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Foraging habits in a generalist predator: Sex and age influence habitat selection and resource use among bottlenose dolphins (*Tursiops truncatus*)

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ABSTRACT

This study examines resource use (diet, habitat use, and trophic level) within and among demographic groups (males, females, and juveniles) of bottlenose dolphins (*Tursiops truncatus*). We analyzed the $\delta^{13}C$ and $\delta^{15}N$ values of 15 prey species constituting 84% of the species found in stomach contents. We used these data to establish a trophic enrichment factor (TEF) to inform dietary analysis using a Bayesian isotope mixing model. We document a TEF of 0‰ and 2.0‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. The dietary results showed that all demographic groups relied heavily on low trophic level seagrass-associated prey. Bayesian standard ellipse areas (SEA_b) were calculated to assess diversity in resource use. The SEA_b of females was nearly four times larger than that of males indicating varied resource use, likely a consequence of small home ranges and habitat specialization. Juveniles possessed an intermediate SEA_b, generally feeding at a lower trophic level compared to females, potentially an effect of natal philopatry and immature foraging skills. The small SEA_b of males reflects a high degree of specialization on seagrass associated prey. Patterns in resource use by the demographic groups are likely linked to differences in the relative importance of social and ecological factors.

Key words: bottlenose dolphin, *Tursiops truncatus*, stable isotopes, foraging ecology, habitat use, diet, individual specialization, generalist, Sarasota Bay.

The use of particular food resources or habitats by members of a population impacts the intensity of intraspecific competition, social interactions, and risk of predation or parasitism (Bolnick *et al.* 2003). Further, a wealth of recent literature documents that ecological inequality within a population results in differential use of the total resource pool (*e.g.*, habitat or prey type) by individuals or assemblages within

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that population (Bolnick *et al.* 2003, Newsome *et al.* 2009, Torres and Read 2009). Such intraspecific variation in resource use can confer both benefit and detriment to the long-term viability of a population. For example, differential habitat use among assemblages within a population can result in increased population viability amid the loss of a specific habitat type (Tyler and Rose 1994). However, loss of a habitat upon which all or most juveniles are dependent would likely result in population decline, emphasizing the importance of studying variation in resource use among demographic groups (Dahlgren *et al*. 2006). The impact on certain demographic groups, and thus population viability, is of particular concern for wildlife populations in close proximity to human development because resources within these communities are more likely to experience disturbance (*e.g.*, habitat loss, competition with humans for resources). Marine mammals are of particular interest as they are large predators that often inhabit metropolitan coastal areas where habitats have undergone degradation and increased fishing pressure.

The bottlenose dolphins (*Tursiops truncatus*) of Sarasota Bay (SB), Florida, represent a model system to study patterns in resource use within and between demographic groups. SB dolphins are year-round, multigenerational residents that have been intensively studied for nearly five decades (Wells *et al.* 1987; Wells 2003, 2014). Previous stomach content studies of stranded deceased dolphins from the SB population (Barros and Wells 1998, Berens McCabe *et al.* 2010) provide estimates of diet that reflect recently ingested prey. Additionally, dolphin foraging has been assessed using molecular prey detection on fecal samples (Dunshea *et al.* 2013). Unlike stomach content analysis, molecular prey detection is not limited to salvaged individuals. However, the time period represented by the molecular data is similarly short. Together stomach content data and molecular prey detection are excellent indicators of the prey species commonly consumed by SB bottlenose dolphins. Yet, to date, there is no information on potential differences in resource use among demographic groups within the long-term resident community.

Carbon and nitrogen stable isotope analysis of bottlenose dolphin tissues complements stomach content and molecular techniques by providing information on habitat use, trophic position, and diet over a long time period (half-life of months for skin and years for muscle) (Newsome *et al.* 2010). The foraging habits of a large number of individuals can be obtained because, in addition to tissues from salvaged animals, analysis can be conducted on biopsies from extant members of the population. Unique types of information can be derived from stable isotope data. Carbon isotope values ($\delta^{13}C$) are indicators of primary production at the base of the food web. $\delta^{13}C$ values differentiate seagrass from phytoplankton and nonseagrass habitat (mangrove and open bay) (Peterson and Fry 1987). For Sarasota Bay bottlenose dolphins, high $\delta^{13}C$ values indicate frequent foraging in seagrass habitat (Rossman *et al.* 2013). Nitrogen isotope values ($\delta^{15}N$) generally increase by 3‰–4‰ with each step in the food chain, offering a good indicator of trophic level (Peterson and Fry 1987); although, recent studies indicate trophic dynamics may be lower for high trophic level organisms (Hussey *et al*. 2014). The information provided by stable isotope analysis is particularly valuable for cryptic foragers such as bottlenose dolphins who capture and consume prey underwater. Because of the ecological information derived from stable isotope approaches, mass-balance models using multiple isotopes are well established tools for determining the relative contribution of various prey sources to a population's diet (Harrigan *et al*. 1989, Phillips *et al*. 2005).

Recently, dietary assessments using stable isotopes have been advanced *via* the development of Bayesian mass balance models. By incorporating variability in prey

and consumer isotope values, Bayesian diet modeling programs, such as Stable Isotope Analysis in R (SIAR) (Jackson *et al.* 2011) have a unique advantage over earlier mass balance models (Harrigan *et al*. 1989, Phillips *et al*. 2005). Unlike the earlier models that report the fractional contribution of prey to the diet as a range, Bayesian models provide a true probability distribution for each prey item (Parnell *et al*. 2010).

While SIAR provides an estimate of the average contribution of each prey item to the diet, the degree of variation within a population or demographic group is also an important descriptor of foraging ecology. Stable isotope Bayesian ellipses in R (SIBER) (Jackson *et al*. 2011) uses $\delta^{13}C$ and $\delta^{15}N$ values to construct ellipses that represent two dimensional equivalents of the standard deviation. While these ellipses were originally intended to compare isotopic variability among species within a community they can also be used to quantify variability within and between demographic groups and to infer differences in habitat use and trophic diversity.

In this study we assess resource use (diet, habitat use, and trophic level) among male, female, and juvenile bottlenose dolphins (demographic groups). We first compare diet among the groups using stable isotope-based Bayesian dietary estimation. We then compare variation in resource use among the groups *via* stable isotope Bayesian standard ellipses. These tools provide important insight into a cryptic forager and the manner in which the unique ecology of the demographic groups relates to resource use at the population level.

Methods

SB is a complex series of shallow bays (<4 m deep, 40 km long) on the central west coast of Florida, communicating with the Gulf of Mexico through narrow, deep passes separating a series of narrow barrier islands. The study area encompasses a diverse array of habitats, including seagrass meadows, mangrove fringing forests, human-altered shorelines, and open bay (Rossman *et al.* 2013). Fish commonly found in the diet of bottlenose dolphins were collected for isotopic analysis during fish abundance surveys 2009–2012 (Table 1) (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013). In total, 15 species and 234 individual samples were processed for isotope analysis. Sampling targeted fish between 100 and 300 mm, the size range most often found in stomach contents of bottlenose dolphins (Barros and Wells 1998). Bottlenose dolphin skin samples were obtained from a community of *ca.* 160 individuals, mostly of known age and sex that are resident to SB (Wells 2003, 2009). Skin samples were taken during health assessments when dolphins were briefly captured, biopsied, and released (Wells *et al*. 2004). In the field, tissues were stored in liquid nitrogen and retained frozen prior to analysis. Isotope values for bottlenose dolphin muscle tissue used to determine the trophic enrichment factor (TEF) were taken from Rossman *et al.* (2013). Because muscle data derive from stranded, deceased dolphins it is independent from the skin samples used for diet estimation in SIAR.

Sample Preparation

White muscle tissue from fish and bottlenose dolphin skin were freeze-dried, lipid extracted, and homogenized to a fine powder in a high-energy ball mill (SPEX SamplePrep) and a 1 mg aliquot of homogenate was transferred to tin capsules for stable carbon and nitrogen isotope analysis. Isotope values were determined using an

Table 1. Bottlenose dolphin prey species $\delta^{13}C$ and $\delta^{15}N$ values (means ± standard deviation), the number of samples used to determine the average isotope value (*n*) dietary indicators, SCA and DNA and prey cluster designation. SCA and DNA are the fractional contribution of each species to the diet of bottlenose dolphins as determined by stomach content analysis or molecular prey detection (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013). Prey cluster refers to the cluster designation as determined by *k*-means cluster analysis. Asterisk indicates instances where Dunshea *et al.* 2013 report genus sp., the genus and species are provided here.

Species	Common name	$\delta^{13}C$	$\delta^{15}N$	*n*	SCA	DNA	Prey cluster
Elops saurus	ladyfish	−17.5 ± 1.6	11.7 ± 1.1	11	0.013*	0.059*	1
Centropomus undecimalis	snook	−16.1 ± 0.7	11.1 ± 1.0	3	0.024	0.020	1
Leiostomus xanthurus	spot	−16.7 ± 2.1	10.3 ± 1.4	24	0.029	0.085	1
Caranx hippos	crevalle jack	−15.5 ± 1.5	11.5 ± 0.5	4	0.012*	0.009*	2
Cynoscion nebulosus	spotted seatrout	−14.3 ± 1.7	11.5 ± 1.7	27	0.013*	0.0230*	2
Lutjanus synagris	lane snapper	−14.6 ± 1.1	8.7 ± 1.1	9	0.002*	0.000*	3
Gerreid sp.	mojarra	−13.8 ± 1.0	7.8 ± 0.7	16	0.006*	0.003*	3
Orthopristis chrysoptera	pigfish	−14.3 ± 0.9	9.3 ± 0.8	27	0.020	0.008	3
Sciaenops ocellatus	red drum	−14.1± 1.2	9.4 ± 0.8	4	0.002*	0.000*	3
Archosargus probatocephalus	sheepshead	−14.9 ± 1.6	9.0 ± 0.8	15	0.018	0.028	3
Opsanus beta	Gulf toadfish	−13.8 ± 1.1	8.7 ± 2.2	14	0.327*	0.110*	3
Mugil cephalus	striped mullet	−12.9 ± 1.6	9.9 ± 4.0	15	0.022	0.008	3
Lagodon rhomboides	pinfish (seagrass)	−13.7 ± 1.2	8.0 ± 1.3	27	0.309	0.456	3
Lagodon rhomboides	pinfish (non-seagrass)	−16.1 ± 1.2	9.0 ± 0.7	20			4
Opisthonema oglinum	threadfin herring	−17.5 ± 1.7	9.2 ± 0.4	11	0.039*	0.003*	4
Harengula jaguana	scaled sardine	−16.2 ± 2.2	9.4 ± 1.4	7	0.0001	NA	4
Total				234	0.836	0.812	

elemental analyzer (Eurovector) interfaced to an Isoprime mass spectrometer (Elementar). Isotope values are expressed as:

$$\delta X = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \times 1,000$$

where X represents ^{13}C or ^{15}N, and R represents the abundance ratios: $^{13}C/^{12}C$ or $^{15}N/^{14}N$ respectively. In-house standards used for $\delta^{13}C$ and $\delta^{15}N$ were calibrated with respect to international scales V-PDB and air respectively. In-house precision was 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values.

Statistical Analysis

To delineate factors impacting prey fish isotope values, we assessed the influence of standard length, habitat, season, and location on $\delta^{13}C$ and $\delta^{15}N$ values of each of five prey fish species whose sample size was sufficient for general linear modeling (GLM). These species included spot, *Leiostomus xanthurus*; spotted seatrout, *Cynoscion nebulosus;* pigfish, *Orthopristis chrysoptera*; pinfish, *Lagodon rhomboides*; and sheepshead, *Archosargus probatocephalus*. The variable habitat included three levels: seagrass, mangrove, and open bay. Tukey's HSD was used to test for pairwise differences in mean $\delta^{13}C$ or $\delta^{15}N$ value between habitats. For the variable "season," fish were grouped based on the calendar date of capture: spring (21 April–6 June), summer (21 June–20 September), fall (21 September–20 December), and winter (21 December–21 April). For the variable location, latitude and longitude were combined into a single variable *via* principal components analysis (PCA). The first PCA, retained for modeling efforts as the variable "location," explained 97% of the variation in latitude and longitude. All statistical analyses were conducted in R 3.0.1 (R Development Core Team 2013).

Bottlenose dolphin demographic groups were defined as follows: males (>6 yr of age), females (>6 yr of age), and juveniles (2–6 yr of age). Dolphins younger than 2 yr of age are not included in health assessments and, thus, not represented in this study. Nearly all calves leave their mothers around 6 yr of age, thus the age ranges for males and females (>6 yr of age) only reflect foraging by males and females independent from their mothers (Wells 1991). The package, Stable Isotope Analysis in R (SIAR) 4.2 (Parnell and Jackson 2013) was run within R 3.0.1 (R Development Core Team 2013) to provide dietary estimates for each bottlenose dolphin demographic group. SIAR requires isotope values for consumers, isotope values of prey species, and a TEF. Because SIAR cannot differentiate prey items with similar isotope values (Phillips *et al*. 2005), we used a *k*-means cluster analysis to group prey fish into four clusters. The resulting clusters differed by trophic level and/or source of primary production at the base of the food web. The TEF value used in this study was based on stomach content data, molecular prey detection, prey isotope values, and muscle isotope values of stranded deceased dolphins from SB. First, a weighted average $\delta^{13}C$ value of bottlenose dolphin diet was calculated as follows:

$$\delta^{13}C_d = \sum_{i=1}^{n} F_i \delta^{13}C_i$$

Where $\delta^{13}C_d$ is the average carbon isotope value of bottlenose dolphin diet, F_i is the fractional contribution of diet item i based on stomach content analysis or molecular

prey detection (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013), and $\delta^{13}C_i$ is the average carbon isotope value of diet item i as reported in this study. To determine the $\delta^{13}C$ TEF the isotope value of the bottlenose dolphin diet ($\delta^{13}C_d$) was subtracted from the average SB dolphin muscle $\delta^{13}C$ value (Rossman *et al.* 2013). The same method was then applied to determine the TEF for $\delta^{15}N$. With only two TEF values we could not provide an estimate of variance associated with trophic fractionation which was assumed to be negligible compared to other sources of isotopic variation. Because the TEF derives from isotope values of bottlenose dolphin muscle and the dietary estimates used isotope values of skin, the TEF determination was independent of data used in Bayesian dietary estimation.

Stable isotope Bayesian ellipses in R (SIBER) including standard ellipse areas were produced using SIAR (Jackson *et al.* 2011). To test for significant differences we ran 100,000 Markov-chain Monte Carlo iterations for SEA_b and constructed 95% credible intervals around the mean of each subgroup. The probability that there was a significant difference in SEA_b between demographic groups was determined by calculating the proportion of times the posterior estimate for one demographic group was smaller than another (Turner *et al.* 2010). We considered the two SEA_b to be significantly different when no more than 5% of the posterior estimates for one group were smaller than those of another group ($\alpha = 0.05$). For graphical representations we used standard ellipse areas controlled for small sample size (SEA_c).

Results

We assessed isotope values of prey species constituting 81% (stomach content analysis) or 84% (molecular prey detection) of bottlenose dolphin diet (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013). Species average $\delta^{13}C$ values ranged from −17.5‰ (ladyfish, *Elops saurus*, and threadfin herring, *Opisthonema oglimum*) to −12.9‰ (striped mullet, *Mugil cephalus*), and average $\delta^{15}N$ values ranged from 7.8‰ (mojarra, *Gerreid* sp.) to 11.7‰ (ladyfish) (Table 1). Habitat, length, season, and location did not significantly influence the isotope values of pigfish, spot, sheepshead, or spotted seatrout. Pinfish $\delta^{13}C$ values were significantly related to habitat and location ($F_{2, 42} = 36.09$, $P < 0.001$, $F_{1, 42} = 5.20$, $P = 0.028$, respectively). $\delta^{13}C$ values decreased from northwest to southeast and from seagrass (mean standard deviation: −13.7‰ 1.2‰) to open bay (−15.5‰ 1.0‰) to mangrove habitat (−17.1‰ 1.0‰) (seagrass *vs.* open bay: $P < 0.001$, seagrass *vs.* mangrove: $P < 0.001$, mangrove *vs.* seagrass: $P < 0.001$). Length and season did not appear to influence pinfish $\delta^{13}C$ values. Pinfish $\delta^{15}N$ values demonstrated a significant relationship with habitat and length ($F_{2, 42} = 6.43$, $P = 0.004$, $F_{1, 42} = 5.80$, $P = 0.021$, respectively) but not location or season. $\delta^{15}N$ values of pinfish increased with length and were higher in open bay *vs.* seagrass habitat (9.3‰ 0.5‰ *vs.* 8.0‰ 1.3‰, $P = 0.003$). $\delta^{15}N$ values from mangrove pinfish (8.6‰ 0.7‰) did not significantly differ from those of seagrass or open bay.

The *k*-means cluster analysis of prey fish isotope values combined fish species that shared a common food web base ($\delta^{13}C$ values) and trophic level ($\delta^{15}N$ values) (Fig. 1). High $\delta^{13}C$ values are indicative of seagrass based food webs (*e.g.*, seagrass grazing pinfish, −13.7‰) and low $\delta^{13}C$ values are associated with open bay and mangrove primary production (*e.g.*, clupeids whose food web is generally phytoplankton based: threadfin herring, −17.5‰, scaled sardine, *Harengula jaguana*, −16.2‰). Cluster 1, contained high trophic level nonseagrass prey and included snook (*Centropomus*

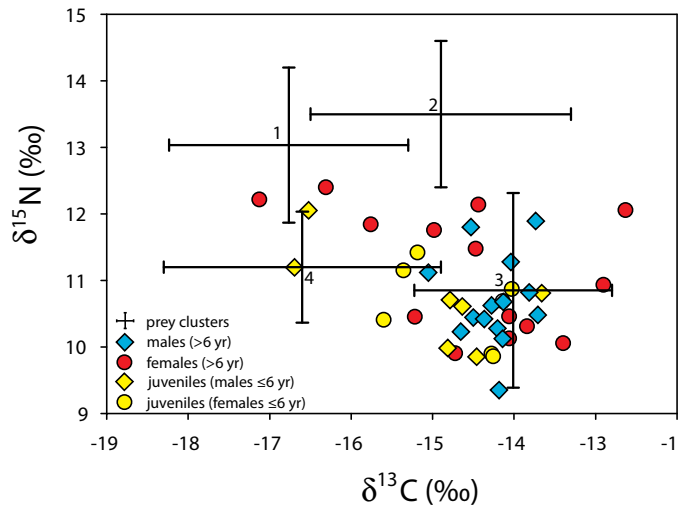


Figure 1. $\delta^{13}C$ and $\delta^{15}N$ values of prey clusters and bottlenose dolphin skin from different demographic groups including males (>6 yr old), females (>6 yr old), and juveniles (2–6 yr old). Prey clusters show mean with error bars depicting the standard deviation. Prey clusters were adjusted for trophic enrichment (cluster average + TEF). TEF estimates derive from this study ($\delta^{13}C$: 0.0‰, $\delta^{15}N$: 2.0‰), not the literature.

undecimalis), ladyfish, and spot. Cluster 2 consisted of high trophic level prey associated with seagrass and consisted of seatrout and crevalle jack (*Caranx hippos*). Cluster 3 included low trophic level, seagrass-associated species and consisted of Gulf toadfish (*Opsanus beta*), seagrass pinfish, pigfish, red drum (*Sciaenops ocellatus*), lane snapper (*Lutjanus synagris*), sheepshead, mojarra, and striped mullet. Cluster 4 contained low trophic level nonseagrass associated prey and consisted of threadfin herring, nonseagrass pinfish, and scaled sardine. Because pinfish isotope values significantly differed between habitats, pinfish were separated by habitat prior to the cluster analysis. This resulted in cluster 3 containing seagrass pinfish and cluster 4 containing nonseagrass pinfish with low $\delta^{13}C$ values (open bay and mangrove). The mean isotope values and associated standard deviation for all species within a cluster were used to estimate cluster averages and standard deviation, which were implemented as sources in the Bayesian dietary estimation.

The weighted average $\delta^{13}C$ and $\delta^{15}N$ of SB bottlenose dolphin diet based on the relative contribution of prey from stomach content analysis or molecular prey detection was −14.2‰ and 8.9‰ and −14.5‰ and 8.9‰, respectively (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013). Given the average isotope value for bottlenose dolphin muscle (−14.4‰ and 10.8‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) the TEF estimate based on stomach content analysis was −0.1‰ for $\delta^{13}C$ and 2.0‰ for $\delta^{15}N$. The TEF estimate based on molecular prey detection was 0.1‰ for $\delta^{13}C$ and 2.0‰ for $\delta^{15}N$. The TEF used in this study was an average of the two values: 0.0‰ for $\delta^{13}C$ and 2.0‰ for $\delta^{15}N$.

The mean skin isotope values, reported as mean standard deviation, for the three demographic groups were similar to one another: juveniles ($\delta^{13}C$ = −14.9‰ 0.9‰, $\delta^{15}N$ = 10.6‰ 0.6‰, n = 14), females ($\delta^{13}C$ = −14.6‰ 1.3‰, $\delta^{15}N$ =

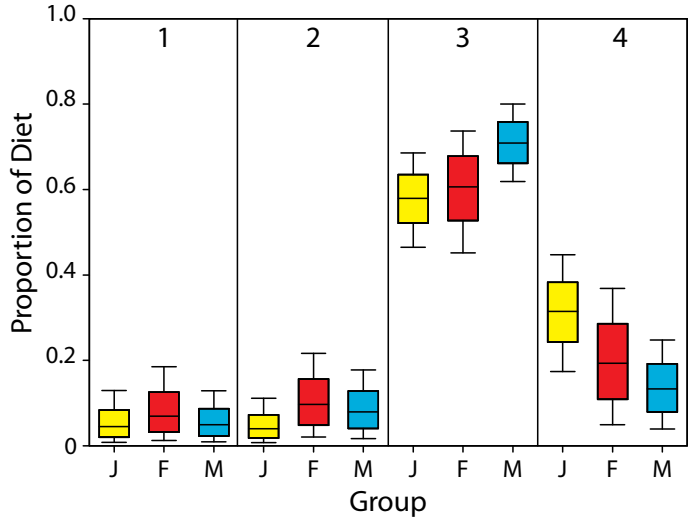


Figure 2. SIAR results for bottlenose dolphin demographic groups: juveniles (J; 2–6 yr old males and females), females (F; >6 yr old), and males (M; >6 yr old). Horizontal lines within boxes represent mean dietary contributions of each prey cluster to the demographic group. Boxes enclose the 50% credible interval and vertical lines with end caps depicting the 95% credible interval. Cluster 1, contains snook, ladyfish, and spot. Cluster 2 contains seatrout and crevalle jack. Cluster 3 contains toadfish, seagrass pinfish, pigfish, red drum, lane snapper, sheepshead, mojarra, and striped mullet. Cluster 4 contains nonseagrass prey fish, threadfin herring, nonseagrass pinfish, and scaled sardine.

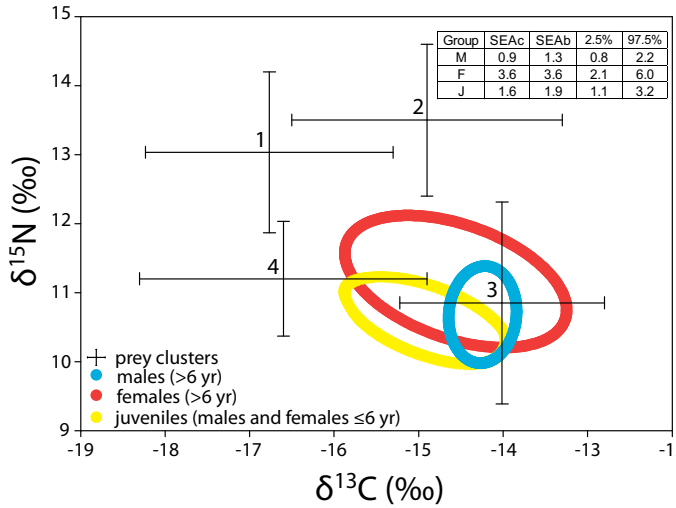
11.2‰ 0.9‰, n = 14) and males (δ^{13}C = -14.2‰ 0.4‰, δ^{15}N = 10.7‰ 0.7‰, n = 14) (Fig. 1).

The results of the Bayesian mass balance model, given as mean standard deviation, showed that juveniles consumed prey cluster 3 in the highest proportion (0.58 0.09) (Fig. 2) followed by cluster 4 (0.31 0.11), cluster 1 (0.06 0.05), and cluster 2 (0.05 0.05). Females consumed cluster 3 in the highest proportion (0.60 0.11), followed by cluster 4 (0.20 0.12), cluster 2 (0.11 0.08), and cluster 1 (0.09 0.07). Males consumed prey cluster 3 in the highest proportion (0.71 0.07) followed by cluster 4 (0.14 0.08), cluster 2 (0.09 0.06), and cluster 1 (0.06 0.05).

Females had the largest SEA_b at 3.59‰^{2} (95% CI: 2.15‰^{2}–6.00‰^{2}) followed by juveniles at 1.93‰^{2} (95% CI: 1.10‰^{2}–3.21‰^{2}), and males at 1.29‰^{2} (95% CI: 0.77‰^{2}–2.14‰^{2}) (Fig. 3). The SEA_b of males was significantly smaller than that of females (P = 0.003) but not juveniles (P = 0.144). The SEA_b of juveniles was significantly smaller compared to the SEA_b of females (P = 0.046). SEA_c was calculated for graphical representations of standard ellipse area (Fig.3).

Discussion

Male, female, and juvenile bottlenose dolphins possess unique combinations of ecological, physiological, and social constraints (Wells 2003, 2014), all of which may



Group	SEAc	SEAb	2.5%	97.5%
M	0.9	1.3	0.8	2.2
F	3.6	3.6	2.1	6.0
J	1.6	1.9	1.1	3.2

Figure 3. Carbon and nitrogen isotope values of prey clusters and standard ellipses controlled for small sample size (SEA_c) for female, male and juvenile bottlenose dolphins. The upper right inset table provides SEAc area (‰^{2}), mean Bayesian standard ellipse area (SEA_b) (‰^{2}), and the lower (2.5%) and upper (97.5%) bounds for the 95% credible interval around the mean SEA_b for males (M; >6 yr old), females (F; >6 yr old), and juveniles (J; 2–6 yr old).

impact how these different demographic groups find and consume prey. We probed differences in the foraging ecology of these three groups using stable isotope analysis and Bayesian modeling. Because our analyses included a large number of prey species (15) we performed cluster analysis to group prey. This resulted in ecologically significant clusters differentiated by source of primary production at the food web base and/or trophic level.

Our Bayesian mass balance modeling benefited from a TEF estimate that was, (1) based on prey data specific to the SB bottlenose dolphin food web, (2) independent of our skin isotope data used in SIAR, and (3) derived from two independent estimates of population diet, one based on stomach content analysis and the other on molecular prey detection (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013). In using the average isotope value of muscle to produce a TEF that was later applied to Bayesian modeling based on skin data, we assumed that the TEF of muscle and skin were similar. This assumption is consistent with the findings of Borrell *et al.* (2012) and Fernández *et al.* (2011), who documented identical average $\delta^{13}C$ and $\delta^{15}N$ values for skin and muscle from cetaceans. For SB bottlenose dolphins, the mean $\delta^{13}C$ and $\delta^{15}N$ isotope values of skin and muscle differed by <0.1‰.

The average TEF values calculated in this study were 0‰ for $\delta^{13}C$ and 2.0‰ for $\delta^{15}N$. While our $\delta^{15}N$ TEF is low compared to the often cited average of 3.4‰ (Post 2002), a growing body of literature documents widespread variability in TEF across and within taxa (McCutchan *et al.* 2003, Lecomte *et al.* 2011). Our values are in agreement with a low $\delta^{15}N$ TEF expected for a consumers with a high protein diet and who utilize marine environments (Vanderklift and Ponsard 2003).

Results from the Bayesian mass balance model indicate that all bottlenose dolphin demographic groups predominantly depend on low trophic level, seagrass-associated prey fish (prey cluster 3). Among the clusters, prey cluster 3 contains the largest number of species including both prey fish frequently small (*e.g.,* pinfish, pigfish, and mojarra) and more massive prey items (*e.g.,* mullet). Prey cluster 3 is likely the most important dolphin diet because seagrass serves as an excellent foraging habitat, supporting high densities of prey fish and providing safety from predators in SB (*e.g.*, bull sharks) (Barros and Wells 1998, Gannon *et al.* 2009, Mann *et al.* 2000, McHugh *et al*. 2011). Our findings are consistent with those of Barros and Wells (1998) documenting seagrass as an important habitat for bottlenose dolphins. In addition to prey cluster 3, juveniles, in particular, appeared to consume low trophic level, nonseagrass prey (cluster 4) to a larger extent than male or females. This may be related to physiological and behavioral constraints that are unique to juveniles. The acquisition of foraging skills by calves is likely a slow process; upon nutritional weaning (typically in second year of life), calves may not yet possess skills associated with complex foraging behavior typical of adults. For example, the detection and capture of prey species associated with structures (*e.g.,* Gulf toadfish) or fast-moving high trophic level fish may be too difficult for young dolphins (Berens McCabe *et al.* 2010). The small gape size of juveniles may work in conjunction with undeveloped foraging skills to constrain diet to small, easily detectable, low trophic level prey, such as all members of prey cluster 4 and pinfish, pigfish and mojarra in prey cluster 3. However, the finding that high trophic level prey were not a large contributor to the diet of any demographic group is consistent with the observation that high trophic level prey species occur in only low abundances and may be too energetically costly for consumption at the population level.

An increasing body of literature suggests that variation in resource use within and between individuals of a population is an important ecological parameter that has profound implications for conservation biology (Bolnick *et al.* 2003, Johnson *et al*. 2009). To assess variation in the foraging behavior between male, female, and juvenile bottlenose dolphins, we used SEA_b as a quantitative indicator of variation in resource use (Jackson *et al.* 2011). Male and female bottlenose dolphins appear widely divergent in their diversity of resource use. Males possess a significantly small SEA_b, nearly one fourth the size of the female SEA_b. The small SEA_b size indicates that differences in foraging habits among males are small. Even though most male bottlenose dolphins possess home ranges larger than those of females (Wells 2003, Urian *et al*. 2009) and have access to numerous habitat types, the position and small size of the male standard ellipse indicates a predominant reliance on seagrass-associated prey. This may occur because seagrass habitat has one of the highest densities of prey fish of any habitat (Gannon *et al.* 2009) often including numerous large prey species (*e.g.*, mullet), which generally provide more calories compared to smaller fish. Because gape size can be a constraint, the larger gape size of males offers an advantage. More importantly, consuming large prey allows males, relative to females and juveniles, to maximize their caloric intake while minimizing energy expenditure.

In contrast to the males, the large SEA_b of females indicates broader foraging habits. The large SEA_b predominately derives from the wide range of $\delta^{13}C$ values, an indicator of habitat use (*i.e.*, seagrass *vs*. open water). This suggests that individual female dolphins consistently utilize a subset of available habitats (habitat specialization). Observations of SB bottlenose dolphins suggest a high degree of habitat specialization among females. For example, females occupy smaller home ranges compared to males (Wells 2003, Urian *et al*. 2009). For reproductively active

females, habitat familiarity, predator avoidance, and proximity to familiar female associates favor a small home range and place limitations on foraging habitat. Thus, some females in the SB population may specialize on prey from seagrass habitats while others may consume prey associated with phytoplankton based food webs. Thus, it appears that while most males specialize on seagrass-associated prey, females may specialize on a variety of habitats or prey resources. Furthermore, female bottlenose dolphin habitat selection appears correlated with trophic level. Females who forage in seagrass also consume lower tropic level prey compared to females who forage in open water. This likely results from seagrass associated female dolphins utilizing the abundant low trophic level prey commonly found in seagrass habitat. While low trophic level species are found in open water (*e.g.*, clupeids) they do not substantially contribute to the diet of female bottlenose dolphins as indicated by SIAR results, stomach content analysis and molecular prey detection (Barros and Wells 1998, Berens McCabe *et al.* 2010, Dunshea *et al.* 2013).

Samples obtained during health assessments are, out of necessity, generally from dolphins traveling in shallow habitats. This possibly introduces a bias favoring individuals who frequently utilize seagrass, a common habitat type for shallow water. However, a bias of this nature would likely impact males and females similarly yet, we document an SEA_b for females significantly larger than that of males.

Juveniles possessed an intermediate SEA_b between males and females. Relative to females, the ellipse for juveniles is similar in spatial orientation but smaller in total area. The shape of the ellipse for juveniles is contracted in $\delta^{13}C$ and lower in $\delta^{15}N$ compared to females. The similarity in shape between the female and juvenile ellipses is likely the result of maternal habitat selection and/or the high degree of philopatry demonstrated by calves newly independent of their mother (McHugh *et al.* 2011). The lower $\delta^{15}N$ values suggest that juveniles feed at a lower trophic level than females possibly resulting from limitations of a small gape size and less developed foraging skills.

Bottlenose dolphins have traditionally been described as opportunistic generalists (Shane *et al.* 1986). However, recent studies have demonstrated that bottlenose dolphins do not indiscriminately capture and consume prey; instead, they specialize on a subset of available prey, especially soniferous fishes (Berens McCabe *et al.* 2010), yet the manner in which dietary variability and specialization is partitioned within dolphin populations remains uncertain. In this study, we found an ecologically significant disparity in the diversity of resource use by male and female bottlenose dolphins, with females accounting for the majority of the variation in foraging habits at the population level. Differences in resource use among male, female, and juvenile bottlenose dolphins likely resulted from trade-offs associated with social interactions, predator avoidance, and energetic needs related to body size, activity levels, and reproductive condition. This dichotomy in resource use may have impacts for conservation and management. Because specialization in resource use within a population impacts social interaction and exposure to habitat degradation, certain subsets of the population may be more likely to strand as the result of disturbance. This is because individuals who utilize a particular foraging habitat may be predisposed to stranding or increased mortality if nutritional stress results from habitat loss or disturbance (Johnson *et al.* 2009). In addition, an elevated mortality risk may result from increased exposure to pathogens or diseased individuals, phenomena that may be promoted by some types of foraging specialization. Consequently, foraging habits may play a critical role in understanding the ecology of phenomena such as unusual mortality events (Gulland and Hall 2007).

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