

NUTRITION AND HABITAT DRIVEN FORAGING OF WILD DOLPHINS IN THE
BAHAMAS: A RECIPE FOR PREY USE

by

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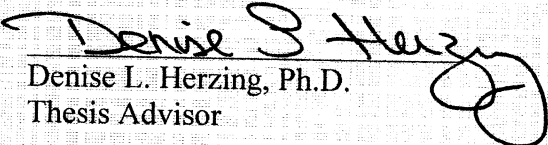
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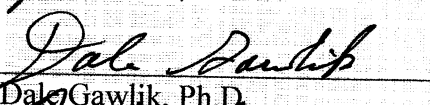
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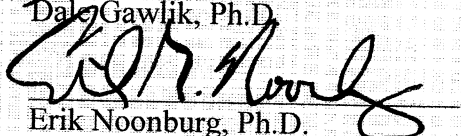
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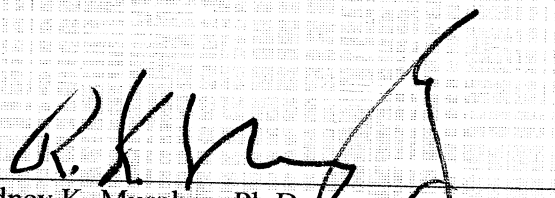
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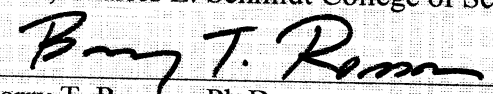

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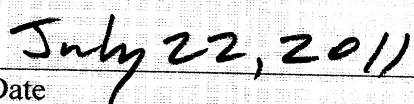

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ABSTRACT

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Two sympatric dolphin species, *Stenella frontalis* and *Tursiops truncatus*, resident to Little Bahama Bank, Bahamas were found to mostly forage independent of one another, but occasionally foraged in mixed groups. Analysis of over 20 years of data revealed the degree of overlap to be minimal with spatially distinct regions identified for both species, environmental segregation based on depth, bottom type, temperature, and time of day. Results based on observational data indicated significant differences in group size and selected prey.

For *S. frontalis*, lactating females had the most distinct diet, which differed from that of non-reproductively active (NRA) females. Pregnant females had ambiguous prey use results, but diet differences were revealed through nutritional analysis. Lactating females had a higher intake of all nutrients (% moisture, % lipid, % protein, and calories) than pregnant females but lower than NRA females. Mother and calf pairs selected prey for caloric and moisture values. The influence of calves on foraging groups was reflected

through discrete differences in all nutrients. Males and females appeared to select the same major prey, but female prey use was much more diverse.

NUTRITION AND HABITAT DRIVEN FORAGING OF WILD DOLPHINS IN THE BAHAMAS: A RECIPE FOR PREY USE

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INTRODUCTION

Patterns of habitat use by large-bodied apex predators are often a reflection of foraging strategy and prey choice. Specialized foraging tactics of groups or individual dolphins have been correlated with spatial heterogeneity, habitat features, and prey availability (e.g. Young & Cockcroft, 1994). Dolphins live in oceans and major rivers throughout the world and many are able to adjust their foraging techniques across suitable habitats (Natoli *et al.* 2005; Gannon & Waples, 2004). It has also been suggested that dolphins select habitats that suit their foraging abilities rather than adjusting their behavior for new habitats (Torres & Read, 2009). Successful foraging may therefore be a measure of an animal's ability to either locate suitable habitat or adapt to local habitat characteristics. Alternative foraging strategies allow opportunistic feeding for dolphins with generalized diets and selective feeding when preferred prey are available. With the ability to forage on an assortment of prey and inhabit a variety of marine and even freshwater environments, it is necessary to determine the major factors driving foraging patterns of dolphins in various geographical locations.

Many studies have documented links between foraging behavior, benthic topography, and bathymetric properties such as seafloor gradient and water depth (Hastie *et al.*, 2004). Home ranges and patterns of distribution are greatly influenced by habitat heterogeneity, biological requirements of a species, and availability of resources (McNab, 1963; Balance, 1992). Differences in foraging behavior of bottlenose dolphins

(*T. truncatus*), one of the most extensively studied and geographically distributed dolphins throughout temperate and tropical seas, including various environmental gradients, have provided an excellent example of diverse foraging abilities. For instance, Torres et al. (2009) found that foraging behaviors of *T. truncatus* varied significantly along changes in depth and ecological gradient in Florida Bay. Specifically, this study found correlation with water depth and various habitat types including sea grass, mud, sand, and hard bottom areas composed of sponge and coral structures. In the Moray Firth, Scotland, *T. truncatus* feeding behaviors and preferences for discrete foraging locations were strongly correlated with specific submarine habitat characteristics (Hastie et al., 2004). Sarasota Bay resident *T. truncatus* utilize seagrass beds for foraging, which has been evidenced through long term observation and studies of prey composition in stomachs of stranded animals (Barros & Wells, 1998). Hastie et al. (2004) suggest that habitat preference of *T. truncatus* determines distribution patterns and ultimately foraging efficiency. Determining patterns of both prey and habitat use in wild dolphins is an ecologically important step to understanding their role as predators (Berens McCabe et al., 2010).

Interspecies Habitat and Prey Use

In addition to benthic environmental factors, distribution patterns within a dolphin's home range are influenced by competition for available resources. Competition between two or more similar species for prey can influence individual or group habitat use. Two sympatric species in the Bahamas, Atlantic spotted (*Stenella frontalis*) and *T. truncatus* dolphins, have been observed aggressively interacting; however the implication

of aggressive behavior remains unclear (Herzing & Johnson, 1997). Habitat patchiness has been documented on Little Bahama Bank, Bahamas, with general habitat patterns from shallower to deeper water correlating with grassy to sand benthic characteristics, respectively (Rossbach and Herzing, 1999). Interspecies resource competition here is likely attenuated by utilizing various foraging techniques, feeding on different prey, and by avoiding similar habitats. However, the potential result when overlap does occur is exploitative or interference competition (e.g. Sih, 1993). Although dietary overlap alone does not necessarily determine interspecies ecological competition, frequent aggression between two similar species during foraging events certainly could be the result of competition for resources (Lavigne, 1996). This would likely be reduced for *S. frontalis* and *T. truncatus* in the Bahamas if indeed distinct habitat niches have been formed and disparate patterns of distribution have evolved. Competition avoidance may be energetically beneficial and has been described for cormorants and dolphins in Florida Bay where both species occupied habitats with significantly different characteristics but were found to consume similar prey (Torres *et al.*, 2009).

Atlantic spotted dolphin prey use and nutritional influence on diet

Determining the underlying factors behind prey selection is of great value for developing theories on a predator's role in the environment. In order to provide a better theoretical framework for understanding complex trophic interactions, predator-prey relationships need to be further explored. Enhancing our understanding of these interactions by studying interspecific and intraspecific foraging in large-bodied apex predators provides answers to many ecologically related questions. In dolphins and other

marine mammals, previous and existing techniques (e.g. stomach contents and fecal analysis) have been less than adequate for describing trophic relationships (Lavigne, 1996). However, advances in methods, such as stable isotope ratios (e.g., Walker *et al.*, 1999; Knoff *et al.*, 2008) and studies that utilize combinations of underwater observation, nutrition, and environmental variance, enable us to more fully understand these complex and dynamic interactions. Our extensive knowledge and detailed underwater observations spanning over 25 years of *S. frontalis* in the Bahamas allows us to explore the relationship between prey and 1) life stage, 2) sex, and 3) reproductive status. *S. frontalis*, in comparison to *T. truncatus* and many other species, are relatively ideal for observing in the wild and have provided the opportunity for underwater observations. Development of spots with age allows for individual identification and age class determination over consecutive years. Distinct general coloration phases that correlate with age class include: two-tones (calves) 1-3 years, although this stage can be prolonged up to age 6 as determined by active nursing; speckled (juveniles) 4-8 years; mottled (young adults) 9-15 years; and fused (old adults) 15+ years (Herzing, 1997).

Dietary studies of large marine apex predators are essential to the understanding of trophic interactions and predator-prey relationships that define our ecosystems. In order for marine mammals to meet basic metabolic demands, prey must be captured in a systematic way as to result in net energy gain. Unmasking the underlying factors driving patterns of dolphin foraging behavior can be a complex undertaking. Dolphins are large-bodied, highly active, aquatic mammals requiring a high daily energetic intake. Throughout the life of a typical dolphin, the magnitude of energy and other nutritional components (e.g. protein, moisture) required is largely dependent on factors such as: life

stage, reproductive status, daily activity level, metabolic requirements, and thermoregulatory expenses (Worthy, G.A.J., p. 791). Estimated diet and nutrient requirements of dolphins remains largely uncertain for age structure (Archer & Robertson, 2004), size at age class, sex, and reproductive status (Lavigne, 1996; Meynier *et. al*, 2008).

Prey intake, both frequency and type, is an observable, measurable unit that can be used to assess nutritional requirements. However, there are intrinsic limitations to studying highly mobile protected predators that generally forage at or beneath the water's surface. Most field studies that relate diet to nutrition in marine mammals have been based on stomach contents of stranded individuals, accidental by-catch from fisheries, or intentionally harvested animals (e.g., Barros and Wells, 1998; Benoit-Bird, 2004).

Captive-based studies have allowed for detailed measurements of nutritional requirements and intake rates for individual dolphins (e.g. Kastelein *et al.*, 2003). Higher rates of energy expenditure in a dolphin's own environment (e.g. costs associated with foraging), however, is not accounted for in captivity. For example, wild Hawaiian spinner dolphins (*Stenella longirostris*) were found to consume higher caloric densities of prey than any known captive study of marine mammals (Benoit-Bird, 2004). More comprehensive approaches to understanding feeding patterns and nutritional requirements should apply feeding rates in captivity to natural foraging behavior in the wild.

Nutritional content is deemed an important characteristic of prey, and more "nutritious" prey may be selected for by all dolphins, especially reproductively active or young intensively growing individuals which have higher nutritional needs. All prey can be broken down into three major nutritional components: moisture, protein, and fat

(Worthy, G.A.J., p.813). Nutritional value of prey is thought to be a major factor driving patterns of individual and group foraging (e.g. Brody, 1945; Close *et al.*, 1985; Bernard & Hohn, 1989). However, many studies have only provided details on either energy density and size of prey consumed, or frequency of occurrence (Lavigne, 1996). To allow for meaningful partitioning of diet, the mass of each prey species and the amount of energy provided by each prey needs to be accounted for (Lavigne, 1996) with relation to frequency of prey in diet.

Reproductive status influence on prey use and nutrition in diet

Reproductive status of female dolphins, particularly lactating and pregnant versus non-reproductively active, has been found to significantly affect foraging strategy. Reproductively active cetaceans, most often lactating females, have been observed to feed differently from the rest of the adult population (Bernard and Hohn, 1989; Kastelein *et al.*, 2003). For example, Bernard and Hohn (1989) found pregnant *S. attenuata* to have similar diets to non-reproductively active adults, but lactating females consumed higher quantities of food and altered their prey preference to an almost exclusive diet of flying fish and very low quantities of squid. Throughout lactation, the costs of energy allocation to milk production and loss of fat reserves are quite high. Milk samples collected from nursing long-finned pilot whales (*Globicephala melas*) were composed of about 15-31% fat (Lockyer, 1993). Ridgway *et al.* (1995) found *T. truncatus* milk fat consistency to range from 6 to 27%. To offset these costs, females are likely to eat either greater quantities of food or switch to a diet of greater nutritional value (Brody, 1945; Close *et al.*, 1985; Clutton-Brock *et al.*, 1982; Perez and Mooney, 1986). Prey use is therefore

hypothesized to adequately reflect changes in nutritional demands. For example, Lockyer (1993) found that food consumption of lactating *G. melas* increased by a range of 32-63% depending on stage of lactation. Kastelein et al. (2002b) found *T. truncatus* food consumption to increase little throughout gestation, but significantly (58%-97%) during lactation.

Most diet studies of pregnant females, on the contrary, have shown similar feeding patterns to that of non-reproductively active adults. Kastelein *et al.* (1993; 2002b; 2003) did not find pregnant *T. truncatus*, Commerson's dolphins (*Cephalorhynchus commersonii*), and killer whales (*Orcinus orca*) to significantly increase prey intake throughout pregnancy. Stomach contents collected from a field study on pantropical spotted dolphins (*Stenella attenuata*) indicated that feeding habits of pregnant females were similar to those of the general population (Bernard and Hohn, 1989). More comprehensive studies involving reproductive status and diet are needed to better understand intraspecies foraging behavior differences.

Ontogeny, mother/calf foraging, and sex-specific segregation

The presence of a developing calf could also be a factor affecting foraging behavior in dolphins. *S. frontalis* calves spend on average the first 3 years of life with their mothers, but occasionally prolong dependency up to 5 or, on very rare occasion, even 6 years. Teaching foraging techniques, due to the difficulty involved in finding and catching food, along with prolonged lactation, comes at a high energetic cost to the mother (Whitehead & Mann, 2000; West *et al.*, 2007). Additionally, mothers may modify their diet and potentially shift to prey species that are easier to capture in the

presence of calves. For example, mothers associating with a nursing calf may be less likely to forage on squid, due to foraging restrictions, as this requires deep-diving, which a calf cannot do as deep or for as long a period of time (Noren *et al.*, 2006; Meynier *et al.*, 2008). Ultimately, a diet shift could result from a combination of: 1) more limited physical performance in the presence of a calf; 2) increased energetic demand; and 3) exaggerated foraging compensation.

Diet shifts are known to occur during the beginning stages of a dolphin's life. Throughout the weaning process, calves gradually suckle less and consume more solid food until full independence is reached. In fact, newborns rely entirely on mother's milk for nutrition until an age where they begin the weaning process (Kastelein *et al.*, 2003): 6-19 months for *T. truncatus* (Peddemors *et al.*, 1992; Reddy *et al.*, 1994; Kastelein *et al.*, 2002b), and typically 1-3 years (two-tone phase) for *S. frontalis* on Little Bahama Bank. Weaning calves have heightened nutritional needs due to rapid growth and development (Nicolson, 1982; Archer & Robertson, 2004), and may augment a solid food diet with their mother's milk until they become proficient foragers (Gannon & Waples, 2004). Developing hunting skills necessary to locate and capture prey requires a great deal of time, and young dolphins may consume prey that are less elusive than those pursued by older dolphins (Gannon & Waples, 2004). Diving ability, swimming performance, and sensorial development contribute to diet composition and foraging ability throughout development (Meynier *et al.*, 2008). Weaning juvenile dolphins may make up for a high energy demand respective to their foraging ability by consuming prey that provide a greater caloric return, increasing feeding frequency, or increasing volume of fish consumed (Archer & Robertson, 2004). Research on the harbor porpoise (*Phocoena*

phocoena) (Smith and Read, 1992), franciscana dolphin (*Pontoporia blainvillei*) (Rodriguez *et al.*, 2002), and *T. truncatus* (Gannon & Waples, 2004) have demonstrated feeding patterns of calves to be different from adults. Archer and Robertson (2004) found a significant diet shift in *S. attenuata* calves that foraged more frequently on squid as they got older.

Differential habitat preference by sex-specific social groups sometimes results in ecological segregation, thus reducing intersexual competition for resources during foraging events (Breed *et al.*, 2006). The formation of sex-specific social groups has been reported for many taxonomic levels, from invertebrates to mammals. For example, various ungulate species, such as red deer (*Cervus elaphus*), are known to form sex-specific groups (Clutton-Brock *et al.*, 1982; Breed *et al.*, 2006). Within our study site, Rossbach and Herzing (1999) found that a bottlenose dolphin's closest associate was of the same sex 74% of the time. Along with age segregation and reproductive status, differences in energy requirements and survival strategies between sexes were found to be the primary causes for social segregation in Beaufort Sea beluga whales (*Delphinapterus leucas*) (Loseto *et al.*, 2006).

Studying dolphin foraging, and most behaviors, in the wild is an invariably difficult task due to limitations of viewing behavior only at the surface (Hastie 2004). Most research relies on interpolation between surface and underwater behavior (e.g. Allen *et al.*, 2001) and is therefore potentially biased against subsurface behavior in deeper water and foraging activity not observed (Barros & Wells, 1998; Nowacek *et al.*, 2001). However, our study bridges the gap between surface, pelagic, and benthos through studying two species of dolphin in the typically clear and shallow Bahamian

waters that allow for both surface and underwater viewing of foraging events. Our long-term observational records provide an unprecedented opportunity to study individually identified dolphins, many with known histories, over the course of many years.

For this study, I determined (1) habitat use and spatial patterns of *S. frontalis* and *T. truncatus* on Little Bahama Bank, Bahamas during foraging events. Habitat characteristics (depth, bottom type, water temperature, tidal state) along with group size and time of day used for foraging were compared between species in order to determine potential disparate habitat preferences. Interspecies foraging and habitat correlation allowed for a comparison of ecological niches and gave insight into how these two sympatric species coexist. (2) Selection frequencies of specific prey items were tested to determine differences in interspecies prey use between *S. frontalis* and *T. truncatus*, and intraspecies differences for *S. frontalis*. (3) Nutritional importance in the diets of *S. frontalis* foraging groups was tested for potential influence on prey selection.

METHODS

Study site

The study area is located at the western edge of Little Bahama Bank, from West End, Grand Bahama Island (26°42' N, 79°00' W) to White Sand Ridge (27°15' N, 79°08' W) (Fig. 1). Shallow waters here range in depth from <1 to 20 m, generally increasing from south to north. There is a steep drop-off at the western boundary where our study area meets the eastern edge of the Gulf Stream, which has a depth greater than 500 meters. The study area is approximately 280 km², 56 km north to south and 5 km east to west.

Bahama Banks are thick submerged platforms of calcium carbonate, which provide a diversity of habitats, including: ledges, grassy flats, atolls, fringe reefs, and patch reefs. Sand is the major bottom type found here, along with scattered areas of rock and reef. Vegetation includes small and large patches of seagrass, primarily turtle grass (*Thalassia testudinum*). Various structures and bottom types provide the necessary habitat to support a great diversity of life including the large variety of prey available to dolphins. These clear (average visibility ≥ 30 m (Herzing, 1996)), shallow, and warm waters provide safety for the dolphins and ease of underwater viewing for human observers.

Data collection- Field

Behavioral observations were recorded and field data collected for each dolphin sighting between May and September (1992-2009) aboard The Wild Dolphin Project's vessel R/V *Stenella*, a 20-m power catamaran. Continuous dolphin surveying was conducted between the hours of 0700 to 1900 hours each day. *T. truncatus* dorsal fins were photographed from the boat for identification. Behavior for *T. truncatus* was recorded from the boat with occasional water entry to obtain underwater observational data. Underwater observations along with photography and video were the primary means of obtaining both identification and behavior recordings of *S. frontalis*.

Dolphin groups were defined by any number of individuals exhibiting similar patterns of directional movement and activity (Shane, 1990; Rogers *et al.*, 2004). Environmental data collected for each dolphin group included: date (month/day/year), time of day, GPS location, tide direction, depth, temperature, and dominant benthic bottom type. Bottom type was categorized as: (1) sand, (2) sand/grass, (3) grass, (4) reef, and (5) rock. Tidal state consists of 4 categories: (1) flow (sea level rises), (2) ebb (sea level falls), (3) slack high (tidal current ceases during high tide), and (4) slack low (tidal current ceases during low tide). Observational data included: group size, group composition, and detailed behavioral notes. Female reproductive state was determined by visual inspection and was categorized as pregnant, lactating, or non-reproductively active (NRA) (Herzing & Brunnick, 1997).

Data processing - Lab

Only those encounters involving foraging activity were investigated for this study. From the database for each encounter, I scored the number of times *T. truncatus* and *S. frontalis* were observed foraging, together or separate, and associated habitat characteristics. *S. frontalis* group composition information extracted from observational notes per encounter included: reproductive status of females, presence of mother/calf pairs, age class, sex, and group size. Due to a more limited knowledge base of *T. truncatus*, only sex and group size were scored for group composition. Age of reproductive maturation for males is not well known, but in terms of foraging, juveniles and adults were presumed to have similar abilities to feed based on motor and sensorial development; thus, they were grouped into one category. Calves were considered a separate category in terms of foraging ability due to underdeveloped motor and sensorial abilities. Females were considered reproductively mature if mottled or fused (adult category), and were assumed non-reproductively active adults for these age classes if not pregnant or lactating. To confirm that reproductive status was accurate and that early pregnancies were not mistaken for NRA from visual observations of outward appearance, encounter notes from following years were checked for the presence of calves. Group size was defined by only those individuals observed actively foraging, even if overall group size was larger.

Additional information extracted from observational notes included foraging behavior and identified prey. Prey for individual encounters were scored for selection frequency by each feeding group. This study was based on observed foraging events and

was therefore limited by visibility and only daytime feeding events. Only clearly identified prey encounters were used for analysis.

Prey collection & processing

In order to conduct a sub-analysis of prey selection based on nutrition of prey, known and potential prey were collected for nutritional analysis during 2009/2010 field seasons (May-September) aboard R/V *Stenella*. Although the Bahamas are not likely to experience seasonal changes in fish and squid communities to the extent of more temperate regions, consistent prey collections during the same months of foraging observations controlled for potential seasonal effects. Due to the great diversity of prey known for *S. frontalis* and *T. truncatus* in our study area (Herzing, 2004), a variety of methods were used for prey capture. (1) For demersal fish, sedentary traps were baited and set for periods averaging 24 hours. Traps were placed on chosen sites and habitat types to maximize capture success. (2) A 5 ft x 100 ft (1.5 x 30.5 m), half-inch (~ 5/4 cm) mesh gill net was used to catch small benthic and benthic-pelagic prey. In order to control for current and net drift, one end was attached to the boat and the other end (downstream of the current) was anchored to the ocean floor. Swimmers swam out to set the net and then continuously monitored the soaking net. A technique of spooking fish into the net, when fish were near, was also used by swimmers with moderate success. (3) Pole spearing was a method used to collect demersal fish and proved to be a very successful technique. (4) Hook and line allowed for capture of pelagic and benthic-pelagic fish. (5) Hand netting was a successful method for capturing slow moving pelagic squid and fish, and some benthic species. This method was used mostly at night

to capture offshore prey in the Gulf Stream. (6) Underwater fishing was accomplished using an Ugly Stick Ice Rod equipped with a multiple-small hook design. A snorkeler would swim out to locate benthic fish and then hover with baited hooks in attempt to snag or hook them.

Field measurements for each specimen included species identification (whenever possible), total and standard lengths, with additional mantle length for squid, and total wet mass. Environmental and collection data were also recorded: capture method, soak time, time of day, water depth, water temperature, bottom type, and GPS location. Each specimen caught was packaged, labeled, and temporarily frozen at -20°C immediately following capture. Samples were subsequently frozen in a -40°C freezer until they could be processed for nutritional content in a laboratory. In the laboratory, detailed pictures were taken of each specimen and species identification was confirmed. Squid were the only specimens not identified down to species level. For the purpose of this study, they were pooled and generically classed as “squid”.

Nutritional analysis – Proximate composition

To better understand prey use, collected prey specimens were analyzed for nutritional composition. Frozen fish and squid were thawed and ground using equipment appropriate for specimen size: coffee grinder (smallest); blender (medium-small); food processor (medium-large); bowl chopper (largest). Samples were ground until tissue was completely homogenized. Methods for analysis were based on simple, rapid, and precise lipid extraction methods derived from Lee et al. (1996). Samples were placed in a drying oven at 110°C until all moisture was extracted and a constant weight was reached.

Moisture content was calculated by taking the difference between wet and dry weight, and then multiplying by 100 in order to express this fraction as a percent. Total lipid was extracted from samples using 10 ml of an appropriate solvent/g of sample: [fattier fish] 2:1 chloroform (CHCL₃):methanol (MeOH) solvent ratio was used; [medium fat fish] 1:1 CHCL₃:MeOH; [low fat fish] 1:2 CHCL₃:MeOH (Lee *et al.*, 1996). Fat content for determining solvent ration was estimated based on species' physiological characteristics, and if available, relative measurements of similar species from other geographical locations (e.g. Donnelly *et al.*, 1993; Eder and Lewis, 2005; Hastie *et al.*, 2004; Bouriga *et al.*, 2010). Ash content was determined by heating the dry sample in a muffle furnace at 550°C until the sample was completely “ashed” ([%ash = ash/initial sample weight] x 100). Protein content was determined by subtracting % lipid and % ash from % solid (100 - %moisture). Energetic values were determined indirectly by using average values of caloric conversions (lipid = 9 kcal/g; protein = 4 kcal/g) (Brody, 1945) in an equation with measured lipid and protein values: Calories = (lipid x 9) + (protein x 4) = cal/100 g. Caloric values of cal/100g were converted to joules by assuming that 1 cal=4.184J (Schmidt-Nielson 1997; Williams *et al.*, 2004). Three aliquots were taken from the homogenate of each sample; therefore, all presented nutritional values are means of triplicate analytical determinations.

Objectives (Hypotheses Tested)

Interspecific Hypothesis (Atlantic spotted and bottlenose dolphins)

Hypothesis 1:

Ho: During foraging events, there is no significant difference between Atlantic spotted and bottlenose dolphin habitat use and prey use.

Ha: During foraging events, there is a significant difference between Atlantic spotted and bottlenose dolphin habitat use and prey use.

Intraspecific Hypotheses (Atlantic spotted dolphins)

Hypothesis 2:

Ho: There is no significant difference in prey use and nutritional intake between reproductively active females and non-reproductively active females.

Ha: There is a significant difference in prey use and nutritional intake between reproductively active females and non-reproductively active females.

Hypothesis 3:

Ho: The presence of age 1 calves and all other age calves has no significant influence on group prey use and nutritional intake.

Ha: The presence of age 1 calves and all other age calves has a significant influence on group prey use and nutritional intake.

Hypothesis 4:

Ho: The presence of mother/calf pairs has no significant influence on group prey use and nutritional intake.

Ha: The presence of mother/calf pairs has a significant influence on group prey use and nutritional intake.

Hypothesis 5:

Ho: There is no significant difference in prey use between males and females.

Ha: There is a significant difference in prey use between males and females.

Data Analysis

Interspecies Variation in Habitat and Prey Use

To ensure statistical independence for all tests, only the first encounter each day was considered for analysis.

Interspecies foraging data was analyzed with Classification and Regression Tree (CART) using the rpart package (Therneau *et al.*, 2010) in R (R Development Core Team 2010) to describe the relationship between *T. truncatus* and *S. frontalis* with predictor variables: habitat characteristics and time of day. A CART analysis is a nonparametric statistical test having no assumptions of linearity and homogeneity of variables, or independence of data. CART is a multivariate regression tree model created by recursively partitioning data using an algorithm to split explanatory variables at each node, maximally distinguishing the response variable at each split (Breiman *et al.*, 1984; De'Ath, 2002; Torres *et al.*, 2009; Crawley, 2007). Splitting occurs continuously by

forward selection of variables until the best predictors have been chosen at each branch and relative homogeneity is reached where there can be no further reduction in deviance (Crawley, 2007) and all points are classified (Breiman *et al.*, 1984). This approach to cluster analysis is useful for describing patterns of species assemblage and dependence on environmental characteristics (De' Ath, 2002). Data were extracted from the existing database for each foraging observation of *T. truncatus*, *S. frontalis*, and mixed species encounter and were classified relative to the following habitat characteristics: benthic habitat type, tidal pattern, depth, time of event, and temperature. In order to simplify the model and avoid over-elaboration, a cross-validation procedure was used in CART analysis to prune the tree at the point where classification error was minimal (Crawley, 2007).

G-tests for goodness of fit were used to investigate differences between dolphin species in 1) prey use, and to further assess 2) benthic habitat type use. G-tests were used for both species separately to test for significant deviation from random with regard to prey use and benthic habitat type. Prey use was compared at the family level in concordance with general identifications recorded for foraging events. As a preliminary step, due to low frequency counts for some prey, both Pearson's chi-squared tests and G-tests were run on raw data to determine which test was most appropriate. G-test results were used for this analysis unless chi-squared p-value results were found to be more conservative and to be above the threshold of significance (i.e. $p > 0.05$). A second analysis was done for prey use using both chi-squared and G-tests on data with small frequency values eliminated from the data set in order to determine potential effects of small count data.

One-way nonparametric Kruskal-Wallis Analysis of variance (ANOVA) tests were run to test for significant affect of group size on habitat data for both species and mixed encounters. Box plots were created to graphically display differences among species and habitat variables, and between species and group size.

Atlantic Spotted Prey Use and Nutrition

Prey selection frequency was explored among foraging groups using log likelihood ratio statistic G-tests. As a preliminary step, due to low frequency counts for some prey, both Pearson's chi-squared tests and G-tests were run on raw data to determine which test was most appropriate. G-test results were used for this analysis unless chi-squared p-value results were found to be more conservative and to be above the threshold of significance (i.e. $p > 0.05$). A second analysis was done using both chi-squared and G-tests on data with small frequency values eliminated from the data set in order to determine potential effects of small count data. Pairwise chi-squared tests between pregnant, lactating, and NRA females were conducted on individual prey items to determine which prey, if any, were significantly selected. Pregnant, lactating, and NRA females were also analyzed for significant differences in overall prey selection patterns between groups. Individual prey were tested using chi-squared tests in order to determine significantly selected prey between reproductive groups. Since calves are generally associated with their mothers and rarely forage independent of the group, calves were tested for their influence on the outcome of prey selection during foraging events. The presence of mother/calf pairs were also tested for their influence on group prey selection. Sample size was small for encounters that included only age 1 calves (N

= 11), so a subsequent analysis was conducted with a larger sample size which included encounters where age 1 calves were present along with other age calves (ages 2-6) (N= 49). To test for male and female segregation during foraging events, sex-specific prey use was also tested.

Diet differences were further explored through pairwise comparisons of foraging groups. A function was written in R, similar to a t-test, to test the null hypothesis that the nutritional intake difference between two foraging groups had a mean value of zero (e.g. Fig. 2). The purpose of this function was to assess the influence of prey nutritional value on prey selection. The estimated observed frequencies of prey in group G diet (lactating, pregnant, non-reproductively active female (NRA), age 1 calf, other age calf (ages 2-6), non-calf, or mother/calf pair (m/c)) were treated as fixed values. Individual mean prey worth estimates μ are a measure of average nutritional value multiplied by average prey wet mass. Significant differences in group foraging were tested by generating a p-value from the following equation, in which estimated nutritional difference D in \bar{P} means and observed diet difference O are calculated:

$$G_1 = \{g_{11}, g_{12}, g_{13}, \dots, g_{1m}\}$$

$$G_2 = \{g_{21}, g_{22}, g_{23}, \dots, g_{2m}\}$$

where $g_{ij} = \#$ prey type j in diet type i , and g_{ij} draws from a normal distribution for the j 'th prey type is being summed over;

$$P_i = \sum_{j=1}^m \sum_{k=1}^{g_{ij}} x_{jk}$$

where $x_j \sim N(\mu_j, \sigma_j)$;

where x_j is a random draw from a normal distribution with mean μ_j and standard deviation σ_j ;

k prey type is being summed over;

μ_i = average (1) calories, (2) % moisture, (3) %protein, or (4) % lipid of prey types;

σ_i = standard deviation of (1) calories, (2) % moisture, (3) %protein, or (4) % lipid of prey types;

where total diet estimate (N_1 & N_2), respective of G_1 and G_2 , is in terms of either caloric value, % protein, % lipid, or % moisture; G_1 and G_2 represent the observed frequencies of each prey item in the diet of both groups; σ is the standard deviation for individual prey worth estimates;

$$\begin{aligned}\bar{P}_i &= P_i / \sum_{j=1}^m g_{ij} \\ D &= (\bar{P}_1) - (\bar{P}_2) \\ O &= \frac{\sum_{j=1}^m g_{1j} \mu_j}{\sum_{j=1}^m g_{1j}} - \frac{\sum_{j=1}^m g_{2j} \mu_j}{\sum_{j=1}^m g_{2j}} \\ p &= (\sum ((D - O) > |O|) + \sum ((D - O) < -|O|)) / R\end{aligned}$$

where \bar{P} is the average diet estimate; R (replicates) is the number of times the function is run (set to 10000); and p is calculated as the fraction of R , or the total count divided by number of replicates, in which D is at least as large as the observed diet difference O between G_1 & G_2 . The threshold of significance was $\alpha = 0.05$.

In order to determine which nutrients were selected for by pregnant, lactating, and NRA females, frequency graphs were constructed to incorporate relative proportion of nutrients in their diets. To calculate values for each graph, the average nutrients from all prey selected, per foraging group, were averaged and divided by the total number of

observed encounters. For a second set of graphs, the average wet weight of all selected prey was multiplied by the average nutrient. This allowed for interpretation of average prey size as a potential determinant of prey selection.

RESULTS

Interspecies Habitat and Prey Use Variation

Graphically displaying foraging encounters showed varying degrees of geographical separation and overlap between *S. frontalis* and *T. truncatus* throughout our study area (Fig.3). The western extent of Little Bahama Bank, bordering deep waters of the Gulf Stream, had the greatest interspecies overlap and was also the area where most *T. truncatus* were observed foraging. *S. frontalis* were the primary foragers to the north/northeast, and both species sparsely foraged to the south/southeast.

CART analysis selected depth as the primary environmental variable to maximally distinguish *T. truncatus*, *S. frontalis*, and mixed species foraging events; followed by habitat type, time, and temperature, respectively (Fig.4). The largest separation in foraging occurred at depths ≥ 32.5 feet (9.9 m), with a maximum depth of roughly 60 feet (18.3 m), which was dominated by *T. truncatus* (3 mixed/7 *S. frontalis*/34 *T. truncatus*). For the rest of the population, foraging events were best predicted by depths less than 32.5 feet. *S. frontalis* were most strongly associated foraging with shallower depths (205/212) next to mixed groups (53/56) (misclassification error rate: 0.40). For shallower depths (< 32.5 feet), habitat (bottom type) was a key determinant of foraging events; bottom types consisting of sand (habitat a) and grass (habitat c) had the highest rate of foraging with *S. frontalis* being the most dominant

foragers (44 mixed/182 *S. frontalis*/27 *T. truncatus*) (misclassification error rate: 0.34). *T. truncatus* were evenly spread across habitat types at shallower depths. The rest of the population was subdivided into foraging events based on bottom types sand/grass (habitat b) and rock/reef (habitat d) (9 mixed/23 *S. frontalis*/26 *T. truncatus*). For bottom types sand/grass and rock/reef, time of day was the key determinant of foraging; times ≥ 1015 (~17:00) had the lowest foraging rate of anywhere in the data frame for individual species (0 mixed/9 *S. frontalis*/3 *T. truncatus*) (misclassification error rate: 0.23). Those foraging events occurring earlier than 1015 in sand/grass and reef/rock were proportionally dominated by *T. truncatus* (9 mixed/14 *S. frontalis*/23 *T. truncatus*). For groups of dolphins feeding earlier in the day, a key determinant of foraging was temperature (misclassification error rate: 0.28); foraging events taking place at higher temperatures (≥ 84.5 °F/29.2 °C) were dominated by *T. truncatus* (3 mixed/2 *S. frontalis*/12 *T. truncatus*). The remaining encounters at temperatures less than 84.5 °F (6 mixed/12 *S. frontalis*/11 *T. truncatus*) were further divided into time ≥ 831.5 (~ 14:00), followed by the last split of foraging events at times less than 831.5. At earlier times (< 831.5), mixed species were associated with temperatures below 81.5 °F (27.5 °C), and *S. frontalis* were associated with temperatures ≥ 81.5 °F. Tide was determined to be the least important of splits and was the only environmental variable rejected from CART analysis after the regression tree was pruned.

Box plots were constructed to illustrate similar patterns of habitat use by *S. frontalis* (*Stenella*), *T. truncatus* (*Tursiops*), and mixed species foraging relative to depth, time of day, and temperature (Fig.5). Consistent with habitat use results of CART, *T. truncatus* were observed at depths of higher median values than either *S. frontalis* or

mixed groups. Interestingly, the mixed species median value almost perfectly averaged the median value depth ranges of *S. frontalis* and *T. truncatus*. Both mixed group and *S. frontalis* had similar foraging time median values, which were much earlier than that of *T. truncatus*. Median temperature values were close to 85°F (29.4 °C) for *T. truncatus* and lower for both mixed species and *S. frontalis*.

G-test results indicated significant differences from random bottom type use at intraspecific, mixed group, and interspecific levels (Table 1). Consistent with CART, both *S. frontalis* and mixed groups dominated sand habitats while *T. truncatus* split their time almost equally over sand and sand/grass habitats (Fig.6). However, not distinguished in CART, benthic habitats dominated by reef/rock and, to an even lesser degree, grass beds were rarely used for foraging by either species throughout an entire encounter.

Significant differences from random prey use were determined for both *T. truncatus* and *S. frontalis* when considered separately (Table 2). However, when small groups were eliminated from analysis, *T. truncatus* were found to feed at random. Due to small sample sizes for *T. truncatus*, elimination of small count data significantly affected the number of prey accounted for in their diet and lead to the loss of statistical significance. Prey selection was significantly different between *T. truncatus* and *S. frontalis* for interspecies analysis. Prey selection pie charts illustrated dissimilar prey use between species (Fig.7). Both *S. frontalis* and *T. truncatus* shared jacks as major prey items, but other primary prey items differed. The principal prey items for *S. frontalis* were lizardfish, jacks, and flounder; for *T. truncatus* principal prey items included

razorfish, jacks, and eels. Interestingly, *S. frontalis* were observed to feed on a much larger variety of prey than *T. truncatus*.

Nonparametric Kruskal-Wallis ANOVA test results determined a significant difference in group size, defined as all individuals foraging within an encounter, between *S. frontalis*, *T. truncatus*, and mixed species ($df = 2$, $p < 2.2e-16$). When mixed species were removed from the test, the significant difference between both species was still large ($df = 1$, $p < 0.0001$). Illustration of these results (Fig.8) showed *T. truncatus* (mean group size = 9.4) to have much larger group sizes than *S. frontalis* (mean group size = 5.1) during foraging events. The proportion of individuals foraging to total number of individuals present in an encounter was higher for *T. truncatus* (92.8%) than for *S. frontalis* (71.7%).

Atlantic Spotted Dolphin Prey Use

Common prey items of *S. frontalis* (halfbeaks, eels, flounders, flyingfish, jacks, lizardfish, needlefish, and razorfish) varied in consumption between lactating, pregnant, and NRA females. Lactating females were found to have a selective diet in which prey use significantly deviated from random (Table 3). Prey selection was highest for lizardfish, flounder, and razorfish, respectively (Figure 9). When all prey choice data were included for analysis, both pregnant and NRA females significantly selected prey. Pregnant female prey selection was highest for eels, flyingfish, and halfbeaks. Non-reproductively active female prey selection was highest for needlefish and jacks. However, with small count data eliminated from the analysis of NRA females, significance was not found. Prey selection significantly deviated from random for

reproductively active groups combined post hoc or foraging together during encounters (pregnant/lactating). Pregnant and NRA dolphins combined for analysis (pregnant/NRA) gave similar results; prey use significantly deviated from random.

The result of all three reproductive groups (pregnant, lactating, and NRA) tested against each other showed a significant difference in prey selection, thus revealing significant variation in prey use between two or all three groups (Table 3). Separate pairwise comparisons showed significance in prey selection for NRA females tested against pregnant and lactating females. Lactating females were found to feed similarly ($p > 0.05$) to pregnant females when compared directly and when pregnant females were grouped with NRA dolphins (Pregnant/NRA). Therefore, the observed differences in prey selection were not large enough for statistical significance. Lactating females, as expected, were found to feed significantly different from NRA dolphins. However, needlefish were the only significantly selected prey ($\chi^2=4.09$, $p=0.043$) and were chosen more often by NRA females. Pregnant females were found to feed similar to NRA dolphins for both the more conservative test result and after small count data were removed from analysis. Jacks were, however, significantly selected by NRA females at a higher frequency than by pregnant females ($\chi^2=4.19$, $p=0.041$). Pregnant and lactating females foraged at similar frequencies on flounders, lizardfish, needlefish, razorfish, flyingfish, and halfbeaks (Fig. 9). Although not statistically significant, non-reproductively active females selected flounders and flyingfish at lower frequencies than pregnant and lactating females. Pregnant females had low frequencies of jacks in their diet even though this was a major prey item for both lactating and NRA dolphins. Lizardfish were a major prey item for all three reproductive groups.

Results from encounters with calves of all ages (1-6) present in the foraging group tested against encounters with non-calves (juveniles and adults) showed that there is no difference in prey selection between groups (Table 4). The presence of age 1 calves during foraging encounters were also considered individually and found to not deviate from random feeding. Comparisons between first year developing calves, calves ages 2-6, all age calves compiled (1-6), and non-calves present during encounters resulted in no significant differences from random feeding for all groups considered. Lizardfish, jacks, and flounder were the primary prey selected by foraging groups with calves of all ages and non-calves present (Fig. 10). Although mothers are limited with foraging to the abilities of their developing calves, in terms of prey use, mother and calf pairs fed similarly to all others in the population (Table 4). Lizardfish, jacks, and flounder were the primary prey selected by foraging groups that included “mother & calf pairs” as well as “no mother & calf pairs” (Fig. 11). These were the same primary prey observed for age class groups.

Sex differences were not detected for prey use between males and females (Table 4). Females had a more diverse diet than males; however the primary prey items making up both diets were similar. Lizardfish made up nearly half of the adult male diet and roughly a third of the female diet (Fig. 12). Additionally, flounder made up 11% of the selected prey items for both sexes.

Proximate Composition of Prey Species

A total of 192 individual specimens from 14 families of known prey were analyzed for proximate composition and energetic value. The proximate composition

between prey species varied greatly (Table 5, Fig. 13). Water (% moisture) represented the main component of all prey items, as expected, comprising roughly 75% of body mass (ranging from 67% to 76%). Prey that yielded relatively high moisture values included *Congridae* (conger eels), *Bothidae* (lefteye flounders), and squid, respectively. Protein was the second major component after water, comprising approximately 15% of body mass (ranging from 10% to 20%). Lipids were a fairly constant variable, ranging from approximately 2% to 5.5 %. Species high in lipid and protein values were higher in calculated energy values ($[\text{lipid} \times 9] + [\text{protein} \times 4]$). Fish families relatively high in both lipids and proteins, also yielding high energy values, included *Atherinidae* (silversides), *Holocentridae* (squirrelfish), and *Carangidae* (jacks). Wet mass varied greatly, ranging from 390 to less than 2 g (Fig. 14).

Atlantic Spotted Dolphin Nutritional Influence on Diet

Pregnant and NRA females had diets that deviated from random for each nutrient category (calorie, protein, lipid, and moisture), suggesting they selected prey based on nutritional value (Table 6). Lactating females had diets that deviated from random for each nutrient when tested against both NRA and pregnant female groups independently. However, protein in diet was not different between lactating and pregnant females combined with NRA females (“pregnant/NRA”) ($p = 0.067$). A comparison of relative use of each nutrient in the diets of pregnant, lactating, and NRA females revealed % moisture to be highest for lactating females (Fig. 15). However, all other nutrient categories (% protein, % lipid, kJ g^{-1}) were higher for NRA females. When average wet

weight (g) of prey sampled for nutritional analysis was included in the calculation of % nutrient in diet, NRA females had the highest rate of use for all nutrients.

Foraging groups with only non-calves present tested against encounters with age 1 calves present revealed that prey were significantly selected for on the basis of all nutrient categories (Table 7). The effect of calves of all ages (1-6) present in foraging groups compared against non-calves present showed a significant difference for all nutrients. There were no significant differences in % protein, % moisture, % lipid, and energy (kJ g^{-1}) between age 1 calves and other age calves (2-6) present in foraging groups. A comparison of relative use of each nutrient in the diets of foraging groups with calf ages 1-6 present and foraging groups with non-calves showed great variation when wet weight (g) of prey was not included (Fig. 16). Foraging groups with age 1 calves were highest for % moisture in diet, but with wet weight (g) of prey included, non-calf foraging groups were much higher in overall % moisture. Non-calf foraging groups were highest for % lipid with and without wet weight (g) of prey included. Energy (kJ g^{-1}) was high in both calf (age 1) and non-calf foraging groups, but overall energy with wet weight (g) of prey included was much higher for non-calf encounters. Protein was high in foraging groups with calves (ages 2-6) and age 1 calves, but was surprisingly low for all age calf foraging groups combined. Non-calf foraging groups were much higher in protein when wet weight (g) of prey was included in the calculation.

Foraging groups with mother and calf pairs present tested against foraging groups without mother and calf pairs had significant differences in caloric (kJ g^{-1}) and % moisture intake, but there were no significant differences in % protein and % lipid intake. A comparison of relative use of each nutrient in the diets of foraging groups with mother

and calf pairs compared with no mother and calf pairs gave consistent results when wet weight (g) of prey was included in the calculation: foraging groups without mother and calf pairs were highest for all nutrient categories (Fig. 17). When prey mass was not taken into account, foraging groups with mother and calf pairs were highest for % moisture and % protein intake, and were similar to foraging groups without mother and calf pairs for % lipid and caloric (kJ g^{-1}) intake.

DISCUSSION

Interspecies Habitat and Prey Use Variation

Movement patterns, habitat use, and diet are strongly influenced by a predator's foraging preference (Heithaus *et al.*, 2002). Results from interspecies analysis of foraging events on Little Bahama Bank show depth to have the strongest ecological effect on spatial distribution, with *T. truncatus* selecting deeper water more often than *S. frontalis*. This finding is consistent with populations in the Shannon estuary, Ireland where *T. truncatus* exhibited preference for deeper areas (Wilson *et al.*, 1997; Ingram & Rogan, 2002). In other regions where delphinid species coexist, such as snubfin (*orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) of Cleveland Bay, Queensland, one species has shown preference for shallow waters while the other prefers deeper waters (Parra, 2006). Previous studies have also shown depth to be a major factor driving foraging tactics of dolphins. For example, *T. truncatus* in Florida Bay, Florida were found to most closely associate foraging technique and distribution with depth (Torres & Read, 2009). In the present study, depth segregation corresponds with geographical positions of foraging events. Geographical positions are somewhat biased due to a more intensive search effort on the western edge; however, patterns of relative location during foraging events of both *T. truncatus* and *S. frontalis* provide basic information on species overlap. Spatial mapping of both species show *T. truncatus* utilizing the western edge of Little Bahama Bank, which borders deep waters of the Gulf

Stream. *T. truncatus* were also found to forage throughout the southern extent of our study area, which on average has slightly deeper waters in comparison to more northern regions. Comparatively, although there is some overlap in the western region, *S. frontalis* are spatially segregated and feed almost exclusively in the shallower northern region with minimal overlap from *T. truncatus*.

Heterogeneity of bottom types within these depths secondarily influences patterns of foraging. Frequency of bottom type (sand, sand/grass, grass, and rock/reef) selected for foraging varied considerably between species. Sand is the most abundant bottom type throughout Little Bahama Bank and was subsequently exploited by *S. frontalis* during over 85% of their recorded foraging events. Areas with patches of *T. testudinum*, although proportionally scarce relative to sandy flats, appear to be preferred by *T. truncatus*. Despite the relative scarceness of *T. testudinum* patches, nearly half of the observed *T. truncatus* foraging encounter observations occurred over areas of grass and sand, indicating that they are seeking out areas of concentrated vegetation to forage. Sandy habitats barren of vegetation also account for roughly half of *T. truncatus* foraging encounters, which is consequently the bottom type where a majority of overlap occurs between the two species. These results indicate that differences in habitat use is a primary factor maintaining the coexistence of delphinid species in the Bahamas. Distinct habitat preference has been suggested to help maintain coexistence in other sympatric species as well, such as *O. heinsohni* and *S. chinensis* in Cleveland Bay, Queensland (Parra, 2006). Results from this study are consistent with many other studies which have described a clear relationship between habitat characteristics and foraging strategy (e.g. Hastie *et. al.*, 2004), with individual dolphins varying their diet based on habitat type

(Gannon & Waples, 2004). For *T. truncatus*, similar bottom type use to that seen in the Bahamas has been documented for *T. truncatus* in other regions. For example, *T. truncatus* have shown preference for seagrass habitats in Sarasota Bay, Florida (e.g. Wells, 1991; Berens McCabe *et al.*, 2010).

In addition to spatial variation, habitat and prey use can vary on temporal scales. Foraging times were found to vary, with *T. truncatus* foraging later in the day. Particularly in areas where both species have high incidence of overlap, differences in foraging times may reduce potential competition for the same prey or allow foraging on prey that are available at different times. These results support the hypothesis that disparate foraging strategies have evolved for these two sympatric species in order to minimize competition for resources. Interestingly, observational notes from mixed group encounters indicated that aggression or some sort of defensive stance by either species often resulted and lead to the termination of foraging bouts. However, a small percentage of mixed encounters appeared neutral when feeding on schooling prey.

More temporary environmental features, such as temperature and tide, had only subtle ecological effects on predator distribution. Results also showed associations of *T. truncatus* with higher temperatures and *S. frontalis* with lower temperatures even though *S. frontalis* are much smaller in size compared to *T. truncatus*, and thus more constrained in terms of maintaining thermal balance (Worthy, G.A.J., p.795). Worthy, G.A.J. (p. 795) suggested that for smaller odontocetes metabolic demands should result in a correlation with warmer temperatures; however, water temperature differences are relatively subtle in the Bahamas and do not appear to drive movements of *S. frontalis* or *T. truncatus* based on metabolic needs. *S. frontalis* and *T. truncatus* distribution may

instead follow prey distribution or simply forage in slightly different temperature ranges as a result of prey selection and habitat preference. Temperatures recorded during the months of May through September range from mid-70's to low-90's °F (~23 to 32 °C) and have the potential to drive prey distribution.

Minimal tidal effects found for Little Bahama Bank contradicts a study by Ingram and Rogan (2002) who found tidal cycles to greatly affect foraging activity, with a significant increase in feeding during flowing tidal states. Although tidal changes weren't found to be a significant ecological factor on Little Bahama Bank, daily tidal cycles are likely contributors to prey distribution and the timing of foraging events. Therefore, tidal cycles may indirectly affect foraging events. Research has shown activity levels and horizontal distribution patterns of fish to be affected by tidal currents. Gibson (pp.63-80) describes benthic fish (e.g. flatfish) to be least active during high current speeds, in some cases even burying in the sediment to prevent displacement. Gibson (pp.63-80) also describes tidal patterns in schooling fish which follow tidal currents to achieve transport to feeding areas or spawning grounds.

Results from this study indicate significant differences in diet between *S. frontalis* and *T. truncatus*. Many of the same prey are selected by both species; however, the selection frequencies of overlapping prey are very different. For example, *S. frontalis* have an observed diet composition of 34% lizardfish, 17% jack, 8% eel, and 5% razorfish; comparatively, the diet of *T. truncatus* includes 30% razorfish, 27% eel, 19 % jack, and 4 % lizardfish. Aside from overlapping on jacks as common prey, *S. frontalis* and *T. truncatus* have nearly opposite primary prey selections. Interestingly, jacks that are common prey among these two species are schooling prey and not necessarily

associated with a bottom type. Minimally-overlapping prey, on the contrary, inhabit bottom types associated with those selected for foraging by each delphinid species. Razorfish and eels inhabit sand/grass and grass beds and are common prey for *T. truncatus* who forage primarily over grassy habitats. Lizardfish inhabit sandy areas which is the same bottom type that *S. frontalis* primarily use to forage. *T. truncatus* were also found to feed at relatively higher frequencies over rock/reef habitats, primarily on squirrelfish which were never observed being consumed by *S. frontalis*. Furthermore, *S. frontalis* have been observed consuming a greater variety of prey with observations of 14 known families; whereas *T. truncatus* have been observed foraging on only 9 families of prey. Having a more generalist diet gives *S. frontalis* the ability to select from a wider variety of prey when diet changes are necessary or prey abundance patterns fluctuate. Moreover, it has been suggested that prey use can be an inadequate measure of feeding preference because diet studies typically lack foraging location information and are plagued by small sample sizes from stomach contents of stranded, bycaught, or harvested animals (e.g. Berens McCabe *et al.*, 2010.). However, this study utilizes over 25 years of prey use observation in the high-visibility Bahamian waters; thus providing an accurate estimate of *S. frontalis* and *T. truncatus* diet composition in known foraging locations.

Larger prey species (Fig. 14) were generally selected by *T. truncatus*, which could be an indication of nutritional need relative to their larger body size. In fact, using mean body mass calculations for both species from Trites and Pauly (1998) (*S. frontalis* = 65.4 kg; *T. truncatus* = 187.5), and average food % intake rate during non-reproductive periods of *T. truncatus* from Kastelein *et al.* (2003) (~ 5% body mass/day), it is estimated that the energy demand of *T. truncatus* (9.4 kg food/day) is roughly triple (~2.6 x) that of

S. frontalis (3.2 kg food/day). Maintenance requirements of striped dolphins (*Stenella coeruleoalba*), a close relative to *S. frontalis*, have been estimated at 54 kcal/kg of dolphin per day (Kastelein, *et al.*, 2002a); for other delphinids in captivity the energy demand has been estimated as 50 kcal/kg of dolphin per day (personal communication with J. Pawloski and M. Breese as cited in Benoit-Bird, 2004, p. 437). Using these energy requirement and body mass estimates, it is estimated that *S. frontalis* and *T. truncatus* have maintenance needs of 3531.6 kcal/day and 9375 kcal/day, respectively. *S. frontalis* may afford the time spent foraging for smaller prey, whereas *T. truncatus* have higher energy requirements and must consume larger prey or feed more often to compensate for substantially higher metabolic demands.

A variety of unique feeding techniques are utilized by resident *T. truncatus* and *S. frontalis* on Little Bahama Bank. Although both species have similar approaches to surface feeding and benthic echolocation, only *T. truncatus* use echolocation to “crater feed” and scan ledges and holes for prey (e.g. Rossbach & Herzing, 1997; Rossbach, 1999; Herzing, 2004). Additionally, *S. frontalis* are frequently observed venturing offshore into deeper waters of the Gulf Stream at night to feed on nocturnally vertically migrating squid and pelagic schooling fish (e.g. flyingfish) (Herzing, 1996). Relatively high consumption rates of squid and flyingfish by *S. frontalis* may be critical components to their diet. However, it is important to note that nocturnal feeding events are not included for this study due to inherent difficulties of collecting foraging data at night. *T. truncatus*, on the contrary, have only been observed foraging during daylight hours and on the shallow sandbanks of Little Bahama Bank (Herzing, 1996; Rossbach & Herzing, 1999) and were not observed foraging on squid or flyingfish for this study. Observed

variations in feeding behavior for these two species reflect differences in both prey and habitat use.

Foraging strategy was detected through group size as well. Not only did the two resident species of dolphins exhibit distinct group sizes, but they also varied in the proportion of individuals foraging compared to the total number of dolphins present during encounters. Therefore, group size was defined by only those individuals observed to be foraging, even if the overall number of dolphins present during encounters was larger. *S. frontalis* had on average 50% fewer individuals per group and also fewer individuals actively foraging (71.7%) per encounter in comparison to *T. truncatus* (92.8%). For *S. frontalis*, smaller group size with a greater proportion of non-foraging individuals could indicate a foraging strategy that minimizes predation risk during foraging events. Since shark predation on Little Bahama Bank is visible through the many shark bite scars on resident dolphins, it is possible that the role of non-foraging individuals is to monitor for threats from sharks during foraging events. Although larger group size has been shown to correlate with higher predation risk (Heithaus & Dill, 2002), the higher number of non-foraging dolphins with *S. frontalis* on Little Bahama Bank may be a trade-off to smaller group size. However, the role of non-foragers was not analyzed for this study. Group size differences for each species may also indicate respective optimal foraging size. In order to account for their relatively greater body mass, it is suggested that larger group sizes observed for *T. truncatus* allow for greater group efficiency where many individuals can actively forage over patchy landscapes of *T. testudinum*. Larger group size for *T. truncatus* is beneficial for frequent use of a scarcer bottom type. Habitat that requires longer search time to locate is likely to be foraged

more intensively and by larger groups. Since the same area is being foraged by many individuals, similar prey are likely to be consumed during these foraging events, which is consistent with the narrower range of prey items observed for *T. truncatus*. Larger group size during foraging events is also indicative of animals that need to feed more often to fulfill a higher energy requirement. *T. truncatus* were often observed group feeding, whereas *S. frontalis* had relatively fewer observed coordinated foraging bouts.

Cooperative and group feeding has been documented among *T. truncatus* near Grand Bahama Island, Bahamas as well. Kelly Rossbach (1999) found *T. truncatus* to feed in groups both cooperatively and relatively independently within group formations. Small group size and frequent independent feeding within a group for *S. frontalis* is consistent with their use of a broader landscape in which less search effort is necessary to find prey. When prey becomes available, foraging is likely to ensue regardless of group size. These results are consistent with previous observations of other odontocetes, including coastal bottlenose dolphins. Previous studies have found cooperative foraging to correlate with schooling and more concentrated prey, while solitary foragers tend to target non-schooling and scarcer prey (Wursig, 1986; Allen *et al.*, 2001).

Atlantic Spotted Dolphin Prey Use

A comparison between pregnant, lactating, and NRA female groups revealed significant foraging differences between one or more groups. Additional pairwise comparisons between pregnant and lactating females suggested similar prey use. For further analysis both pregnant and lactating foraging groups were combined into one category inclusive of all reproductively active individuals, which allowed for comparison

with NRA females. These results showed reproductively active female prey use to be different from that of NRA females. However, pregnant female prey use was also consistent with NRA female prey use when tested independent of lactating females. This result partly contradicts the hypothesis that reproductively active females feed differently from NRA females; however, exploratory results suggest pregnant females to have diets more similar to lactating females than to NRA dolphins. It is important to point out that G-test results showed significant differences between pregnant and NRA female prey use ($p=0.0164$); however, more conservative chi-squared results ($p = 0.0838$) suggest prey use differences to not be significant. Nonetheless, similar prey use patterns were observed between pregnant and lactating females. In fact, flounder and flyingfish were preyed on by both pregnant and lactating females at distinctly higher frequencies than NRA dolphins. Flounder are benthic prey and were observed to be much slower and easier to catch, potentially allowing for more successful capture rates especially when lactating mothers were in the presence of a calf. In addition to being a more certain meal for reproductively active females that have dietary restrictions, these prey may also offer some nutritional benefit to both lactating and pregnant females to aid in milk production or fetal development, respectively. On the contrary, NRA dolphins selected jacks and needlefish at significantly higher rates ($p < 0.05$). Both jacks and needlefish are pelagic schooling fish and were observed to be relatively faster prey. This may make these prey items more available to NRA dolphins that are not overshadowed by dietary or foraging restrictions. Similar prey use patterns between lactating and pregnant females *S. frontalis* contradicts the results of Bernard and Hohn (1989) who found differences in feeding patterns between pregnant and lactating female *S. attenuata* in the eastern tropical

Pacific. However, consistent with their findings, lactating females fed differently from NRA females. Somewhat ambiguous results from prey use comparison between pregnant females and the other 2 reproductive groups makes it necessary to take a closer look at the nutritional quality of prey in order to determine more definite diet partitioning between pregnant, lactating, and NRA female foraging groups.

Results from individual groups tested by themselves also showed pregnant and NRA females to randomly select prey; however, lactating females were found to have definite feeding patterns. With 14 families of prey identified for *S. frontalis* on Little Bahama Bank, it is likely that individual dolphins free of foraging or dietary restrictions (i.e. NRA females) feed more opportunistically, and even more randomly, on a wider range of prey. Results for pregnant and NRA females indicate that feeding, as a whole, is random with respect to available prey. On the contrary, lactating females have to make up for an energy deficit due to the energetic cost of milk production. Foraging ability in females is also often hindered by a paired calf. Therefore, it may be beneficial for lactating females to have a more selective diet of prey that offer the greatest return in nutrition while maximizing capture success. It is important to note that conclusions for pregnant and NRA dolphins are based on results from data with small counts eliminated. Pregnant females undoubtedly have heightened dietary needs in response to fetal growth and development. However, pregnant females are not restricted by a foraging calf and therefore don't have an extreme shift in diet like that of lactating females.

Ontogenic changes were not reflected through our results on prey use: calves present during group foraging did not affect the frequency of overall group prey selection from that of foraging without calves present. It is important to note that calves were

always accompanied by an adult during foraging events (not necessarily the mother). Encounters varied in group composition from only m/c pairs to both males and females present. Prey reported for each encounter were those being selected by the foraging group as a whole; therefore, it is possible that foraging adults skewed results. In fact, the major prey categories selected during calf foraging events - lizardfish, jacks, and flounder- were the same prey selected by the general population. Consistent with these findings, lizardfish and flounder were also found by Bender *et al.* (2008) to be the major prey items of mother and calf (m/c) pairs on Little Bahama Bank. Lactating mothers associated with their calves in these encounters were expected to contribute to variation in prey use, but our results do not reflect this assumption. In the presence of calves, mothers have been observed chasing prey for longer periods of time and in an exaggerated fashion as a form of social learning (Bender *et al.*, 2008); therefore, it is suggested that females will forfeit their own needs while teaching their calf how to forage. However, lactating females were not always accompanied by a calf during foraging encounters and may have been compensating for increased dietary needs by feeding independent of their calves.

Significant differences in prey use between adult males and females were not detected for this study. This contrasts what was expected based on findings of spatial foraging strategy differences between males and females in previous studies on non-migratory mammals, such as sex-specific differences in a population of grey seals (*Halichoerus grypus*) at Sable Island, Nova Scotia (Breed *et al.*, 2006). Mixed sex foraging is common for *S. frontalis* on Little Bahama Bank and results suggest major prey to be similar between sexes when reproductive status is not taken into account.

Adult females did however appear to have a greater diversity of prey in their diet. Few studies, to my knowledge, have been done to determine sex-specific prey selection in cetaceans.

Proximate Composition of Prey Species

Nutritional quality of lean mass has been reported for many commercially important species, however, nutritional value of commercial and non-commercial whole specimens is often unknown (Eder & Lewis, 2005). Nutritional compositions for this study are of whole specimens, which is greatly important for understanding requirements of cetaceans who eat their prey whole. Important prey for cetaceans may shift in response to increasing or decreasing nutritional value of individual prey. In this study, however, prey were captured in the same months that foraging encounters were observed. Therefore, potential seasonal variation in nutritional value of prey is assumed to have no effect on the results of this study. Furthermore, the Bahamas is a tropical/subtropical environment and is not subject to extreme seasonal changes in coastal fish communities that more temperate regions undergo, so seasonal effects should be minimal.

Atlantic Spotted Dolphin Prey Use and Nutrition

Of the prey collected and analyzed from Little Bahama Bank, squid energy value (kJ/g) was third after squirrelfish and jacks. The specimen with the lowest lipid and energy levels are flounder. Moreover, lipid values for squid were highest of all specimens analyzed. This result contrasts values from other nutritional reports in which fish are generally considered to be higher in caloric content, particularly from fats, than

invertebrates such as squid (Croxall & Prince, 1982; Clarke, 1986). For example, a study on prey of *S. attenuata* in the eastern tropical Pacific reported higher energy values for fish than for squid (per 100 g muscle mass: mean = 420 kJ/fish; mean = 310 kJ/squid) (Bernard & Hohn, 1989). Therefore, results from this study don't necessarily represent high energy levels for squid, but rather low energetic composition for fish. Results do follow moisture expectations of squid, such as that found for ommastrephid squid (*Ommastrephes bartrami*) from the North Pacific, which were measured to be higher in water content than flying fish from the same area (Sidewell *et al.*, 1981). Squid were found to have nearly the highest % moisture, falling just short of lefteye flounders. While squid are primarily fed on nocturnally, and for this study rarely observed in daytime foraging encounters, they are known to be a major prey item for *S. frontalis*.

A closer look at the nutritional components of selected prey revealed more definite significant differences in diet than were found in looking only at prey selection frequency. Even small deviations in prey selection among groups were detected for this analysis if nutrient differences for selected prey were large. Unlike the somewhat ambiguous differences found in looking only at prey selection with pregnant females, diet composition comparisons between pregnant and NRA females revealed significant differences for each nutrient tested (calorie, protein, lipid, moisture). In agreement with our prey selection results, lactating females compared separately with NRA dolphins and pregnant females were found to have diets varying in nutritional composition. Lactating females had relatively higher consumption (per gram of food) of % moisture, % lipid, % protein, and energy content (kJ g^{-1}) than pregnant females, but lower demands than NRA females for all nutrients other than % moisture. Since pregnant females were found to

have diets significantly lower in nutrients than both lactating and NRA females, our results suggest that pregnant females are not selecting prey based on higher nutrient content. Pre-formed moisture (% moisture) in the diet of lactating females was found to be significantly higher than pre-formed moisture in the diet of pregnant and NRA females. Moisture is an important prey characteristic because marine mammals derive water from their fat reserves in order to produce milk (Worthy, G.A.J., p.800). This suggests that in order to replenish their heightened use of water from fat reserves, prey with high % moisture are selected. Since NRA females have diets higher in % protein, % lipid, and energy (kJ g^{-1}) it is likely that because they are not constrained by a nursing calf or by a developing fetus that they can feed freely and allocate energy to growth and to build up energy reserves for use during reproductively active periods.

In contrast to the findings of this study, previous nutritional studies on pregnant odontocetes have shown no difference in food consumption from that of NRA females (Kastelein *et al.*, 1993; 2002b; 2003), although slight increases in consumption shortly before parturition have been reported (e.g. Reddy *et al.*, 1994). Consistent with the findings from this study, previous research has shown the cost of pregnancy to be much less than that associated with lactation (Worthy, G.A.J., p.805). In other mammals with similar gestation and lactation periods, like hamsters and humans, increases in energy consumption during lactation have been found as well (Day *et al.*, 2002; Dufour *et al.*, 2002). Results from this study revealed lactating females to increase nutrient intake relative to pregnant females, which was also the result of captive studies by Kastelein *et al.* (2002b; 2003) on captive odontocetes. However, Kastelein *et al.* (2002b; 2003) found lactating females to increase nutrient intake relative to NRA females (Kastelein *et al.*,

2002b; Kastelein *et al.*, 2003). Although lactating females were revealed to have significantly different nutritional intake in the current study, lactating females consumed lower levels of % lipid, % protein, and energy (kJ g^{-1}) than NRA females.

Many ontogenic differences in calf diet were reflected through nutritional analysis that were not revealed in looking only at prey selection. Foraging groups with age 1 calves present were found to have a different nutritional intake than non-calf foraging groups for % moisture, % protein, % lipid, and energy (kJ g^{-1}). Since age 1 calves are most closely associated with their lactating mothers, similarities in nutritional intake were also consistent with that of lactating females. Similar to lactating females, % moisture intake (per gram of food) for foraging groups with age 1 calves present was highest relative to other calf (ages 2-6) and non-calf group encounters. Energy (kJ g^{-1}) intake in age 1 calf group encounters was also relatively high. Dietary differences, however, were not significant for % moisture, % protein, % lipid, or energy (kJ g^{-1}) between different ages of calves present in foraging groups. Even though energy (kJ g^{-1}) and % moisture intake levels were observably higher for age 1 calf foraging groups, statistical analysis revealed that all age calf (1-6) foraging groups had similar nutritional intake at every stage of weaning. Therefore, the difference in nutritional intake between foraging groups with all age calves was not high enough to elicit statistical significance. When mass of prey (g) was included for the calculation of relative use of nutrients, non-calf (juveniles and adults) group encounters had higher levels of intake than all calf foraging groups for every nutrient in their diet (% moisture, % lipid, % protein, and energy (kJ g^{-1})). This is mostly due to the higher frequency of larger-sized prey in the diet of older dolphins.

Findings from nutritional analysis are consistent with previous studies that have shown developing calves to have higher rates of consumption and different nutritional needs than adults (e.g. Kastelein *et al.*, 2003). Elevated metabolic rates, about twice that of adults, along with increased energy requirements have been found for many species of immature and actively growing mammals (Worthy, G.A.J., p.793). Young and fast growing weaning calves from previous studies have also demonstrated a compensation for high energy demands by individuals consuming prey of greater caloric value (Archer & Robertson, 2004). A shift in diet occurs at some later stage of calf development, eventually transitioning into juvenile status. Once juvenile status is reached, individuals feed entirely on solid food and are therefore more likely to have diets similar to that of adults.

Differences not detected in prey use patterns for foraging groups including m/c pairs compared with foraging groups not including m/c pairs were recognized by nutritional analysis. Energy (kJ g^{-1}) and % moisture intake were significantly lower for m/c pair foraging groups compared to no m/c pair foraging groups when size of prey was used for analysis; however, when nutrient per gram of prey was considered without total prey size, % moisture and % protein intake were both observably higher for m/c pair foraging groups. Since the relative proportion of % lipid intake, the major contributor to energy value of prey, is similar for m/c pair and no m/c pair foraging groups, it is not surprising that energy (kJ g^{-1}) intake was similar. This diet analysis is, to our knowledge, the first to look at diet and nutrition in dolphin foraging groups with calves and m/c pairs in the wild.

This study has allowed us to more fully understand the complexities of feeding systems on Little Bahama Bank and the relationship of two sympatric dolphin species with each other and their environment. Finding a correlation between foraging and habitat characteristics for *S. frontalis* and *T. truncatus* has helped us to better understand their roles as predators in the ecosystem and in developing theories on how they coexist with the use of different habitats. Analyzing foraging events from over 20 years of pre-existing data has provided adequate sample sizes for all foraging groups. This long-term study of foraging accounts has also allowed for a more complete interpretation of foraging patterns than has been accomplished with most other studies on prey use. Underwater observation of foraging events has added a unique element to this study, whereas most other studies have relied on surface to sub-surface interpolation or stomach content analysis.

Prey use analysis proved useful as a baseline for interpreting observable patterns of intraspecific and interspecific foraging patterns. Complementing prey use analysis using nutritional data made it clear that observed prey use, even for long-term studies, may alone not be an adequate measure for interpreting underlying factors driving prey selection. Implementing a code developed for R that incorporated nutritional composition of prey has provided a more developed explanation for why dolphins of different life stages, reproductive status, and sex may select certain prey. Nutritional value of prey applied to observed underwater foraging events, by correlating prey quality with prey use, gives valuable insight into prey preference for different groups of foraging *S. frontalis*. Furthermore, a better understanding of the relationship between nutrient intake with intensive growth periods of calves and the heightened dietary needs of

reproductively active females is essential to the understanding of nutritional and energetic constraints on marine mammals. Nutritional and energetic requirements for cetaceans are still largely unknown (Worthy, 2001), and this research is one of the first field studies to estimate prey selection based on reproductive status and life stage in terms of nutritional importance. Also, with mixed results from previous research on dietary and nutritional requirements of reproductively active and NRA individuals, this study offers a more comprehensive approach to determining these differences. Results from this study can provide useful knowledge for nutritional needs and prey selection of odontocetes in both captivity and other regions around the world.

Predator and prey interactions are vulnerable to disruption through human activity, especially for marine systems close in proximity to land. With the knowledge of important prey as well as important habitats selected by both species of dolphin, we can construct better management plans to protect prey and habitats foraged by resident dolphins in the Bahamas. Management priority is not often placed on fish that are not of great economic value. Since most of the prey selected by resident dolphins on Little Bahama Bank have little economic or commercial value, it is important to impose fisheries management and bi-catch regulations for these species in order to protect the dolphin's food supply. Little Bahama Bank is also subjected to strong weather systems, including hurricanes, during summer months. Catastrophic events, such as the hurricanes Frances and Jeanne in 2004, have the potential to completely change the dynamic of this ecosystem. Knowledge of important prey will allow for proper management and the potential recovery of prey species should such catastrophic events decrease their abundance.

APPENDIXES

Table 1. Results from G-tests (G) of intraspecific (*T. truncatus*, *S. frontalis*), interspecific (*T. truncatus*/*S. frontalis*), and mixed foraging group bottom type use (sand, sand/grass, grass, reef/rock) during foraging events.

Group	N	G	df	P
<i>T. truncatus</i>	87	68.84	3	< 2.2e-16
<i>S. frontalis</i>	212	431.87	3	< 2.2e-16
Mixed	56	87.68	3	< 2.2e-16
<i>T. truncatus</i> * <i>S. frontalis</i>	299	62.98	3	< 2.2e-16
<i>T. truncatus</i> * <i>S. frontalis</i> * Mixed	355	64.49	6	< 2.2e-16

“*” = feeding groups being compared

Table 2. Prey use results from G-tests (G) and chi-squared tests (χ) of intraspecific and interspecific significance in deviation from random feeding. Probability (P) values in bold represent the most conservative values for each test. Probability values for tests run with small count data are only in bold if they gave a different result.

Group	N	G	χ	df	P (G)	P (χ)
<i>T. truncatus</i>	27	23.31	26.00	8	0.003	0.0011
[<i>T. truncatus</i>]	21	0.91	0.86	2	0.635	0.6514
<i>S. frontalis</i>	295	334.5	425.36	13	< 2.2e-16	< 2.2e-16
[<i>S. frontalis</i>]	291	223.7	282.55	10	< 2.2e-16	< 2.2e-16
<i>T. truncatus</i> * <i>S. frontalis</i>	322	82.22	103.95	16	< 2.2e-16	< 2.2e-16
[<i>T. truncatus</i> * <i>S. frontalis</i>]	317	65.87	81.39	9	< 2.2e-16	< 2.2e-16

“[]” = significance tests run with small count data eliminated

“*” = feeding groups being compared

Table 3. Results from G-tests (G) and chi-squared tests (χ) of significance in deviation from random prey use for reproductive female groups (lactating, pregnant, or non-reproductively active (NRA)). Probability (P) values in bold represent the most conservative values. Probability values for tests run with small count data are only in bold if they gave a different result. Faded lines are redundant significant values and not used for interpretation of results.

Group	N	G	χ	df	P (G)	P (χ)
Pregnant	29	17.48	23.45	8	0.0255	0.0028
[Pregnant]	27	12.45	16.30	6	0.0527	0.0123
Lactating	60	44.20	61.87	7	< 2.2e-16	< 2.2e-16
[Lactating]	51	29.33	35.96	4	< 2.2e-16	< 2.2e-16
NRA	41	21.41	23.20	7	0.0032	0.0016
[NRA]	33	5.05	4.94	3	0.1684	0.1763
Pregnant /Lactating	98	111.41	165.02	11	< 2.2e-16	< 2.2e-16
[Pregnant/Lactating]	92	68.09	93.91	7	< 2.2e-16	< 2.2e-16
Pregnant/NRA	76	62.29	78.87	10	< 2.2e-16	< 2.2e-16
[Pregnant/NRA]	70	28.18	36.00	6	< 2.2e-16	< 2.2e-16
Pregnant * Lactating * NRA	130	43.24	38.31	20	0.0019	0.0081
[Pregnant * Lactating * NRA]	125	29.62	24.17	14	0.0086	0.0438
NRA * Pregnant/Lactating	138	29.40	26.63	12	0.0034	0.0087
[NRA * Pregnant/Lactating]	130	20.33	19.18	7	0.0049	0.0076
Lactating * Pregnant/NRA	136	15.67	13.48	10	0.1096	0.1981
[Lactating * Pregnant/NRA]	131	9.70	9.32	7	0.2064	0.2306
Lactating * NRA	99	23.57	19.69	8	0.0027	0.0116
[Lactating * NRA]	97	19.78	16.74	7	0.0061	0.0191
Lactating * Pregnant	89	14.52	12.27	9	0.1050	0.1985
[Lactating * Pregnant]	86	7.57	6.09	7	0.3719	0.5293
Pregnant * NRA	70	21.77	16.60	10	0.0164	0.0838
[Pregnant * NRA]	64	12.43	9.56	6	0.0531	0.1444

“[]” = significance tests run with small count data eliminated

“/” = feeding groups compiled or together in encounter

“*” = feeding groups being compared

Table 4. Results from G-tests (G) and chi-squared tests (χ) of significance in deviation from random prey use for mother & calf pairs (m/c), life stage groups (calves: ages 1-6, all others (juveniles and adults)), and sex groups (male and female). “Age 1 calves only” differentiates from “Age 1 present” with the former including encounters where no other age calves were present and the latter being inclusive of other age calves. Probability (P) values in bold represent the most conservative values. Probability values for tests run with small count data are only in bold if they gave a different result. Faded lines were redundant significant values and not used for interpretation of results.

Group	N	G	χ	df	P (G)	P (χ)
Age1 calves only	11	4.15	3.60	9	0.9010	0.9357
<i>[Age 1 present * Non-calves]</i>	<i>161</i>	<i>8.45</i>	<i>8.88</i>	<i>8</i>	<i>0.3908</i>	<i>0.3523</i>
Age 1 present * Other calves (ages2-6)	138	16.81	14.76	12	0.1569	0.2548
<i>[Age 1 present * Other calves (ages2-6)]</i>	<i>133</i>	<i>12.55</i>	<i>11.87</i>	<i>8</i>	<i>0.1283</i>	<i>0.1569</i>
All age calves * Non-calves	255	21.49	17.93	13	0.0638	0.1601
<i>[All age calves * Non-calves]</i>	<i>246</i>	<i>9.42</i>	<i>9.27</i>	<i>8</i>	<i>0.3078</i>	<i>0.3198</i>
m/c * Non-m/c	295	18.55	15.27	13	0.1378	0.2909
<i>[m/c * Non-m/c]</i>	<i>283</i>	<i>5.91</i>	<i>5.70</i>	<i>8</i>	<i>0.6573</i>	<i>0.6807</i>
Males * Females	136	7.84	6.40	11	0.7273	0.8454
<i>[Males * Females]</i>	<i>126</i>	<i>3.35</i>	<i>3.14</i>	<i>6</i>	<i>0.7638</i>	<i>0.7917</i>

“[]” = significance tests run with small count data eliminated

“&” = paired groups

“*” = feeding groups being compared

Table 5. Numbers of each prey species used (N), and number of samples after pooling (n), for proximate composition analysis (% moisture, % solid, % ash [% of wet total body mass], % lipid, % protein), energy content (kJ g⁻¹), mass (g), and total length from Little Bahama Bank, Bahamas.

Family	Species	Common Name	N	n	% Moisture	% Solid	% Ash	% Lipid	% Protein	Energy (kJ g ⁻¹)	Mass (g)	Total length (cm)
Belonidae	<i>Platybelone argalus</i>	keeltail needlefish	8	6	70.8 ± 1.1	29.2 ± 1.1	6.5 ± 1.2	3.4 ± 1.0	19.2 ± 1.3	4.5 ± 0.5	20.6 ± 7.2	29.7 ± 2.7
Bothidae	<i>Bothus ocellatus</i>	eyed flounder	20	15	75.8 ± 2.2	24.2 ± 2.2	7.7 ± 2.1	2.5 ± 0.5	14.1 ± 2.1	3.3 ± 0.5	8.0 ± 3.0	10.3 ± 1.4
Carangidae	<i>Caranx crysos</i>	blue runner	3	3	73.7 ± 1.3	26.3 ± 1.3	3.1 ± 0.2	4.8 ± 1.2	18.4 ± 0.5	4.9 ± 0.4	392.1 ± 102.5	34.7 ± 2.6
Exocoetidae	<i>Hemiramphus balao</i>	balao	1	1	72.00	28.10	5.2	2.6	20.2	4.4	75.8	32.1
Exocoetidae	<i>Hemiramphus brasiliensis</i>	ballyhoo	8	7	73.4 ± 1.1	26.6 ± 1.1	4.4 ± 0.5	2.7 ± 0.1	19.6 ± 0.7	4.3 ± 0.1	14.9 ± 6.5	18.1 ± 3.1
Exocoetidae	<i>Cheilopogon melanurus</i>	atlantic flyingfish	14	7	73.3 ± 2.4	26.7 ± 2.4	6.2 ± 1.8	2.5 ± 0.7	18.0 ± 1.4	4.0 ± 0.4	61.4 ± 44.3	19.7 ± 6.9
Exocoetidae	<i>Prognichthys gibbifrons</i>	bluntnose flyingfish	2	2	71.0 ± 0.2	29.0 ± 0.2	5.9 ± 0.2	3.9 ± 0.5	19.2 ± 0.9	4.7	80.0	24.8 ± 2.0
Exocoetidae	<i>Hirundichthys speculiger</i>	mirrorwing flyingfish	4	4	74.0 ± 2.9	26.0 ± 2.9	5.1 ± 1.1	3.4 ± 1.7	17.5 ± 0.8	4.2 ± 0.7	107.2 ± 29.5	24.9 ± 2.0
Exocoetidae	<i>Parexocoetus brachypterus</i>	sailfin flyingfish	6	4	70.7 ± 1.1	29.3 ± 1.1	6.5 ± 0.3	3.0 ± 0.5	19.9 ± 0.7	4.4 ± 0.2	10.3 ± 6.4	12.2 ± 2.7
Haemulidae	<i>Haemulon aurolineatum</i>	tomtate	3	3	72.5 ± 0.6	27.5 ± 0.6	7.3 ± 0.5	3.4 ± 0.5	16.8 ± 0.5	4.1 ± 0.2	32.1 ± 7.2	—
Haemulidae	<i>Haemulon plumieri</i>	white grunt	7	7	73.7 ± 1.5	26.3 ± 1.5	6.5 ± 1.0	3.7 ± 1.5	16.2 ± 1.1	4.1 ± 0.5	130.6 ± 74.5	20.8 ± 4.8
Holocentridae	<i>Holocentrus adscensionis</i>	squirrelfish	6	6	67.2 ± 1.9	32.8 ± 1.9	9.1 ± 0.9	4.7 ± 1.5	19.0 ± 1.2	4.9 ± 0.5	151.2 ± 35.9	25.8 ± 2.2
Labridae	<i>Xyrichtys splendens</i>	green razorfish	11	5	76.4 ± 0.4	23.6 ± 0.4	5.0 ± 0.2	2.4 ± 0.4	16.2 ± 0.1	3.6 ± 0.2	3.8 ± 0.3	8.3 ± 0.2
Labridae	<i>Xyrichtys novacula</i>	pearly razorfish	6	6	74.3 ± 1.8	25.7 ± 1.8	5.0 ± 0.4	3.9 ± 3.9	16.8 ± 1.7	4.3 ± 0.3	29.3 ± 16.7	13.8 ± 3.3
Labridae	<i>Xyrichtys martinicensis</i>	rosy razorfish	1	1	73.00	27.0	5.6	5.5	15.9	4.7	21.9	15.0
Labridae	<i>Halichoeres poeyi</i>	blackear wrasse	6	6	73.6 ± 1.6	26.4 ± 1.6	5.9 ± 0.8	3.3 ± 1.1	17.2 ± 1.8	4.1 ± 0.2	11.3 ± 9.6	10.8 ± 2.4
Labridae	<i>Thalassoma bifasciatum</i>	bluehead wrasse	1	1	73.50	26.5	6.7	3.9	15.9	4.1	9.5	10.9
Labridae	<i>Halichoeres bivittatus</i>	slippery dick	15	7	74.8 ± 1.2	25.2 ± 1.2	6.1 ± 0.7	1.9 ± 1.2	17.1 ± 1.4	3.6 ± 0.3	24.7 ± 14.9	13.1 ± 3.1
Lutjanidae	<i>Lutjanus synagris</i>	lane snapper	8	8	73.7 ± 0.8	26.3 ± 0.8	5.9 ± 0.9	3.4 ± 1.3	17.1 ± 1.0	4.1 ± 0.4	123.7 ± 72.8	21.0 ± 4.8
Lutjanidae	<i>Ocyurus chrysurus</i>	yellowtail snapper	6	6	74.4 ± 2.5	25.6 ± 2.5	5.4 ± 1.3	2.3 ± 2.3	17.9 ± 1.3	3.9 ± 0.8	206.0 ± 89.0	29.2 ± 3.9
Mullidae	<i>Pseudupeneus maculatus</i>	spotted goatfish	3	3	73.1 ± 2.0	26.9 ± 2.0	6.3 ± 0.4	4.2 ± 1.1	16.5 ± 0.7	4.3 ± 0.5	19.7 ± 4.8	13.0 ± 1.1
Mullidae	<i>Mulloidichthys martinicus</i>	yellow goatfish	2	2	75.0 ± 0.5	25.0 ± 0.5	5.9 ± 0.3	2.7 ± 0.4	16.4 ± 0.1	3.8 ± 0.1	16.5 ± 3.3	12.9 ± 1.2
Scaridae	<i>Cryptotomus roseus</i>	bluelip parrotfish	2	2	74.8 ± 0.1	25.2 ± 0.1	5.8 ± 0.4	2.6 ± 0.6	16.8 ± 0.2	3.8 ± 0.2	10.6 ± 1.6	10.6 ± 0.5
Synodontidae	<i>Synodus foetens</i>	inshore lizardfish	5	5	74.1 ± 0.8	25.9 ± 0.8	5.4 ± 0.9	2.2 ± 0.6	18.3 ± 0.7	3.9 ± 0.3	109.0 ± 52.0	26.8 ± 3.4
Synodontidae	<i>Synodus saurus</i>	bluestriped lizardfish	1	1	73.50	26.5	5.1	4.1	17.2	4.4	18.8	14.9
	Unidentified	squid	43	10	75.7 ± 1.8	24.3 ± 1.8	2.2 ± 0.2	4.9 ± 0.9	17.2 ± 1.7	4.7 ± 0.4	13.4 ± 11.7	20.3 ± 5.7

Table 6. Results of the “diet difference” function written in R of each nutrient category (calorie, protein, lipid, moisture) for female reproductive groups of foraging *S. frontalis* (Preg = pregnant, Lac = lactating, NRA = non-reproductively active). Significant values are in bold.

Group	N	P
Preg * NRA (calorie)	76	< 2.2e-16
Preg * NRA (protein)	76	< 2.2e-16
Preg * NRA (lipid)	76	0.0046
Preg * NRA (moisture)	76	< 2.2e-16
NRA * Preg/Lac (calorie)	138	< 2.2e-16
NRA * Preg/Lac (protein)	138	< 2.2e-16
NRA * Preg/Lac (lipid)	138	< 2.2e-16
NRA * Preg/Lac (moisture)	138	< 2.2e-16
Lac * Preg/NRA (calorie)	136	0.0068
Lac * Preg/NRA (protein)	136	0.067
Lac * Preg/NRA (lipid)	136	0.0228
Lac * Preg/NRA (moisture)	136	0.008
Lac * NRA (calorie)	99	< 2.2e-16
Lac * NRA (protein)	99	< 2.2e-16
Lac * NRA (lipid)	99	< 2.2e-16
Lac * NRA (moisture)	99	< 2.2e-16
Lac * Preg (calorie)	89	< 2.2e-16
Lac * Preg (protein)	89	< 2.2e-16
Lac * Preg (lipid)	89	< 2.2e-16
Lac * Preg (moisture)	89	< 2.2e-16

“/” = feeding groups compiled or together in encounter

“*” = feeding groups being compared

Table 7. Results of the “diet difference” function written in R of each nutrient category (calorie, protein, lipid, moisture) for life stage groups, and mother & calf pairs of foraging *S. frontalis*. Significant values are in bold.

Group	N	P
Age 1 present * No calves (calorie)	166	< 2.2e-16
Age 1 present * No calves (protein)	166	< 2.2e-16
Age 1 present * No calves (lipid)	166	< 2.2e-16
Age 1 present * No calves (moisture)	166	< 2.2e-16
Age 1 present * Other calves (ages2-6) (calorie)	138	0.3904
Age 1 present * Other calves (ages2-6) (protein)	138	0.0937
Age 1 present * Other calves (ages2-6) (lipid)	138	0.3393
Age 1 present * Other calves (ages2-6) (moisture)	138	0.2744
All age calves * No calves (calorie)	255	< 2.2e-16
All age calves * No calves (protein)	255	0.0026
All age calves * No calves (lipid)	255	0.0021
All age calves * No calves (moisture)	255	< 2.2e-16
Mother & calf pair * No mother & calf (calorie)	295	0.0053
Mother & calf pair * No mother & calf (protein)	295	0.0806
Mother & calf pair * No mother & calf (lipid)	295	0.0505
Mother & calf pair * No mother & calf (moisture)	295	0.0017
Only Age1 calves * No calves (calorie)	128	0.0032
Only Age1 calves * No calves (protein)	128	0.0142
Only Age1 calves * No calves (lipid)	128	0.0195
Only Age1 calves * No calves (moisture)	128	0.0011

“&” = paired groups

“*” = feeding groups being compared

Figure 1. Study area on western edge of Little Bahama Bank (image taken from Rossbach and Herzing (1997)).

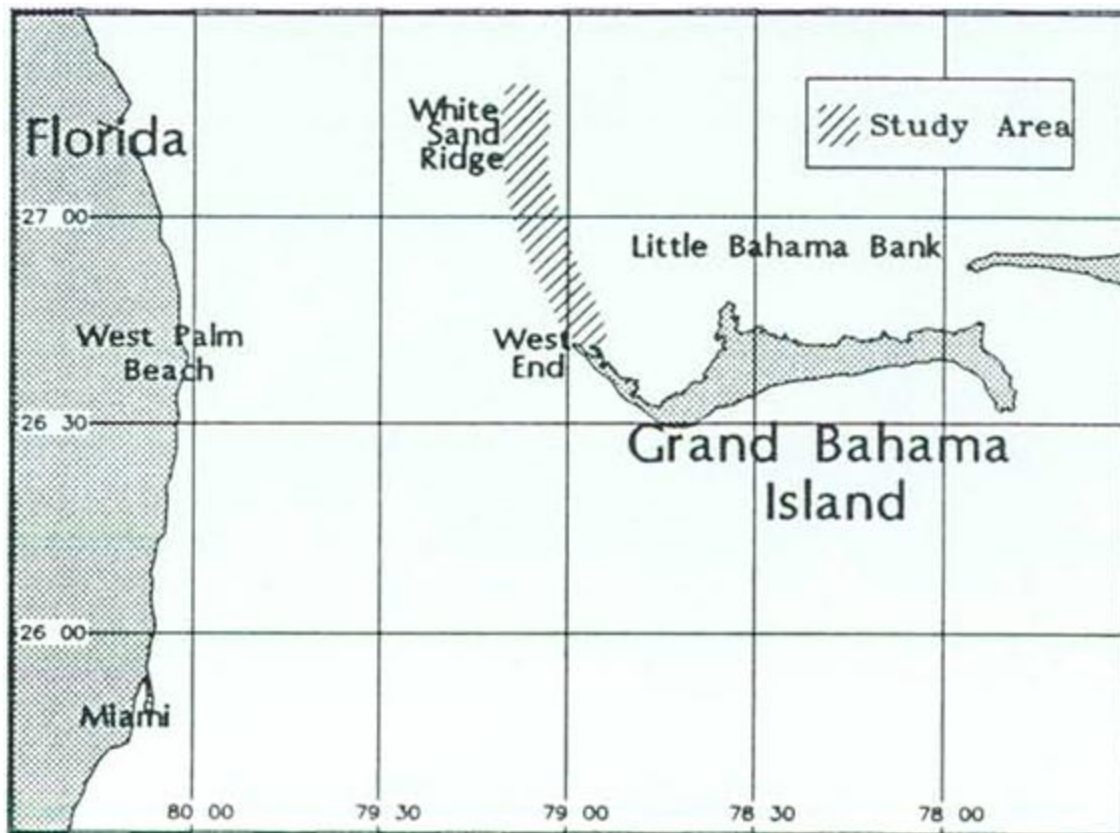


Figure 2. Sample R function used for pairwise comparisons of nutritional intake between foraging groups.

```

nutrient.test<-function(replicates){

  prey.mean=c(26.3,257.9,75.6,412.9,96.6,1919.5,375.5,92.7,40.2,73.1,639.3,63.4,747.1,66.9,
  16.4,8.7,1879.0) #mean caloric content

  prey.sd=c(8.89,194.49,23.42,299.28,104.58,564.01,238.15,28.30,6.86,68.75,326.91,46.07,17
  4.96,5.14,11.91,5.39,564.01) #standard deviation of prey values

  Group1.diet=c(9,5,0,0,3,6,27,3,0,4,0,0,0,0,0,3)

  Group2.diet=c(2,1,0,0,2,8,13,8,0,0,0,0,0,0,0,4)

  diet.difference=array(dim=replicates)

  for(i in 1:replicates){

    calories1=0

    for(j in 1:length(prey.mean)){

      if(Group1.diet[j]>0)
calories1=calories1+sum(rnorm(n=Group1.diet[j],mean=prey.mean[j],sd=prey.sd[j])) }

      calories1.avg=calories1/sum(Group1.diet)

    calories2=0

    for(j in 1:length(prey.mean)){

      if(Group2.diet[j]>0)
calories2=calories2+sum(rnorm(n=Group2.diet[j],mean=prey.mean[j],sd=prey.sd[j])) }

      calories2.avg=calories2/sum(Group2.diet)

      diet.difference[i]=calories1.avg-calories2.avg }

    obs.diff=sum(Group1.diet*prey.mean)/sum(Group1.diet)-
sum(Group2.diet*prey.mean)/sum(Group2.diet)

    p.value=(sum((diet.difference-obs.diff)>abs(obs.diff)) + sum((diet.difference-obs.diff)
<(- abs(obs.diff))))/replicates
  }
}

```

Figure 3. Geographical positions (recorded at the start of each encounter) of *T. truncatus* and *S. frontalis* during foraging events sightings (1992-2009) along our study area, showing the degree of interspecies overlap and separation.

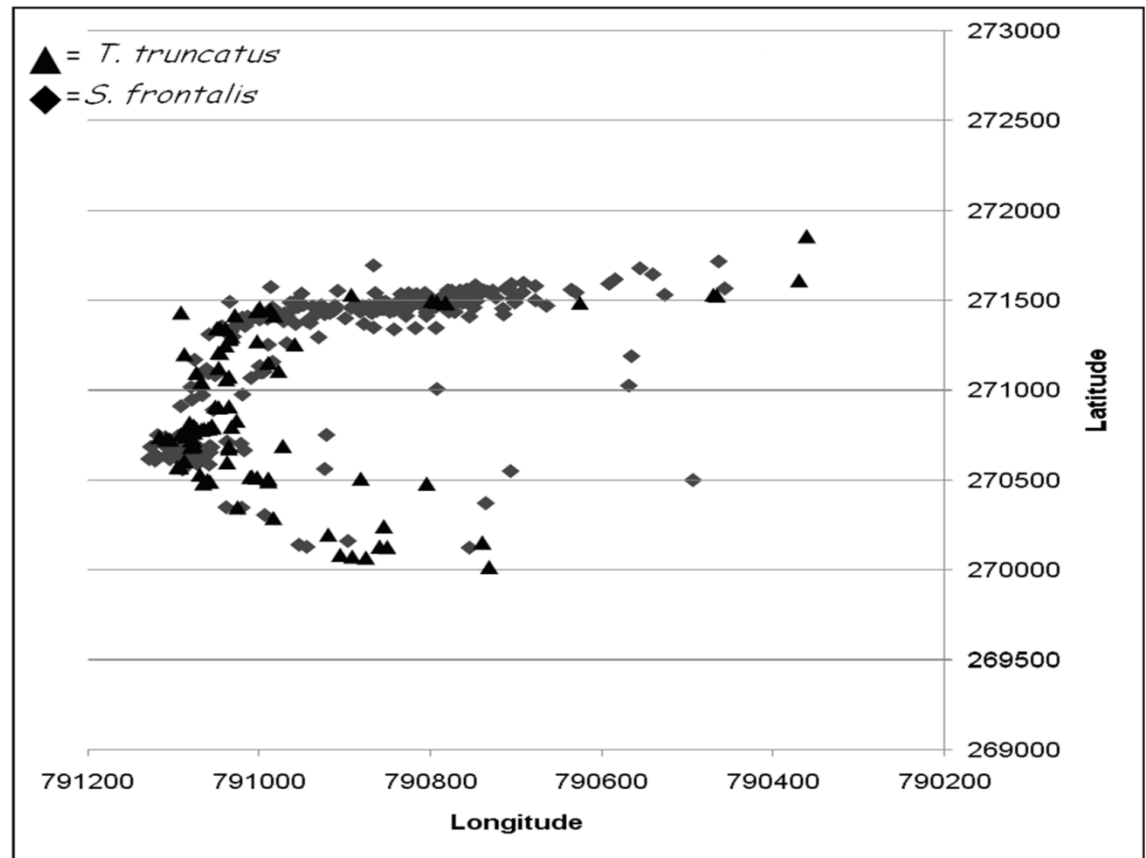


Figure 4. Classification and Regression Tree of *T. truncatus*, *S. frontalis*, and mixed species foraging groups. The explanatory variables are depth (feet), habitat (a=sand, b=sand/grass, c=grass, d=reef), time (# of minutes from 12 a.m.), and temperature (°F). Mean values for selected explanatory variables are given at each split for that subset of data. Proportions (# Mixed/# Stenella/# Tursiops) at each node represent the mean number of each species distinguished at each split. Terminal nodes are indicated by boxes.

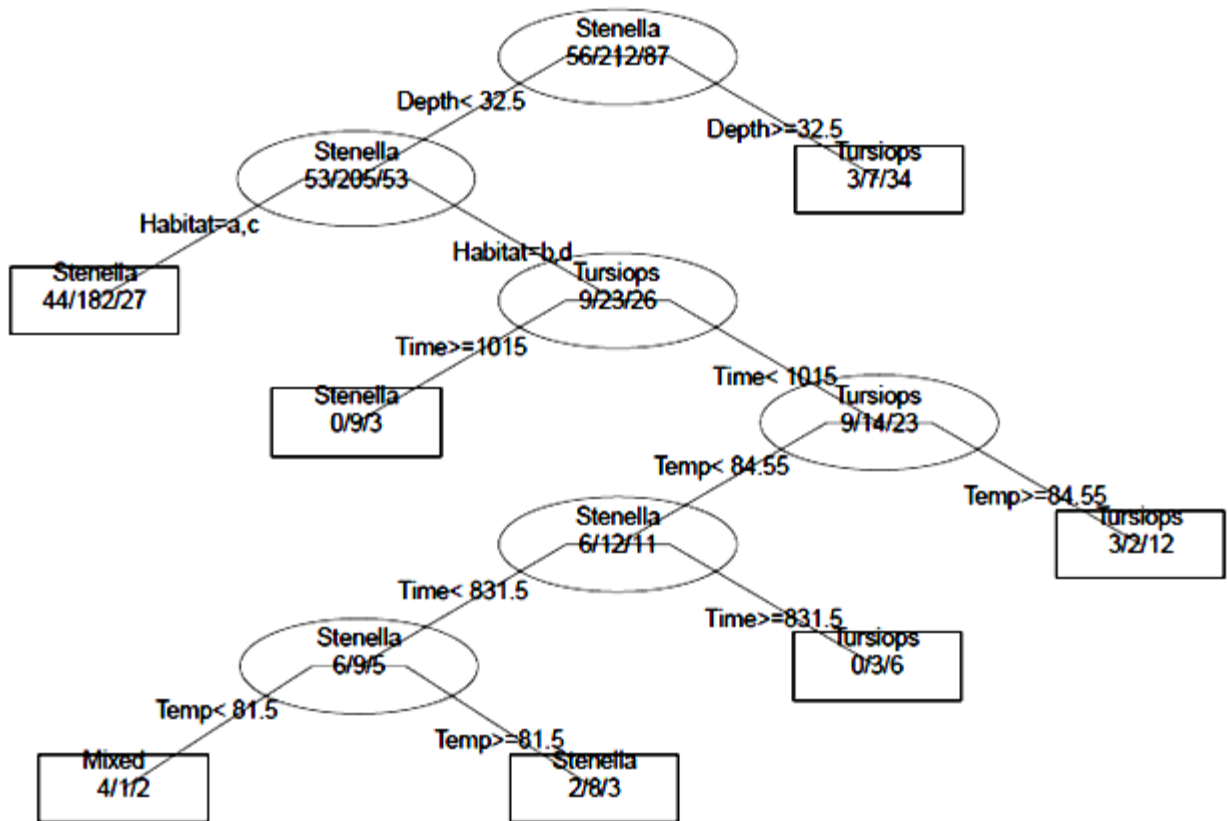


Figure 5. Box plots depicting distributions of *T. truncatus*, *S. frontalis*, and mixed groups relative to environmental factors (depth, time of day (# of minutes from morning [00:00]), and temperature) during foraging events in order of descending influence as determined by CART analysis. Boxes range from 25th to 75th percentiles; solid lines represent the 50th percentile median value; extreme values are found at the end of the whiskers; and open circles represent 5th and 95th percentile outliers.

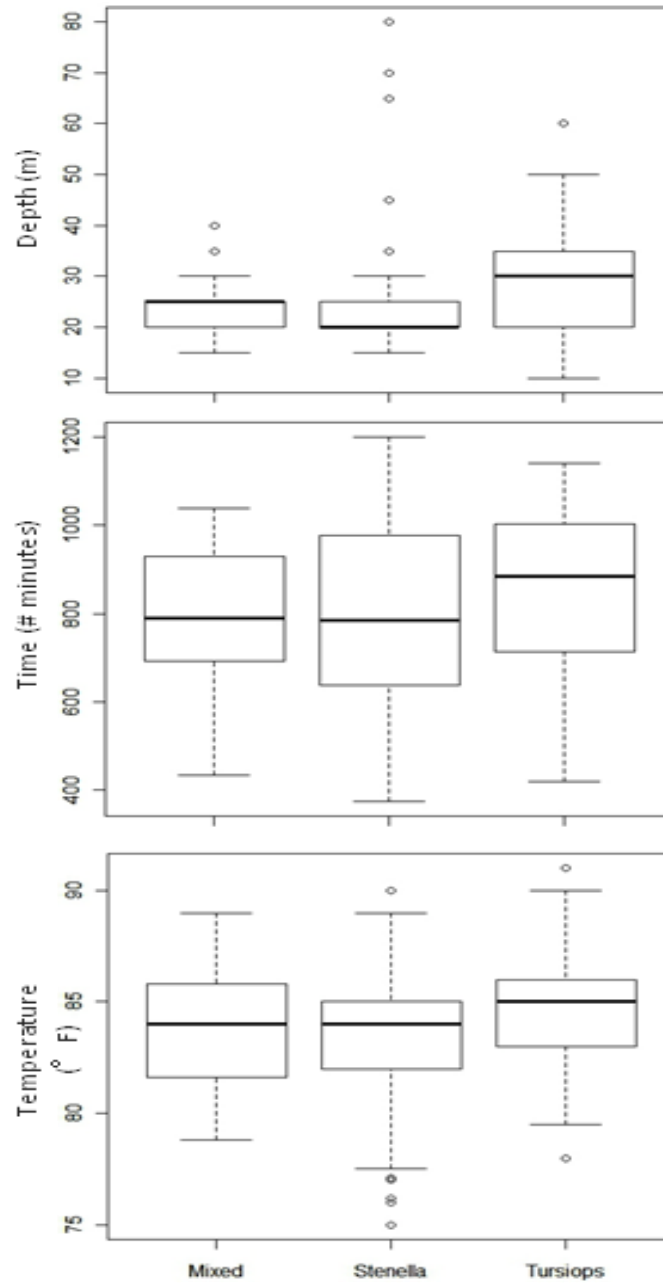


Figure 6. Frequency distribution of foraging *T. truncatus*, *S. frontalis*, and mixed species groups over major bottom types. Total sample size is 417 (*T. truncatus*=95; *S. frontalis*=260; mixed species=62).

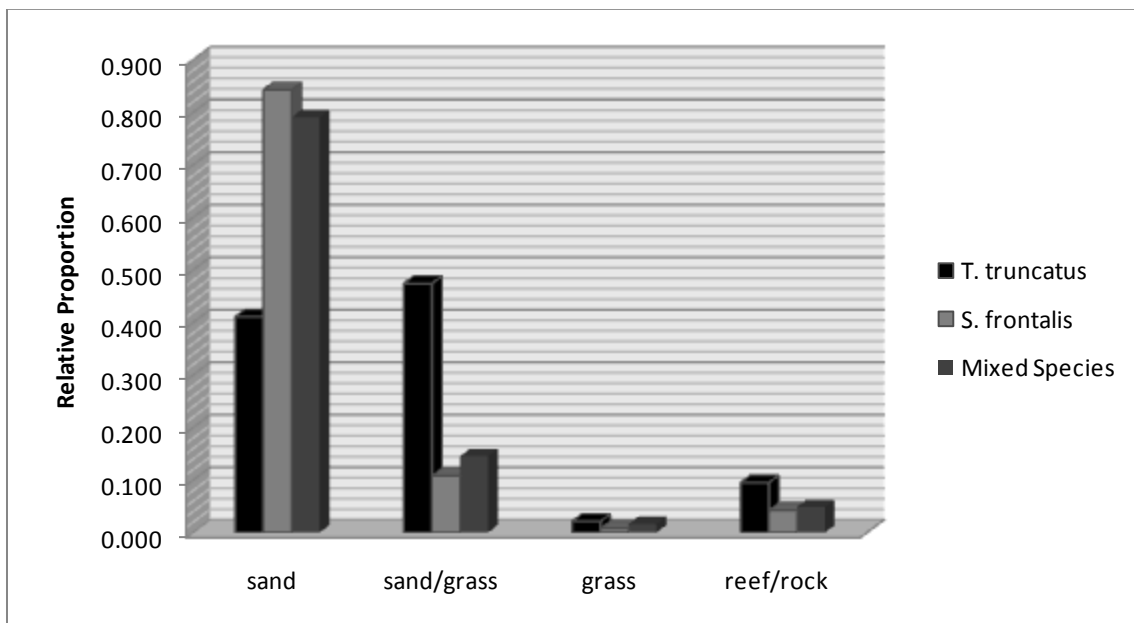


Figure 7. Pie charts displaying differences in frequency and diversity of prey selected by *S. frontalis* and *T. truncatus* during recorded foraging events.

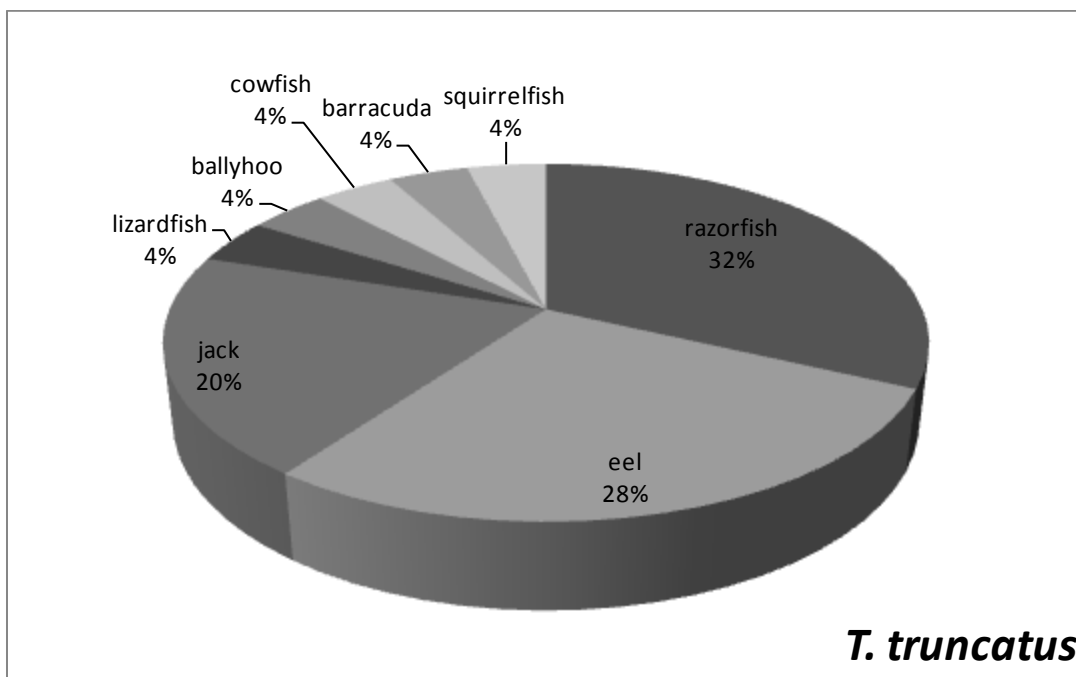
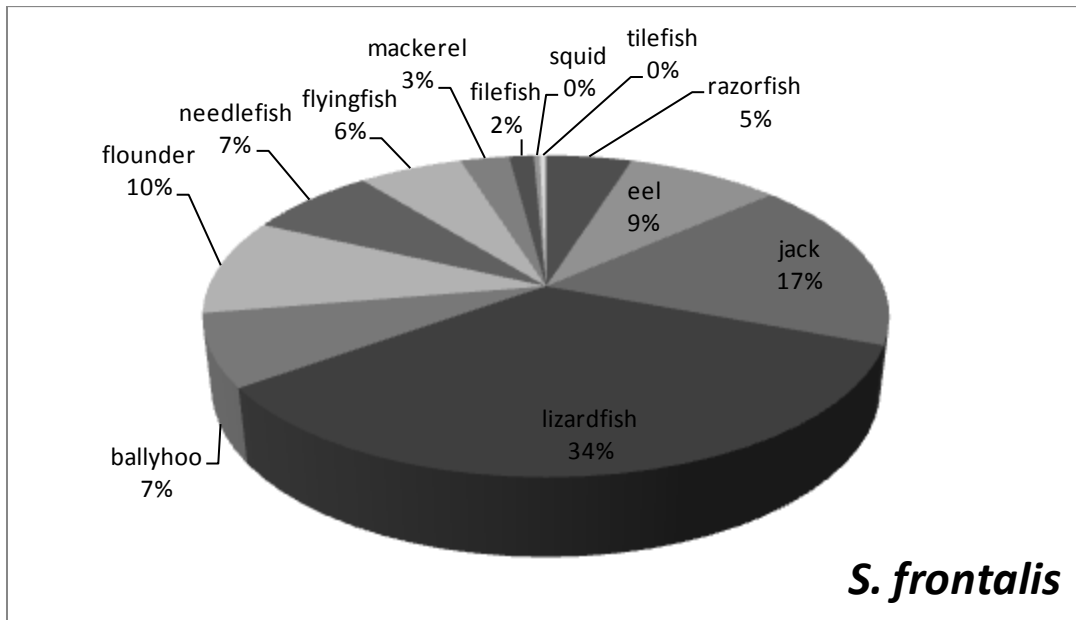


Figure 8. Box plot depicting differences in group size of *S. frontalis* and *T. truncatus*. Boxes range from 25th to 75th percentiles; solid lines represent the 50th percentile median value; extreme values are found at the end of the whiskers; and open circles represent 5th and 95th percentile outliers.

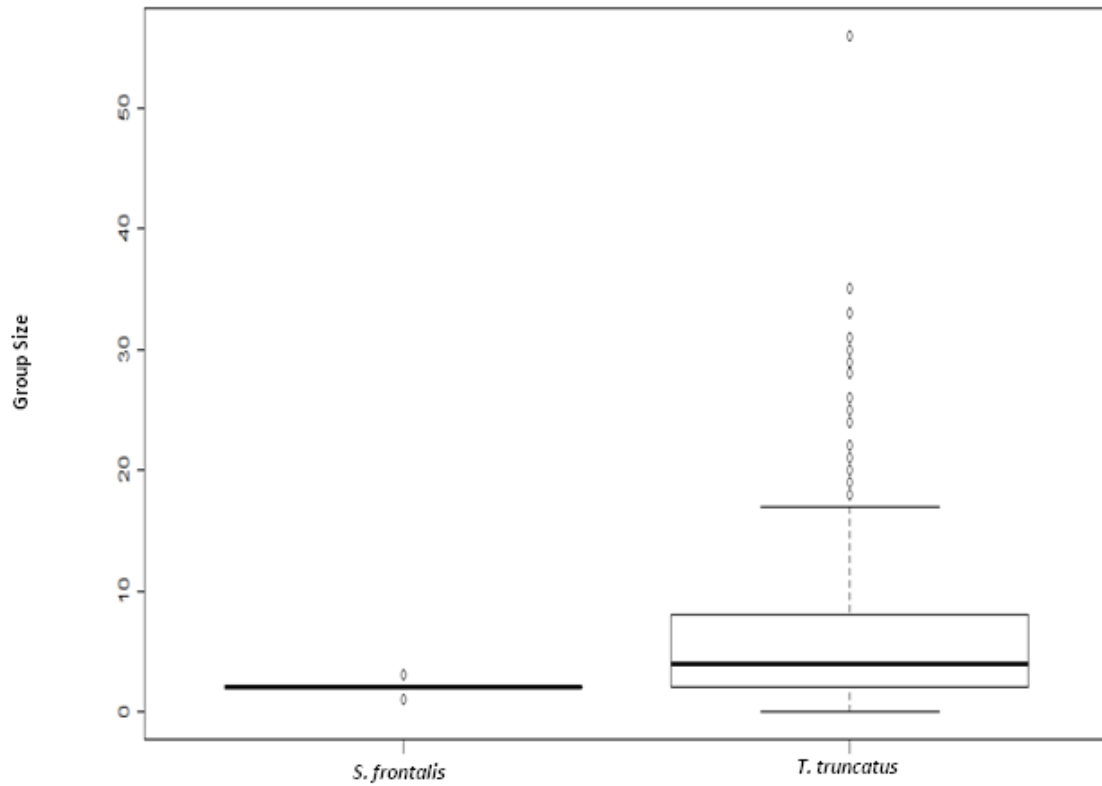


Figure 9. *S. frontalis* prey use comparison of relative frequency between foraging female reproductive groups (Lac = lactating, Preg = pregnant, and NRA = non-reproductively active).

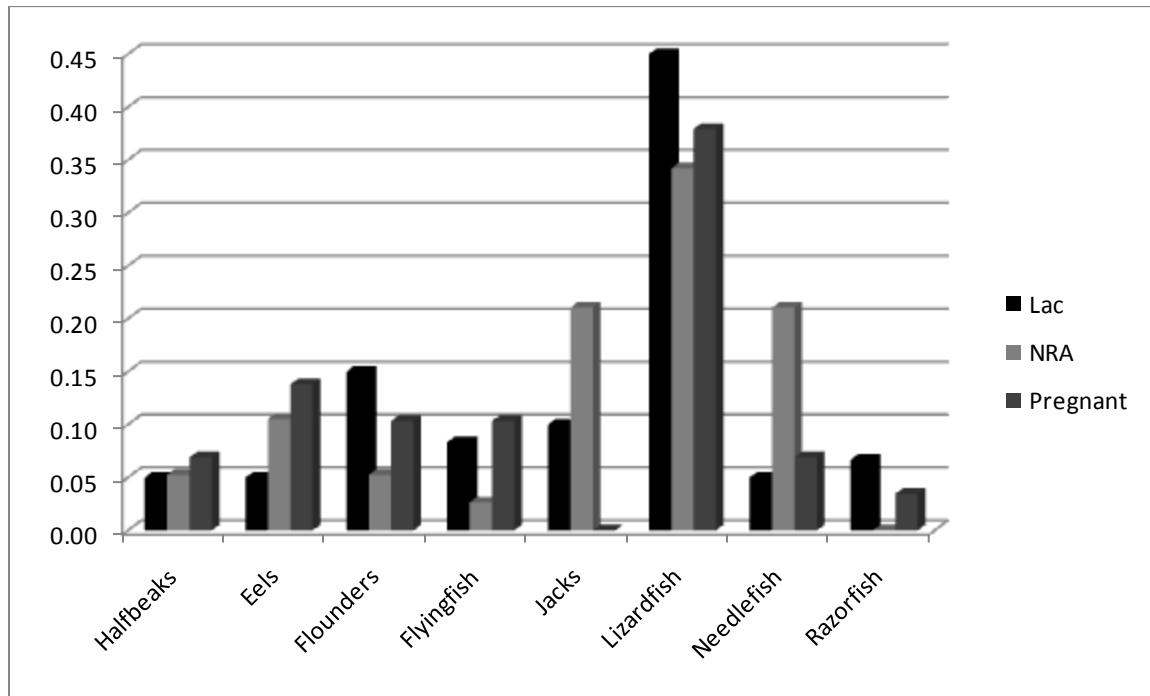


Figure 10. Pie charts displaying differences in frequency and diversity of prey selected by *S. frontalis* during recorded foraging events (a) Calves (Age 1), (b) Calves (Ages 2-6), (c) All Age Calves (1-6), and (d) Non-calves (only adults and juveniles).

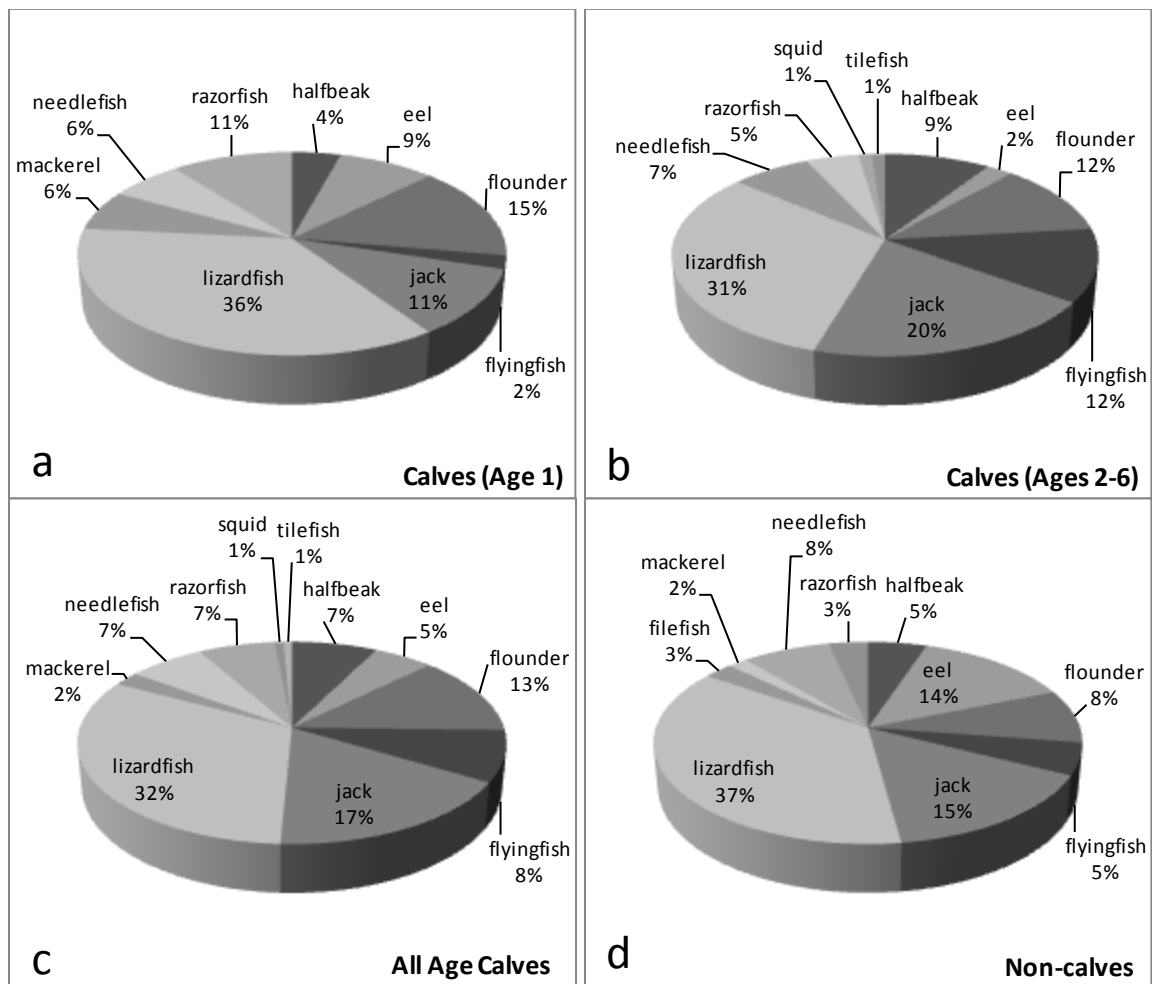


Figure 11. Pie charts displaying differences in frequency and diversity of prey selected by *S. frontalis* mother/calf pairs (m/c pair) and foraging by all groups with the exclusion of mother/calf pairs (No m/c pair).

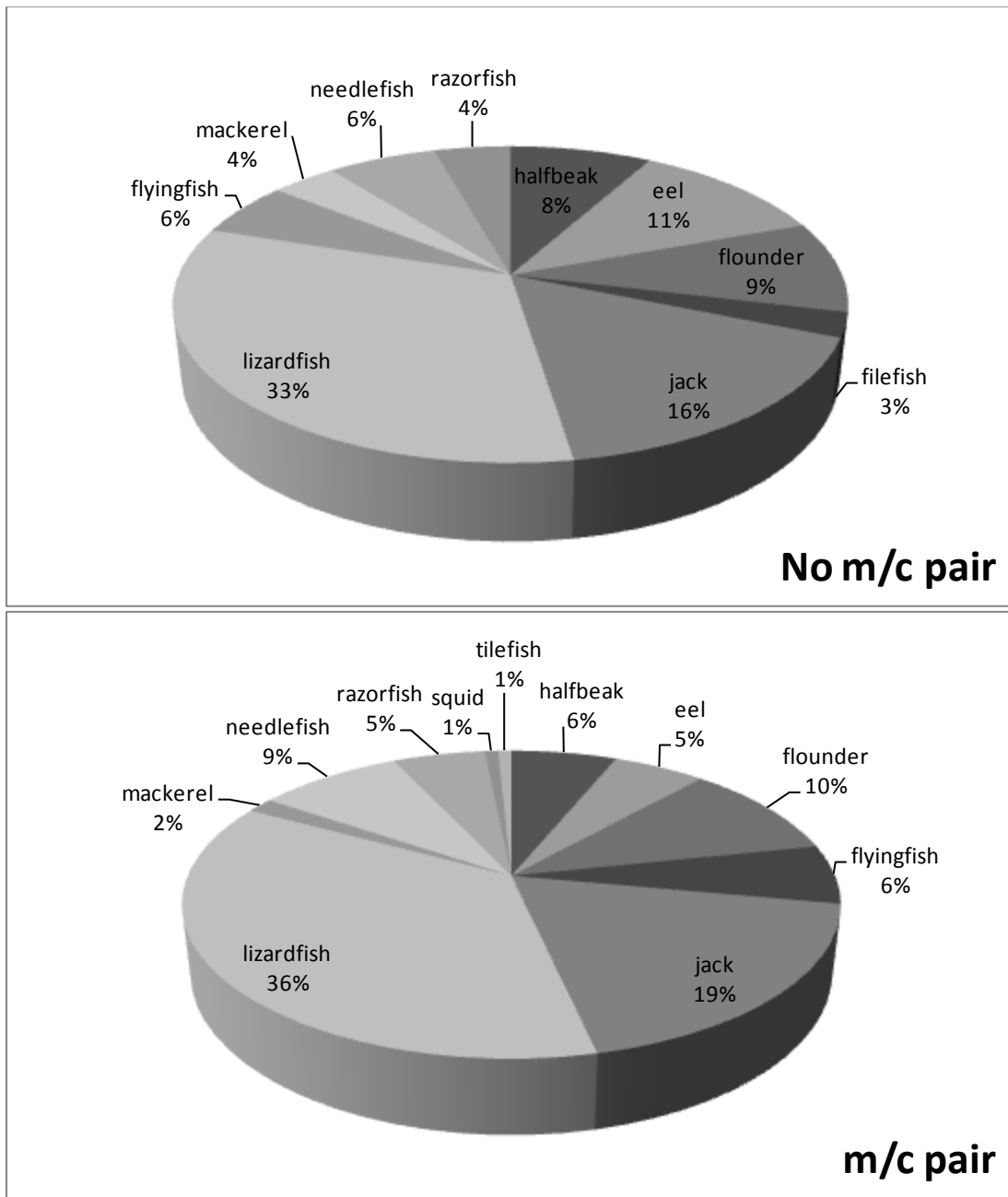


Figure 12. Pie charts displaying differences in frequency and diversity of prey selected by *S. frontalis* males and females.

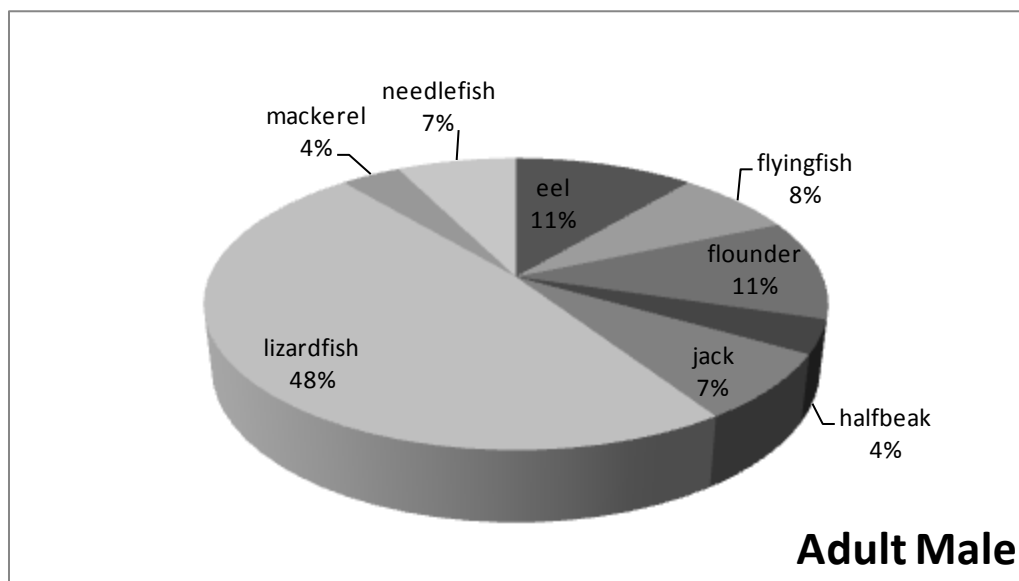
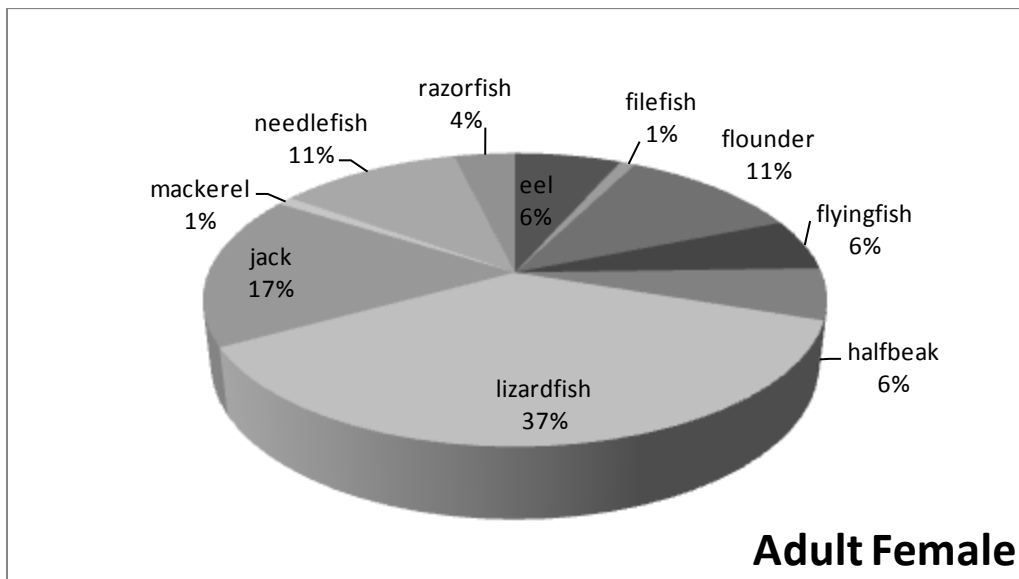
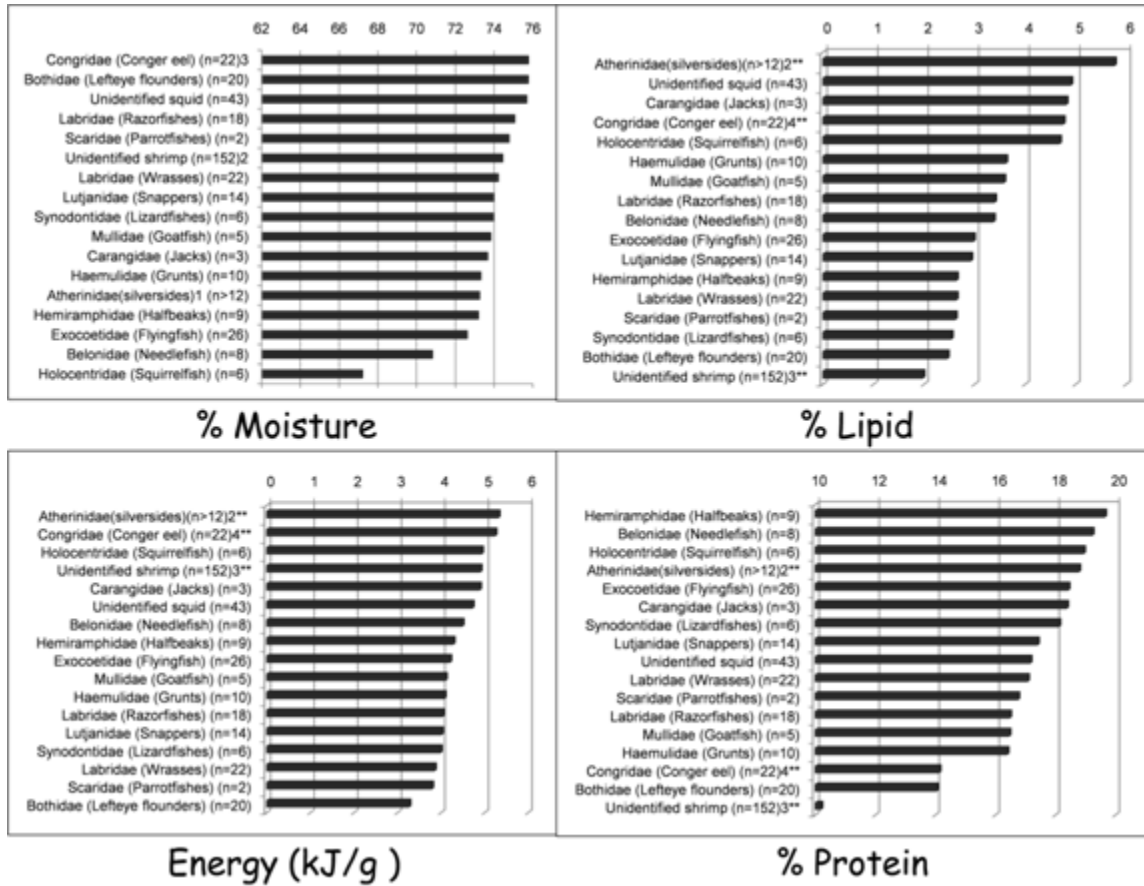
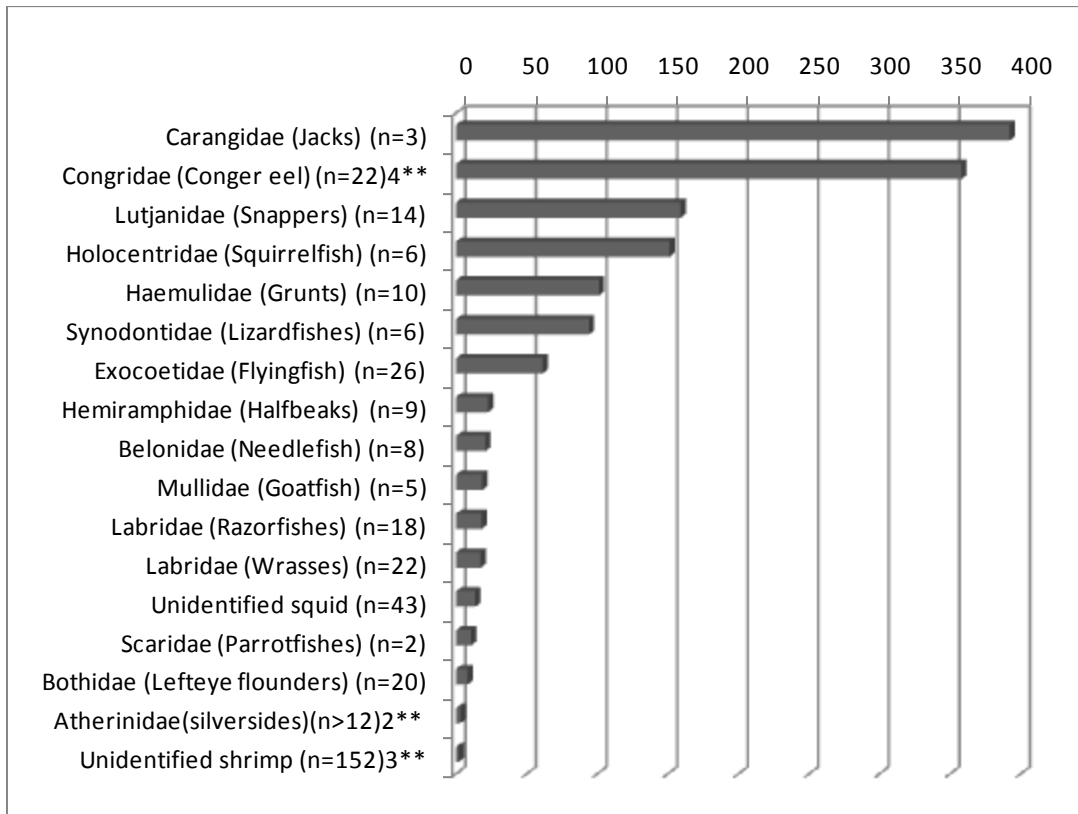


Figure 13. Nutritional value ([a] % moisture, [b] % lipid, [c] energy, and [b] % protein) comparison between dolphin known and potential prey species collected off Little Bahama Bank.



“***” represents prey values obtained from literature: (2**) *Atherinidae* (silversides) (Bouriga et al., 2010); (3**) Unidentified shrimp (Donnelly et al., 1993); (4**) *Congridae* (Conger eel) (E.B. Eder, pers. comm).

Figure 14. Wet weight (g) comparison between dolphin known and potential prey species collected off Little Bahama Bank.



Wet Weight (g)

“***” represents prey values obtained from literature: (2**) *Atherinidae* (silversides) (Bouriga et al., 2010); (3**) Unidentified shrimp (Donnelly et al., 1993); (4**) *Congridae* (Conger eel) (E.B. Eder, pers. comm.)

Figure 15. Comparison of relative nutrient content in the diet of each foraging group (Preg = pregnant; Lac = lactating; NRA = non-reproductively active female) as a measure of (a) ([mean nutrient content per gram of tissue for individual prey] x [frequency of each prey in diet]/[total number of foraging events]); and (b) [relative nutrient content in diet] x [mean wet weight (g) of all individual prey samples].

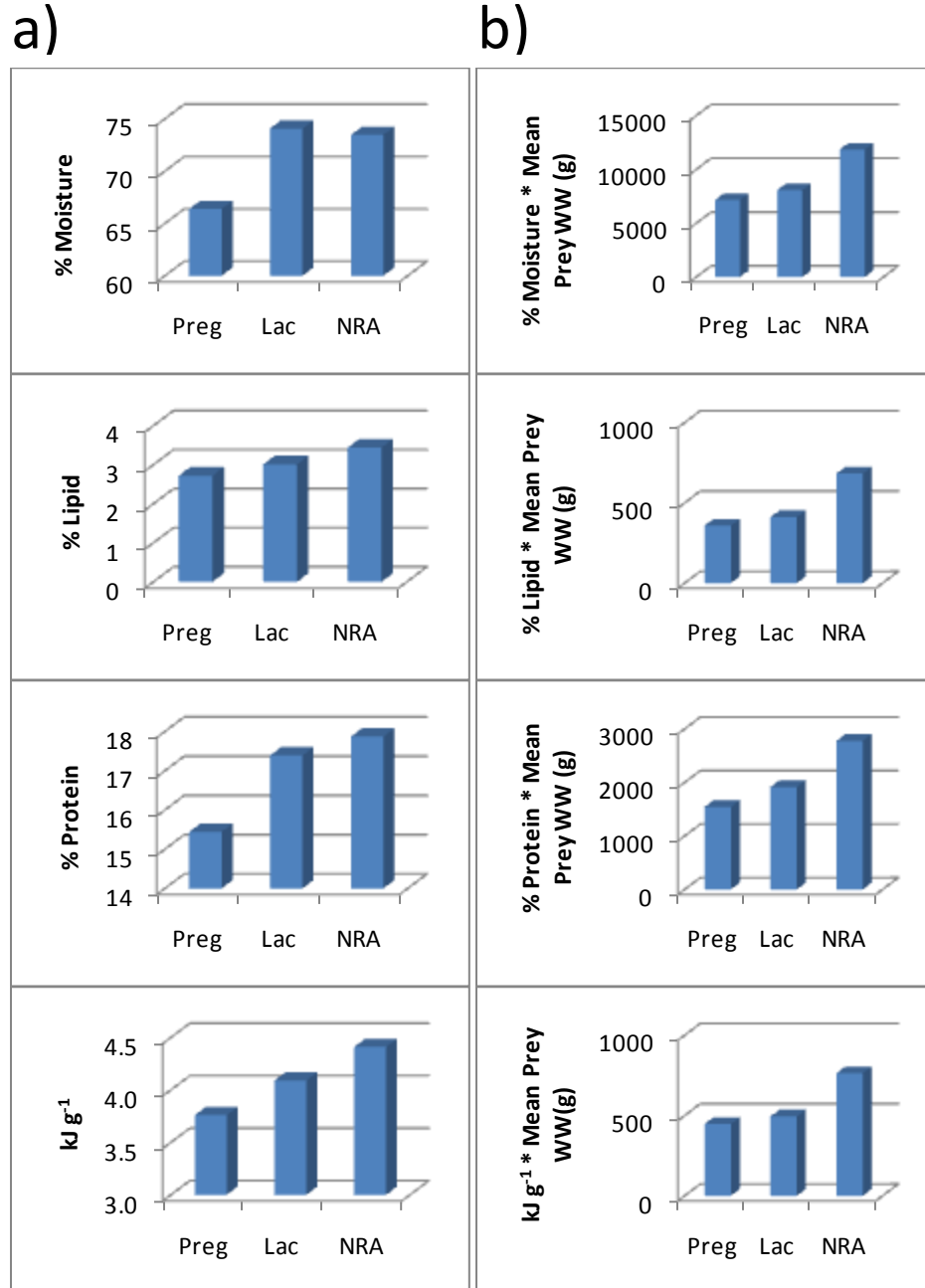


Figure 16. Comparison of relative nutrient content in the diet of each foraging group [Calves (Ages 2-6); Calves (Age 1); All Age Calves (1-6); Non-Calves (juveniles and adults)] as a measure of (a) $[(\text{mean nutrient content per gram of tissue for individual prey}) \times (\text{frequency of each individual prey in diet}) / (\text{total number of foraging events})]$; and (b) $[\text{relative nutrient content in diet}] \times [\text{mean wet weight (g) of all individual prey samples}]$.

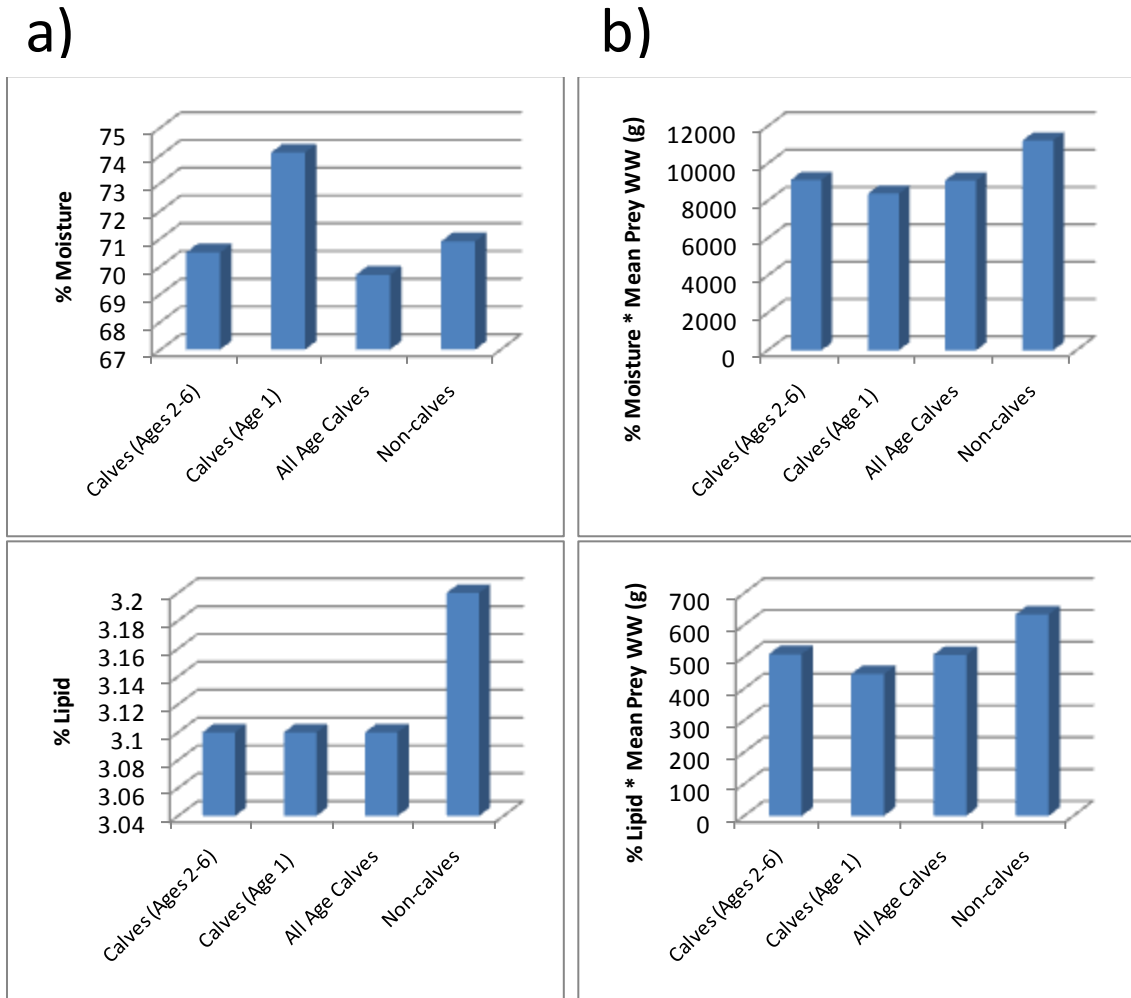
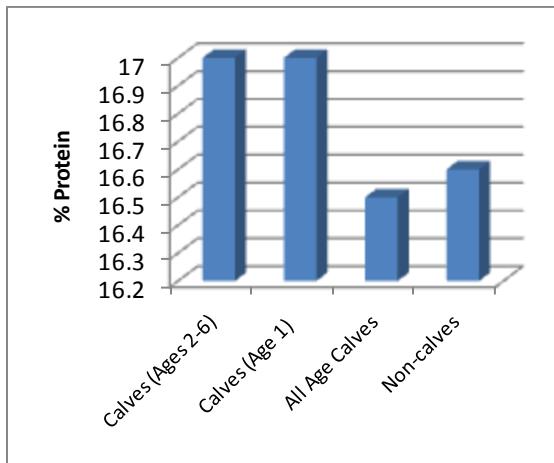


Figure 16. Continued.

a)



b)

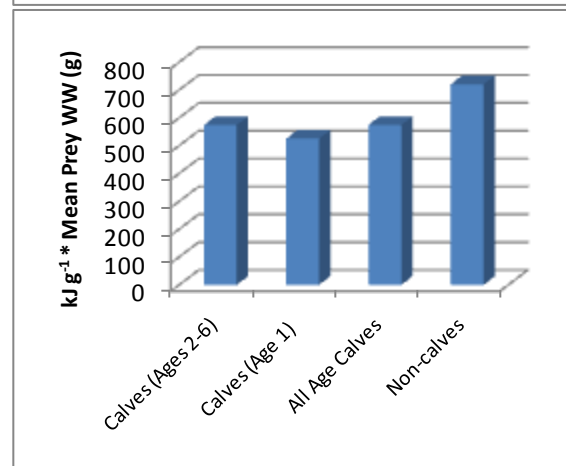
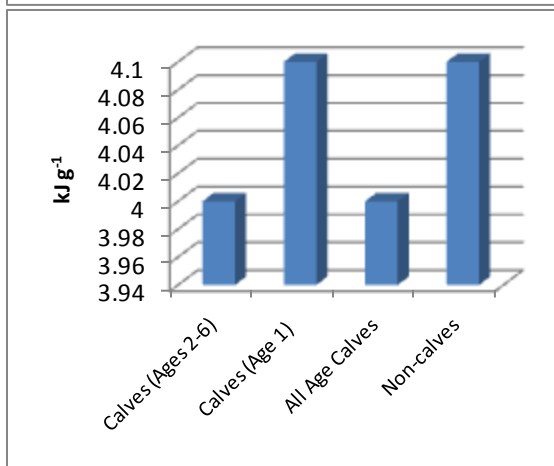
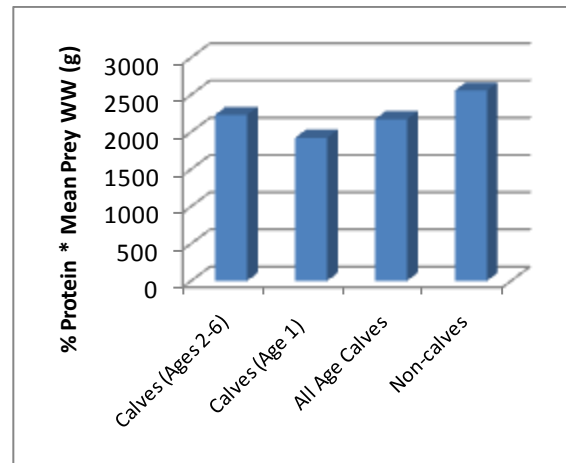


Figure 17. Comparison of relative nutrient content in the diet of each foraging group [no m/c (mother/calf); m/c pair] as a measure of (a) $[(\text{mean nutrient content per gram of tissue for individual prey}) \times (\text{frequency of each individual prey in diet}) / (\text{total number of foraging events})]$; and (b) $[\text{relative nutrient content in diet}] \times [\text{mean wet weight (g) of all individual prey samples}]$.

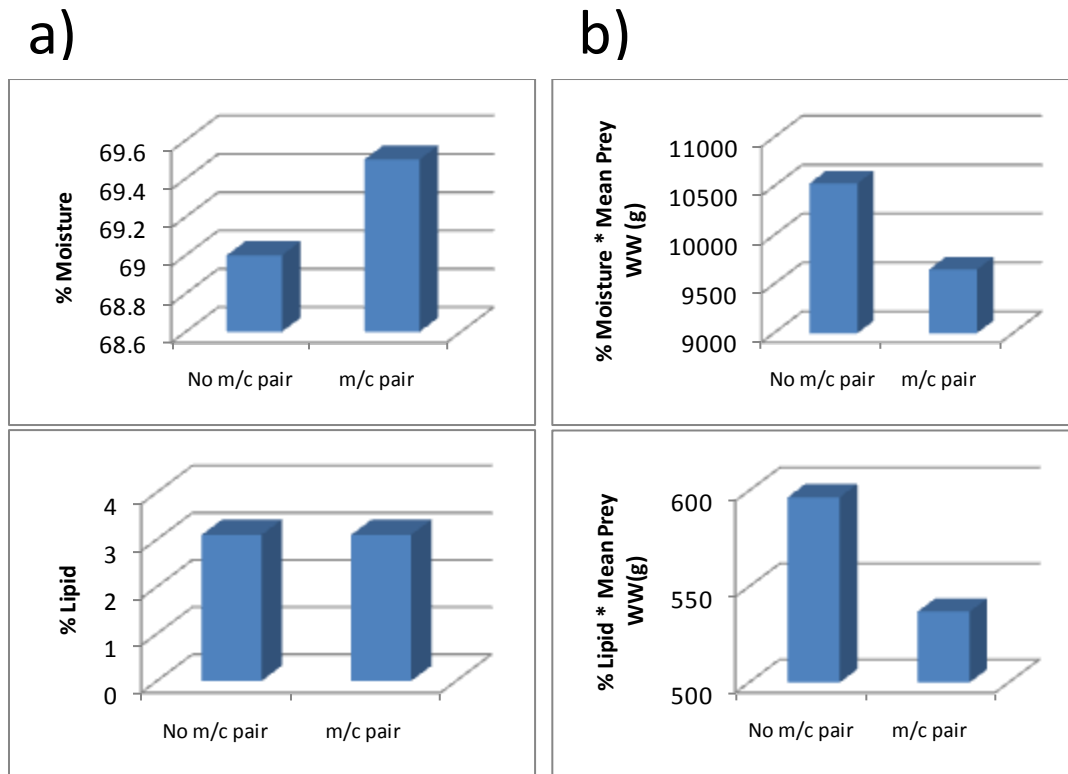
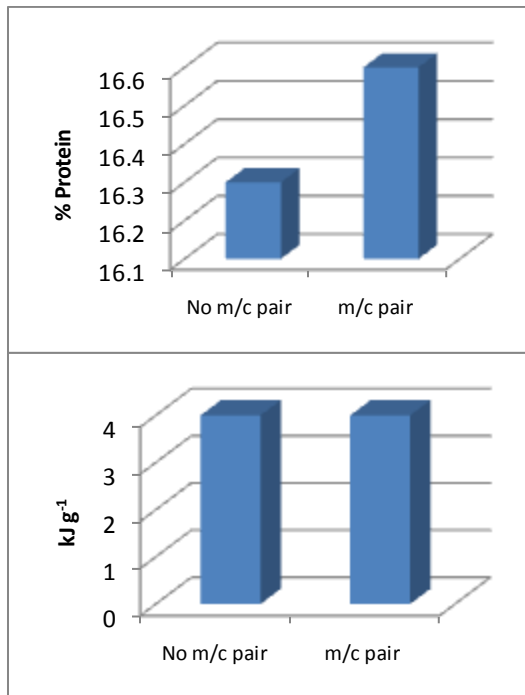
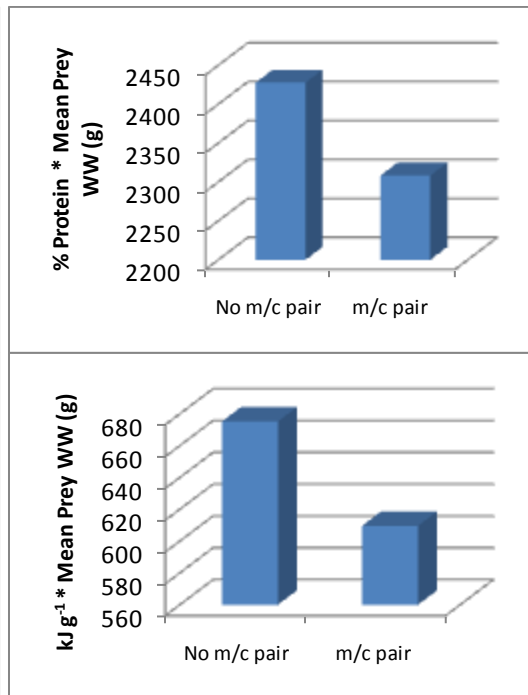


Figure 17. Continued.

a)



b)



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