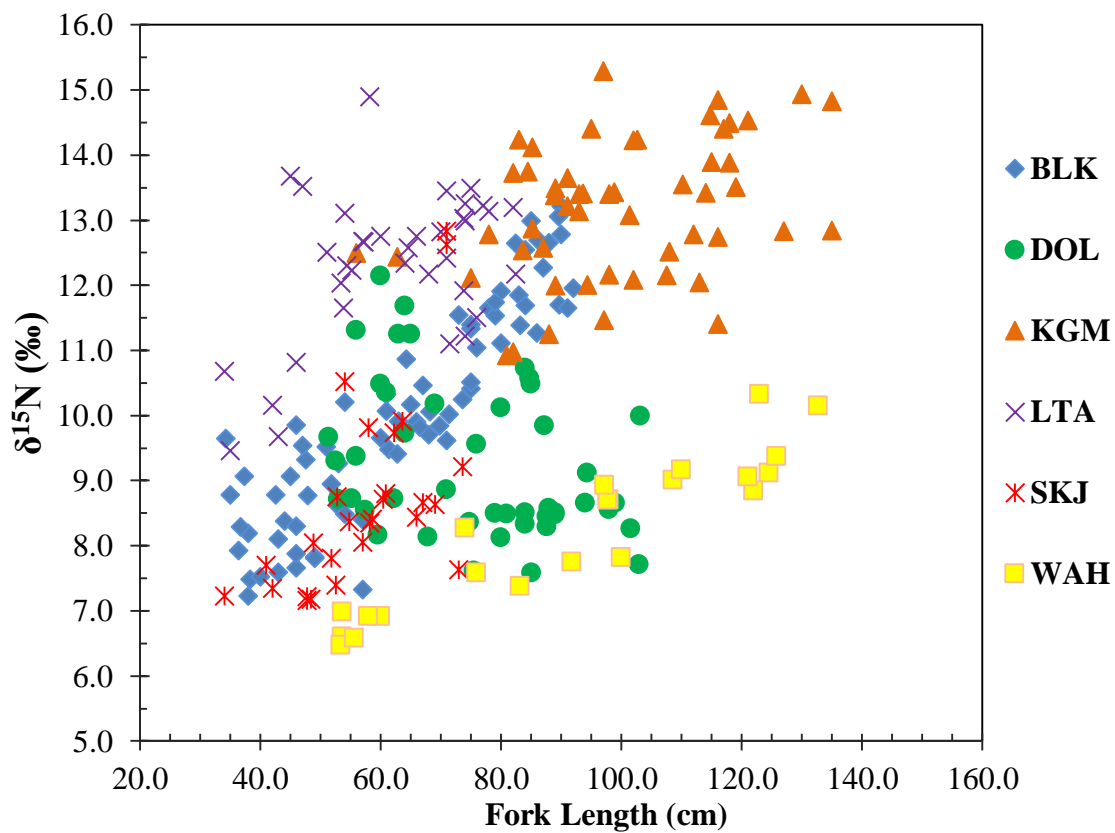


Figure 11. The $\delta^{15}\text{N}$ for individuals from each of the coastal pelagic predator fish species plotted against the fork length (cm) of each individual.

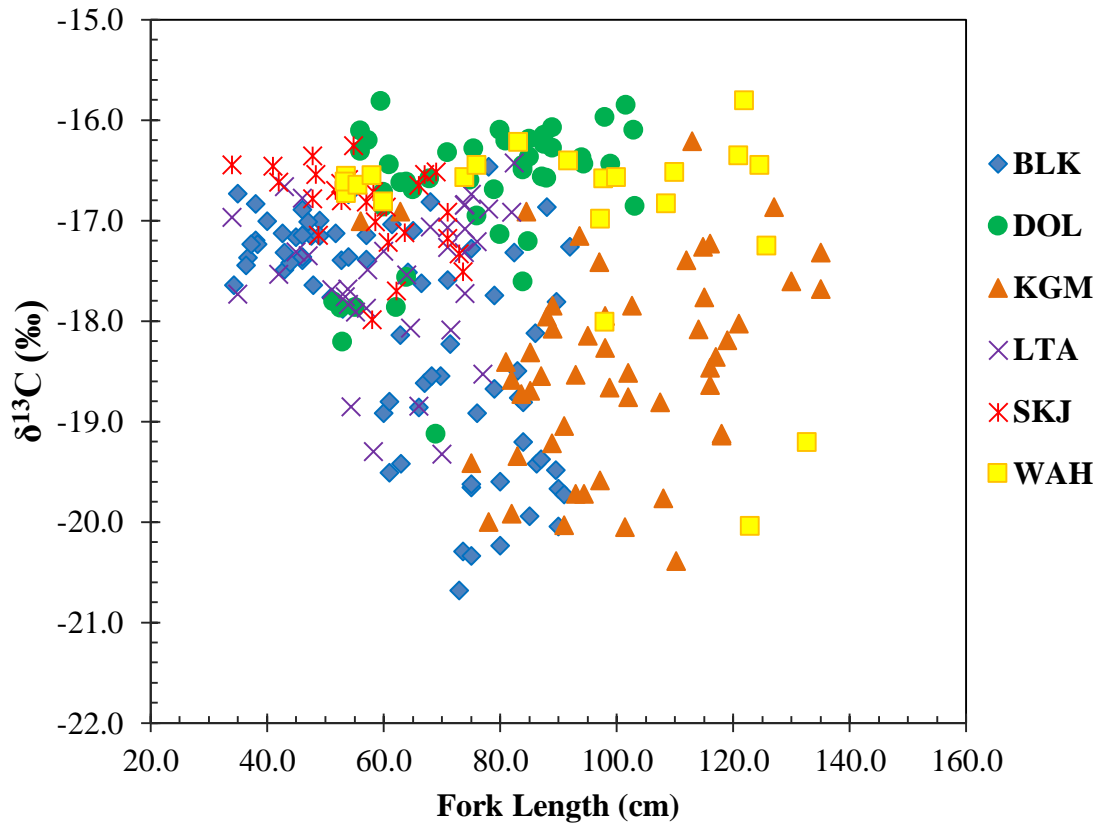


Figure 12. The $\delta^{13}\text{C}$ for individuals from each of the coastal pelagic predator fish species plotted against the fork length (cm) of each individual.

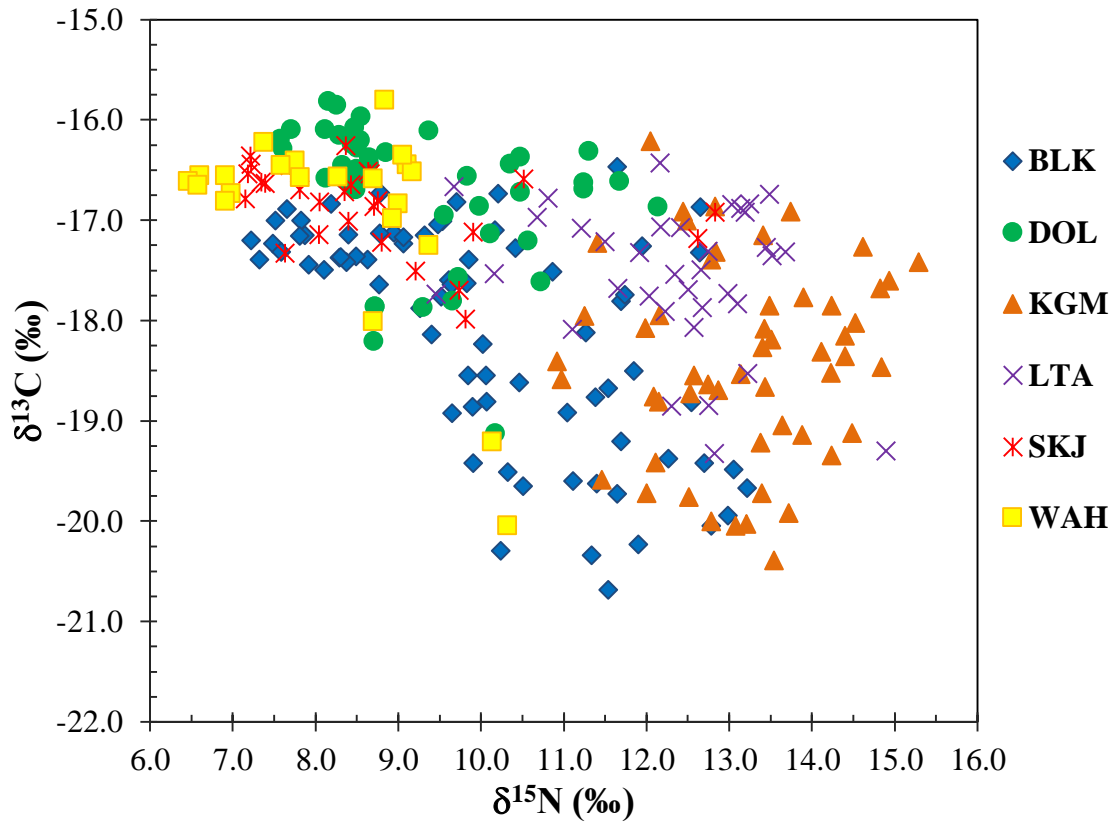


Figure 13. The $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ plotted for individuals sampled from all six coastal pelagic predator fish species.

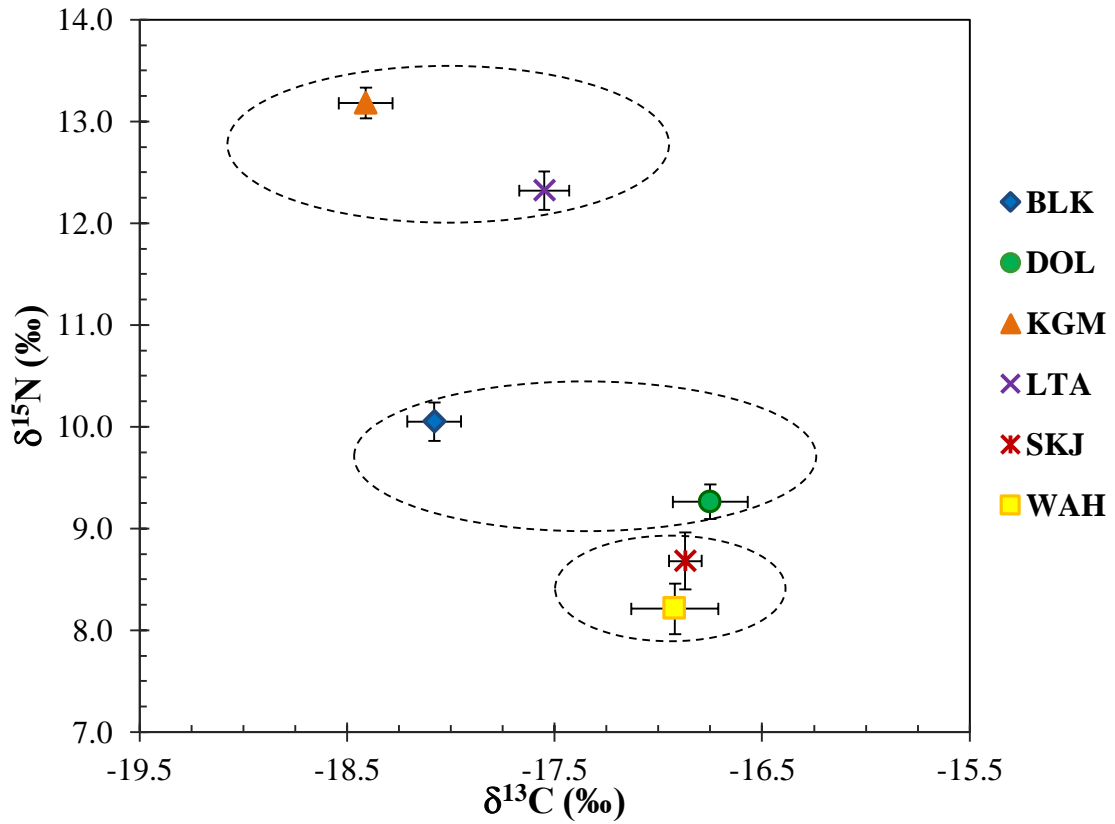


Figure 14. Biplot of the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (± 1.0 SE) of the six coastal pelagic predator fish species showing three broad trophic groups and also showing narrow variation in carbon across the species.

positive and negative) for all six species and (Fig. 11). The Pearson's r correlation test between $\delta^{13}\text{C}$ and fork length indicated a significant negative correlation in blackfin tuna ($n = 75$, $r = -.621$, $p < 0.01$) and skipjack tuna ($n = 22$, $r = -.466$, $p < 0.05$), and a positive relationship in dolphinfish ($n = 47$, $r = .389$, $p < 0.01$).

In conjunction with fork length, each species was divided into two groups (Juvenile and Mature) based on the size at first maturity for each species. A one-way ANOVA was conducted and significant differences were found in $\delta^{15}\text{N}$ between juvenile and mature individuals for the following comparisons: blackfin ($n = 75$, $df = 1$, $F = 41.970$, $p < .0005$); little tunny ($n = 35$, $df = 1$, $F = 5.484$, $p < .05$); and wahoo ($n = 22$, $df = 1$, $F = 29.806$, $p < .0005$). The fish sampled at a mature size range exhibited higher $\delta^{15}\text{N}$ relative to fish within the juvenile size range (Fig. 11). A one-way ANOVA found homogeneity among $\delta^{13}\text{C}$ values in each of the coastal pelagic fish species, except for in blackfin ($n = 75$, $df = 1$, $F = 22.386$, $p < 0.0005$). A comparison of stable isotope values between landing season (i.e., dry season or wet season) was conducted and a significant difference in $\delta^{15}\text{N}$ was only found for blackfin tuna ($n = 75$, $df = 1$, $F = 9.570$, $p < 0.005$) and dolphinfish ($n = 46$, $df = 1$, $F = 8.106$, $p < 0.01$). There was no significant difference in $\delta^{13}\text{C}$ between landing season for any species. A comparison of the isotopic values between gender for each species' gender found a significant difference in $\delta^{15}\text{N}$ only in blackfin tuna ($n = 75$, $df = 1$, $F = 5.358$, $p < 0.05$) and little tunny ($n = 35$, $df = 1$, $F = 4.142$, $p < 0.05$). There was no significant difference in $\delta^{13}\text{C}$ between males and females for any species.

A multiple regression analysis was conducted to examine the effect each variable (fork length, maturity state, landing season, and gender) had on the variability of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among the species. The analysis found that for blackfin tuna, all the variables were significant in explaining 81% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.81$, $df = 4$, $F = 74.133$, $p < 0.0005$). However, only fork length had the strongest influence on the $\delta^{15}\text{N}$ as indicated by the beta value and was statistically significant ($\beta = 0.896$, $p < 0.0005$). For dolphinfish, the analysis found that the variables were significant in explaining 29% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.29$, $df = 4$, $F = 4.319$, $p < 0.01$), and landing season had the strongest influence on $\delta^{15}\text{N}$ as indicated by the beta value and was statistically significant

($\beta = 0.389$, $p < 0.01$). For king mackerel, the analysis showed that the variables significant in explaining only 13% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.13$, $df = 4$, $F = 2.909$, $p < 0.05$), and only fork length had the strongest influence on the $\delta^{15}\text{N}$ as indicated by the beta value was statistically significant ($\beta = 0.532$, $p < 0.01$). In little tunny, the variables together were significant in explaining 31% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.307$, $df = 4$, $F = 3.208$, $p < 0.05$), but none of the variables were statistically significant beta value. For skipjack, the variables together were significant in explaining 38% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.380$, $df = 4$, $F = 3.068$, $p < 0.05$), and fork length had the strongest influence on the $\delta^{15}\text{N}$ as indicated by the beta value was statistically significant ($\beta = 0.686$, $p < 0.01$). In wahoo, the variables together were significant in explaining 90% of the $\delta^{15}\text{N}$ variability ($r^2 = 0.898$, $df = 4$, $F = 32.398$, $p < 0.0005$), and only fork length had the strongest influence on the $\delta^{15}\text{N}$ as indicated by the beta value was statistically significant ($\beta = 0.995$, $p < 0.0005$).

Discussion

Feeding Ecology

In this study, a combination of stomach content and stable isotope analyses were used to examine the feeding ecology of the tunas and mackerel that make up the coastal pelagic complex off Florida's southeastern coast. The stomach content data provided insights into distinct feeding patterns among the predators. Overall, the diets of the species in this complex included a large number of prey taxa that mainly included teleost fishes, cephalopods, and crustaceans. Across all six species, teleost fishes dominated the prey with an average of 64.5% by occurrence, 63.7% by number, and 89.9% by weight. There were two dominant prey families: 1) Clupeidae, which includes herrings, sardines, shads, and menhaden; and 2) Carangidae, which includes species of jacks, scads, and runners. These prey species are generally epipelagic schooling fishes that are not necessarily associated with floating structure. They are commonly referred to as "bait fish" and are common in the waters off southeast Florida with seasonal peaks. The other observed fish families included Exocoetidae (flying fish), Hemiramphidae (ballyhoo), Balistidae (triggerfish), Tetraodontidae (pufferfish), and Monacanthidae (filefish), all of

which are epipelagic species commonly associated with floating structure or “weedlines” of aggregated *Sargassum* sp. macroalgae. Ommastrephid squid, which are associated with pelagic waters, was the most common cephalopod prey taxon.

Selective Feeding Behaviors

In this study, all six species inhabited relatively the same coastal pelagic environment and likely had the opportunity to feed upon the same prey taxa within that environment. However, the results of both the stomach content and stable isotope analyses indicate variability among the diets of all six species. This variability is suggestive of a selective feeding behavior explained by the physiological and biological differences among the six species. The larger predators can exploit forage areas not as easily accessed by small size-class fish species. Furthermore, the schooling and swimming behavior could influence how the predator forages and selects various prey taxa.

Clupeidae occurred more often and in greater number in the tunas (blackfin, little tunny, and skipjack), while Carangidae were more frequent in occurrence and number king mackerel. The higher occurrence of Clupeidae and Carangidae observed in the stomachs of those predators presents evidence of selective feeding behavior. The tunas and mackerel appear to selectively target prey items which school together in large aggregations, colloquially referred to as “bait balls” due to their frequent association with these large fishes targeted by the recreational fishery.

Multiple factors could also explain the selective targeting by the tunas and mackerel. Blackfin tuna, little tunny, and skipjack tuna exhibit intra- and interspecific schooling behavior and it can be suggested that it is easier for a larger group (i.e., school) could locate and target a large aggregation of prey fish. King mackerel do not exhibit as strong as schooling behavior that is associated with tunas (ICCAT, 2006), but schooling could still explain their selective targeting. Secondly, the swimming ability of the tunas and mackerel is far superior to most of the taxa consumed (Altringham, 2001). The selective targeting of prey taxa with less superior swimming ability would require less energy expense by the predator and support the feeding strategy of maximum energy efficiency. Lastly, the size class of the tunas and mackerel sampled in this study can

explain the selective feeding of Clupeidae and Carangidae. The overwhelming majority of tunas and mackerel sampled in this study were of a mature (i.e., larger) size class. The high amount of mature samples was due in part to the sampling bias associated with the use of tournaments and recreational sources for samples.

The selective feeding on Clupeidae and Carangidae is supported indirectly by the stable isotope data, in that blackfin, little tunny, and king mackerel have the highest mean $\delta^{15}\text{N}$ (10.05, 12.32, and 13.18‰, respectively) and the most depleted mean $\delta^{13}\text{C}$ (-18.08, -17.55, and -18.41‰, respectively). These values for blackfin, little tunny, and king mackerel are indicative of feeding on prey types which are higher in proteinous and lipid material (i.e., Clupeidae and Carangidae), and those lipid rich tissues are more depleted in carbon (DeNiro and Epstein, 1978). Skipjack tuna stable isotope signatures did show some signs of diet selectivity, but the data were inconclusive.

There is also evidence of a selective feeding behavior by wahoo based on the results of the stomach content and stable isotope analysis. The high percent occurrence and percent number of Hemiramphidae, Balistidae, Monacanthidae, Ommastrephidae, and Hydrochaitaceae, in conjunction with the conspicuous absence of such families as Exocoetidae and Clupeidae, suggest a selective behavior different from the other scombrid species. Unlike other scombrids, wahoo are solitary pelagic predators that do not exhibit a strong schooling behavior (Collette, 2002). However, they are sometimes found aggregating in pairs or in small “pods” (pers. comm.). Also, wahoo typically inhabit pelagic waters and in this study were found towards the offshore side of the coastal pelagic area. In the resource limited pelagic environment, floating structure such as *Sargassum* sp. aggregations provide some of the only physical habitat for small fishes, crustaceans, and other organisms. In particular, the prey taxa of Hemiramphidae, Balistidae, Monacanthidae are commonly associated with *Sargassum* sp. aggregations when found in the pelagic environment (Rooker, 2006). By using the spatial habitat associations of those prey taxa, it can be surmised that wahoo are selectively feeding in more offshore waters around floating structure. The stable isotope values provide evidence that directly supports the selective feeding strategy of wahoo. Wahoo had the lowest mean $\delta^{15}\text{N}$ (8.21 ‰) of all the coastal pelagic predators. The $\delta^{15}\text{N}$ signature of wahoo is indicative of feeding on prey items that are lower in proteinous material (i.e.,

squids and filefish) and at a lower trophic level. The mean $\delta^{13}\text{C}$ (-16.92 ‰) for wahoo is also more enriched compared to the other predators, which does support the feeding strategy of preying on species at a lower trophic level. The more enriched mean $\delta^{13}\text{C}$ for wahoo can also be explained by biochemical fractions of lipids within the muscle tissue. Since lipids are relatively depleted in ^{13}C , and wahoo muscle tissue has a lower lipid content (i.e. fat), wahoo would have a more enriched $\delta^{13}\text{C}$ signature compared to the other coastal pelagic species (DeNiro and Epstein, 1978).

Consistent with previous studies (Oxenford, 1999; Rudershausen, 2010), there was no observed evidence of diet selectivity in dolphinfish based on the stomach contents. The dolphinfish $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ did not show any diet selectivity as well.

Inshore-Offshore Connections

The coastal pelagic environment is characterized as an ecotone between the inshore (coastal) waters and the offshore (pelagic) waters. By evaluating feeding and trophic dynamics of the coastal pelagic predators at various size classes, inshore-offshore connections among the predators were illustrated. In conjunction with the selective feeding behavior for blackfin, king mackerel, little tunny, and wahoo, the $\delta^{13}\text{C}$ indicate foraging in near shore to offshore waters. Since carbon fractionation is limited, $\delta^{13}\text{C}$ has been used in the pelagic environment to differentiate the major source of carbon input for the organism (Peterson and Fry, 1987). The major carbon sources in the marine environment are typically land based. For the coastal pelagic ecosystem the $\delta^{13}\text{C}$ tends to be enriched (less negative) for nearshore waters, whereas $\delta^{13}\text{C}$ tends to be depleted (more negative) for offshore (pelagic) waters (France, 1995).

The blackfin tuna showed isotopic evidence of a movement from near shore to offshore waters with an increase in size, because the $\delta^{13}\text{C}$ (range -20.68 to -16.47 ‰) were more depleted as the fish fork length increased. The depletion in $\delta^{13}\text{C}$ could be attributed to a change in prey with less lipid content. The blackfin tuna stomach data supports the isotopic values with the presence of prey groups Exocoetidae, Carangidae, and Balistidae that are associated with offshore “mats” or “weedlines” of aggregated *Sargassum* sp. macroalgae.

King mackerel, little tunny, and wahoo showed a similar movement from near shore to offshore waters, evidence of which is shown by the $\delta^{13}\text{C}$ and stomach content data. The $\delta^{13}\text{C}$ for king mackerel (-20.39 to -16.21 ‰), little tunny (-19.33 to -16.43 ‰), and wahoo (-20.05 to -15.81 ‰) became more depleted as the fish fork length increased. Interestingly, wahoo had a mean $\delta^{13}\text{C}$ (-16.92 ‰) that is more enriched than all the other predators and not characteristic of offshore waters. The wahoo $\delta^{13}\text{C}$ in this study can be explained by the mean fork length (91.82 cm), which is smaller than the average size range (100 to 170 cm FL) found in the western North Atlantic waters (Hogarth, 1976; Collette, 2002; McBride, 2008), and likely represents foraging in near shore, or coastal waters. Larger wahoo would presumably have more depleted $\delta^{13}\text{C}$ values which are indicative of the offshore environment (France, 1995).

The stomach content data for king mackerel, little tunny, and wahoo all had the presence of prey items associated with “weedlines” and other offshore characteristics. There was small evidence of a spatial shift in the stomach data for skipjack tuna. However, the evidence is not strong enough to make such a conclusion. There was no evidence in the stable isotope or diet data of a spatial movement in feeding grounds for dolphinfish. Dolphinfish exhibited the greatest diversity in diet, which could not be correlated to near shore or offshore waters. The $\delta^{13}\text{C}$ for dolphinfish also exhibited the least variance of all the coastal pelagic species; the small variance in $\delta^{13}\text{C}$ indicates a diet of prey items with a consistent carbon source. The small variance in $\delta^{13}\text{C}$ can also be explained by their general life history characteristics (Schwenke, 2008) of rapid growth rates and reproductive development.

Diet Overlap

The coastal pelagic ecosystem has multiple middle-top level predators inhabiting the same area. With multiple predator species in the same area, there is the potential for competition of prey resources. This is the first study to compare diet overlap among these six predator species in the southeast Florida coastal pelagic ecosystem. The stomach content analysis showed similarities between the diets of all six species. Furthermore, the Schoener’s Index of diet overlap showed there was diet overlap among

all the predators which is evidence of competition for prey resources. The diet overlap was the highest between king mackerel and little tunny ($\alpha = 0.888$) which is evidence of narrow diet and potential competition. The king mackerel and little tunny diets had the least diversity compared to the other predator species. The lowest diet overlap was between dolphinfish and skipjack tuna ($\alpha = 0.558$). Evidence of the low diet overlap is shown by dolphinfish having a highly diverse diet, whereas skipjack tuna has a low diversity diet.

Trophic Dynamics

In this study, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the muscle tissue showed evidence of movement to higher trophic levels with fish size and of distinct trophic guilds among the coastal pelagic predators. Blackfin tuna, king mackerel, little tunny, and wahoo showed a positive trend between fork length and $\delta^{15}\text{N}$ and a negative relationship with $\delta^{13}\text{C}$. The relationship between fork length and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ supports findings from prior studies where large migratory fish have an increase in fork length associated with an increase in trophic position and a decrease in $\delta^{13}\text{C}$ (Menard, 2007). In particular, blackfin tuna showed a trophic signature across two trophic levels ($\delta^{15}\text{N}$ 7.22 to 13.21 ‰) and a strong relationship ($r = .896$, $p < 0.0001$) between $\delta^{15}\text{N}$ and an increase in fork length. King mackerel and little tunny exhibited a similar relationship between fork length and $\delta^{15}\text{N}$ (king mackerel $n = 53$, $r = 0.367$, $p < 0.0001$) and (little tunny $n = 36$, $r = 0.462$, $p < 0.005$). The findings for king mackerel and little tunny are further supported by the previously mentioned stomach contents. Wahoo showed evidence of a shift in trophic position with the strongest relationship ($r = 0.934$, $p = 0.0001$) between $\delta^{15}\text{N}$ and the increase in fork length.

A trophic shift based on reproductive state (e.g., juvenile or mature) was determined based on the comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and fork length for each predator species. There is strong evidence of an ontogenetic shift at the size of first maturity in blackfin tuna and wahoo. At the size-of-maturity for blackfin (FL < 50 cm; Collette, 2002), a positive shift to a higher trophic position in $\delta^{15}\text{N}$ is shown. The distinct shift towards depleted $\delta^{13}\text{C}$ is visible, which demonstrates a shift in carbon source in the diet at

the time the fish reached reproductive maturity. At the size-of-maturity for wahoo (FL < 105 cm; Hogarth, 1976; Jenkins and McBride, 2009), the $\delta^{15}\text{N}$ showed an increase of one trophic level. There was some evidence of an enrichment in $\delta^{13}\text{C}$ in the wahoo that might be explained by trophic enrichment with size class but the disproportionate sample size of juvenile to mature wahoo prevented better interpretation. Little tunny and skipjack tuna showed little evidence of an ontogenetic shift which can be explained by the sample data. The majority of little tunny and skipjack tuna were above the size-of-maturity because of the fishery-dependent sampling and the legal size limits for each species. Dolphinfish was the only species in this study that showed no evidence of an ontogenetic shift based on the stomach contents and stable isotope signatures. Dolphinfish showing no ontogenetic shift is determined to be a result rapid growth rates (Schwenke, 2008).

In pelagic waters, trophic groups are distinguished based on the mean $\delta^{15}\text{N}$ of the representative fish species (Revill, 2009). In this study, there was evidence of a lower and upper trophic group. The first trophic group was clearly composed of skipjack tuna and wahoo ($\delta^{15}\text{N}$ mean 8.68 and 8.21 ‰, respectively). This grouping holds the lowest relative trophic position compared to the other predators. The second trophic group was composed of king mackerel (13.18 ‰) and little tunny (12.32 ‰) and held the highest relative trophic position. Blackfin tuna and dolphinfish could not be clearly separated into any one trophic group; the mean $\delta^{15}\text{N}$ for blackfin and dolphinfish places them between these two groups. The difference in trophic groups appeared to be primarily due to the diet of the predators. The diets of king mackerel and little tunny exhibited similar patterns, as did skipjack tuna and wahoo. The observed diets of blackfin tuna and dolphinfish were the highest in diversity, which provides reasoning why no clear trophic grouping could be determined for those two predators.

Relationships of Data to Prior Studies

The significant difference between this study and prior research is that it evaluates all six coastal pelagic fish individually by species, as well as together as a fish complex. The findings of this study were compared with previous studies using similar techniques and conducted on the one or more of the same species. However, in the majority of those prior studies, only one fish species or a combination of one to three fish species were

evaluated together. For some of the coastal pelagic species, there were no previous studies in which stomach content and stable isotope analysis were used.

The diet and feeding ecology of the coastal pelagic complex predators demonstrated similar findings to prior studies. The blackfin tuna diet, which consisted primarily of Clupeidae and Exocoetidae, was similar to the results of Headley et al. (2009) which found that the most common prey items were epipelagic species. The blackfin stomach contents and stable isotope data were also consistent with previous studies (Graham, 2007; Headley, 2009) on tunas which indicated that small tunas feed on a wide variety of prey items and as the tuna size increases, there is a shift in diet and trophic position (Graham, 2007; Headley, 2009). This study observed similar feeding ecology in dolphinfish to Rudershausen et al. (2010) and Manooch et al. (1984) in which dolphinfish exhibited a diverse diet consisting primarily of Exocoetidae, Balistidae, and Carangidae as indicated by the %IRI. The high %IRI values for *Sargassum* sp. and prey items associated with *Sargassum* in the diet of dolphinfish were also supported by those prior studies. The observed wahoo diet consisting primarily of Balistidae and Teuthida was supported by Rudershausen et al. (2010) who also observed a high abundance of the same prey items. The little tunny diet observed in this study was similar to that observed by Manooch et al. (1985) in which Clupeidae, Carangidae, and squid were among the most important and abundant in the diet. This study observed some differences in the prey taxa diversity and order of importance based on %IRI in the diets of the coastal pelagic species compared to the prior studies. The difference in study location may explain the disparity in diets among the same species.

The trophic dynamics data observed in this study were compared to previous studies on larger pelagic fish due to the lack of prior work on the smaller to medium sized scombrids. Multiple studies examined the trophic position and diet of bluefin tuna and other large pelagic fishes (e.g., yellowfin, swordfish, and istiophorid billfishes). Prior trophic studies on larger pelagic fishes (Estrada, 2005; Graham, 2007; Menard, 2007; Revill, 2009) found similar patterns in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ associated with an increase in size of the fish. The overall increase in trophic position was generally caused by intra-specific accumulation of heavier isotopes with the increase in size of the fish (Jennings, 2002; Revill, 2009). This current study largely supports that perspective, with $\delta^{15}\text{N}$ and

trophic position mainly increasing with the mean size of the fish, both within and between species. In contrast to Revill et al. (2009), this study did find a significant relationship between $\delta^{13}\text{C}$ and fish size; however, that relationship was only observed in blackfin tuna, dolphinfish, and skipjack tuna. In blackfin tuna and skipjack tuna there was a significant negative relationship between $\delta^{13}\text{C}$ and fork length, while dolphinfish showed a significant positive relationship.

There are no prior studies that evaluate the trophic dynamics or feeding ecology of the blackfin tuna, dolphinfish, king mackerel, little tunny, skipjack tuna, and wahoo together as a fish complex within an ecosystem. The data from this study and prior studies is similar in that the feeding ecology and the relationship among trophic variables (i.e. fork length, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$) consistent in patterns exhibited by the predators. The prey data for stomach content and stable nitrogen and carbon isotope data may differ in the values from prior studies on large scombrids, but the overall trends and relationships in data observed in this study are supported by those prior works.

Conclusion

The waters off the east coast of South Florida are habitat for a multitude of fish species, in particular scombrids. That marine habitat is at a relatively short distance from land due to the extremely short distance of the continental shelf. This shortened distance between the shore and deep water creates a unique ecosystem where coastal species and pelagic species of fish coexist. This study is the first comparison of the trophic dynamics and feeding ecology of blackfin tuna, dolphinfish, king mackerel, little tunny, skipjack tuna, and wahoo in the coastal pelagic ecosystem. The six predator species were evaluated both individually and together on their feeding ecology and trophic dynamics. The combined use of stomach content and stable isotope analysis was pivotal in the evaluation of these species together as a complex. From this study, feeding strategies for the tunas and wahoo based on physiological behavior and habitat association. For blackfin tuna, little tunny, and skipjack tuna, a feeding strategy which selectively targets epipelagic schooling prey fishes was illustrated with its relationship to schooling behavior of tunas. For wahoo, the feeding strategy was also demonstrated in relationship

to the environment and fast swimming behavior. This study was also able to show competition for prey resources with the varying amounts of diet overlap found among the coastal pelagic scombrids.

The combined use of stomach contents and stable isotope ratios lent support to the findings of each analysis conducted. A positive relationship appears to exist between an increase in trophic position and an increase in fork length for blackfin tuna, king mackerel, little tunny, skipjack tuna, and wahoo. Two distinct trophic groups, a higher trophic and a lower trophic level, and one intermediate group for the coastal pelagic species was illustrated with the stable isotope analysis. The degree of trophic grouping was due to the similar feeding ecology and higher diet overlap between certain species compared to others.

The current fisheries management plan has management moving towards an ecosystem-based approach for the future. The coastal pelagic ecosystem, where a multiple fish species utilize the same ecosystem resources as well as support recreational fishery, is a perfect example of a marine environment where ecosystem-based management can work to provide sustainable fisheries for the future. The key component to any ecosystem-based management approach is quality baseline data. The southeast Florida coastal pelagic ecosystem had large data gaps pertaining to the trophic dynamics and feeding ecology of several predator fish. The data and results generated by this study is will finally give insights into the ecosystems dynamics and provide that valuable baseline data for the southeast Florida coastal pelagic ecosystem. Go Pelagic or Go Home!

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