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Foraging behavior, prey distribution, and microhabitat use by bottlenose dolphins *Tursiops truncatus* in a tropical atoll

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ABSTRACT: The study of habitat use by top predators is important for understanding community interactions and is necessary for sound ecosystem management. In marine systems, top predators such as sharks and cetaceans have a strong impact on the structure and function of communities. While the observation of habitat use and foraging behavior of most marine predators is logistically difficult, bottlenose dolphins *Tursiops truncatus* offer less of a challenge due to visible surface behavior and well-documented populations. We examined bottlenose dolphin behavior in relation to microhabitat classes at Turneffe Atoll, Belize. The dolphins were found to feed proportionally more in boundary microhabitats, areas where dense seagrass beds adjoined open sand flats, than in other microhabitats. Fish density, particularly schools of grunts (family Haemulidae), were higher in the boundary microhabitat than in seagrass or sand microhabitats. Extensive acoustic recordings yielded few fish calls, suggesting that passive listening for soniferous fish was not the dominant means of diurnal prey detection. The dolphins' disproportionate use of boundary microhabitats for feeding was likely due to the abundance and accessibility of prey.

KEY WORDS: Habitat use · Microhabitat · Bottlenose dolphin · *Tursiops truncatus* · Passive listening · Tropical atoll

INTRODUCTION

Identifying habitat use by top predators is necessary for understanding community interactions and for defining and implementing management goals. The home range of top predators consists of a mosaic of varying habitat patches that represent different communities of organisms. In contrast to terrestrial systems, top-down control predominates in marine ecosystems (Paine 2002, Shurin et al. 2002, Duffy 2003); predators play a greater role in influencing population and community structures, and ultimately, ecosystem functions (Stachowicz et al. 2007, e.g. Casini et al. 2012). Thus, determining important habitat patches for predation, within the larger home range of a predator, is essential for understanding community interactions and the possible consequences of environmental disturbance, providing important information for implementing management plans.

The impact of marine predators on community structure and function has been described in several well-established examples of top-down control that include the seastar *Pisaster ochraceus* in rocky intertidal communities (Menge et al. 1994) and sea otters in kelp forests (Estes & Duggins 1995, Estes et al. 1998). In addition to these classic examples, studies demonstrate that as large marine predators such as sharks and marine mammals decline, large cascading effects can result (Jackson et al. 2001, Estes et al. 2011). Some of these effects may include shifts in population sizes at different trophic levels, as well as

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changes in the behavior of prey (Dill et al. 2003, Heithaus et al. 2008, Burkholder et al. 2013).

Observation of habitat use and foraging behavior for most marine top predators is logistically challenging due to large home ranges, typically elusive behavior, and low population densities (Heithaus & Dill 2002). The bottlenose dolphin *Tursiops truncatus*, however, is an apex predator that is amenable to foraging studies due to their visible surface behavior, tendency to form groups, and well-documented populations of recognizable individuals.

Dolphin habitat use is likely shaped in part by prey distribution (Allen et al. 2001, Degrati et al. 2012). The mechanisms used by dolphins to detect prey in the wild are not completely understood, but 4 senses may be employed: echolocation, passive listening, vision, and electro-reception (Czech-Damal et al. 2012). While the echolocation abilities (Murchison 1980, Au 1993, Tyack 2000) and visual adaptations (Herman et al. 1975, Mobley & Helweg 1990, Tyack 2000) of dolphins have been well-documented, research efforts have only recently considered passive listening. The abundance of soniferous prey, including scaenid and haemulid fish, in the stomachs of dolphins suggests that passive listening may be an important means of prey detection (Barros & Odell 1990, Mead & Potter 1990, Barros 1993, Barros & Wells 1998, Gannon 2002, Gannon & Waples 2004), particularly over long distances during the search phase of foraging (Gannon et al. 2005).

Our examination of foraging by the dolphin population in Turneffe Atoll, Belize, had 3 research objectives: (1) to identify microhabitat types frequently used for foraging, (2) to characterize the fish communities and therefore potential prey items, and (3) to evaluate the plausibility of passive listening as a potential search method during foraging. Our methodology included 4 major steps. First, we used boat surveys to observe dolphins and record predominant group activity. From these data, we determined locations that were frequently used for foraging and other activities. Second, we returned to dolphin sighting locations to quantify microhabitat types in areas favored by foraging dolphins. Third, we measured fish distribution in favored foraging areas to examine more precisely dolphin foraging microhabitats. Finally, we employed acoustic surveys to determine the likelihood of passive listening as a primary search strategy employed by dolphins.

MATERIALS AND METHODS

Study site

The study was conducted in the southern portion of Turneffe Atoll, Belize (Fig. 1). Observation of dolphin *Tursiops truncatus* behavior is typically limited to surface behavior. However, the shallow and clear water of the Turneffe Atoll, Belize, allowed for underwater observation of dolphins and visual census methods unavailable in other locations. Additionally, dolphins in Turneffe exhibit no evidence of shark wounds (Campbell et al. 2002), suggesting that they are not frequently preyed upon. This indicates that habitat use is unlikely to be influenced by predation risk.

While Belize shares many ecological features with other areas of the Caribbean and Florida, USA, the fish population differs substantially. The highly soniferous Haemulidae, which are absent or uncommon at many other locales, are the most common fish in Belize (Sedberry & Carter 1993) and may be an important prey source.

Turneffe Atoll was designated as a marine reserve on 22 November, 2012. Management planning to identify key conservation issues is currently underway, and information on predator habitat use and community interactions will inform marine reserve conservation plans.

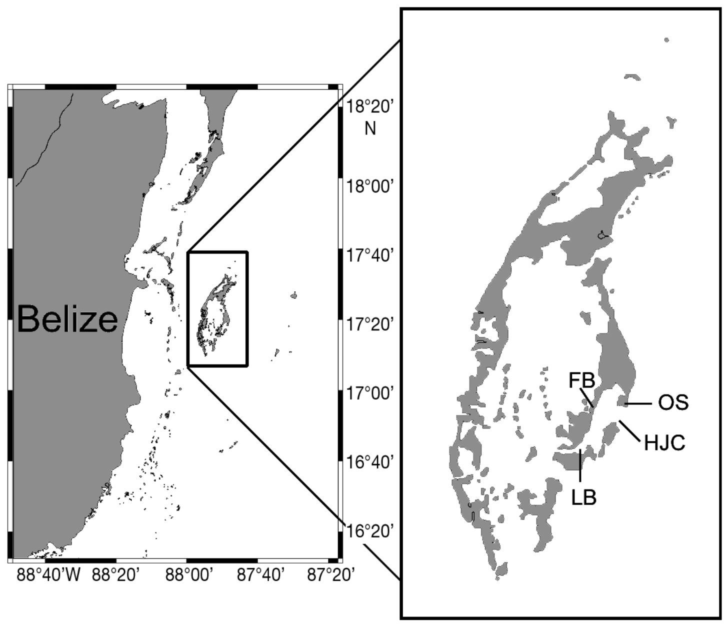

Fig. 1. Turneffe Atoll, Belize, with the locations of fish transect lines indicated, along with the location of the Oceanic Society Field Station (OS) on Blackbird Caye. FB: Fishing Bogue; LB: Long Bogue; HJC: Harry Jones' Cut

Dolphin behavior and microhabitats

Dolphin surveys and microhabitat characterizations were completed from January 2003 through November 2004. Three survey routes, adapted from Bilgre (1998), were used to ensure coverage of the entire survey area each week. Groups were defined using the chain rule (Smolker et al. 1992); dolphins were considered part of the same group if each animal was within 15 m of any other dolphin in the group. Traveling was defined as dolphins moving parallel and steadily in one direction over several minutes. Foraging was defined as active pursuit of prey, regardless of feeding success. Milling was defined as individuals changing orientation with respect to each other. Dolphins were possibly engaged in prey searching during this behavior. However, since no behaviors indicative of hunting were associated with the definition of this activity, milling was not defined as a foraging behavior state for our study. Social behaviors included affilitative, aggressive, sexual, and non-contact displays between 2 or more dolphins. Animals were considered at rest if they were floating at the surface, unmoving, or moving very slowly.

During group-follows, the predominant group activity (defined by orientation, movement patterns, and surface behavior of >50% of the group) was recorded every 2 min. A GPS location was recorded every 20 min during dolphin group-follows. The goal of the repeated 20 min assessments was to obtain an unbiased sub-sampling of behavior states that would be representative of the time dolphins spent engaged in an activity and a random sampling of locations as dolphins moved through the study area. GPS locations were also ground-truthed using observations of underwater topography and triangulation with nearby cayes.

To characterize microhabitats, we returned to the marked GPS locations at the end of group-follows and conducted visual characterizations of benthic habitats while diving. Three radial 20 m transect lines were placed along the bottom substrate, with one shared end staked at the GPS point and the other ends of the lines radiating out at ~120° intervals. Each line was marked every one-tenth of a meter with bold markings at every 1 m point. To measure the bottom habitat coverage of seagrasses, algae, and non-vegetated substrate (Kirkman 1996, Duarte & Kirkman 2001), a 0.25 m^2 quadrat was placed every 4 to 5 m along each radial line. Thus, there were 4 to 5 quadrats on each of 3 lines for a total of 12 to 15 quadrats at each GPS location. Percent seagrass, algae, and bare-substrate cover estimates for each quadrat were recorded on a dive slate by divers. A laminated photocalibration guide of 20, 40, 60, 80, and 100% seagrass coverage was made from representative quadrats and used to standardize estimates (Duarte & Kirkman 2001). The guide was attached to the dive board and consulted during transects to estimate the seagrass coverage to the nearest 10%.

The microhabitat within each quadrat was identified following Mumby & Harborne (1999), which defined 4 major classes of benthic coverage in the Caribbean: coral, algal-dominated, seagrass-dominated, and bare substratum-dominated. Two additional classes were added for this study: mixed vegetation and boundary. The mixed vegetation class was defined as a medium density (as described by Mumby & Harborne 1999) of approximately equal percentages of seagrass and algae. Boundary microhabitats were areas of sharp and distinct convergence of dense seagrass coverage and open sand area. These class characterizations were used, along with depth and site location, to describe microhabitats frequented by dolphins. No imagery is available for Turneffe Atoll at a resolution that allows for a measurable distinction between these micro-scale benthic types.

To quantify the relationship between habitat and behavior, the associations between the predominant group activity of the dolphins and microhabitat class used were compared to an expected distribution. The expected distribution was generated from the proportion of each behavior class totaled across all habitats. Under the null hypothesis that behavior and habitat were unrelated, the proportion of each behavior class calculated from all sightings was applied to the total number of sightings within each habitat. The number of each observed behavior class in each habitat was then compared to the expected number and analyzed by chi-squared tests for independence using R software (R Development Core Team 2011).

Visual census and acoustical transect

Three permanent transect lines, 25 m in length, were placed in each of 3 locations, Fishing Bogue, Long Bogue, and Harry Jones Cut, for visual census of fish communities along the transition from seagrass to sand. These locations were chosen after surveys revealed that they were the most frequent areas used for foraging (combined 53.4% of all foraging observations) and were boundary microhabitats. Transect lines extended 10.5 m on either side of the distinct transition between seagrass and sand. The transect lines were snorkeled, and fish within 2.5 m of either side of the line were counted. Lines were completed in approximately 15 min. Each fish was counted at the meter at which it was observed along the line, and its species was noted. Visual census counts were made at varying times of day and tidal states in order to look for spatial patterns in fish community distribution that were consistent over time.

The fish community distribution along each line was analyzed using a linear mixed-effects model, with different days of observations serving as the random effect.

Coefficient subscripts distinguished their association with a particular factor. The model predicts the log abundance of fish (F) from the fixed effect of the location along the line (L) and the random effect of the day (D):

$$\log F_{ij} = \mu + \beta \times L_i + D_j \quad (1)$$

ANOVA comparisons of null models to models including location along the transect line as the predictor variable were used to determine the statistical significance of location on fish community distribution. The same process was used to analyze the relationship of Haemulidae distribution to location along the transect line. A Bonferroni correction was used to reduce Type I error resulting from the 2 tests — total fish and Haemulidae — using the same data. Analyses were completed using R software (R Development Core Team 2011).

During the summer and fall of 2004, recordings of fish calls were made between 8:30 and 17:30 h, with the time for each line rotating between morning and afternoon. The boat was anchored, and the engine was off for 20 min before recording. Recordings were made at 3 points along each transect line. One point was at the end of the transect line in the grass, one was at the other end of the line in the sand, and the third was directly on the boundary between the sand and the grass. A High-Tech HTI-156-005 hydrophone with an internal preamplifier (High-Tech, Inc.) and a Sony TCD-D8 DAT recorder were used to make each 2 min long recording. The frequency response of the hydrophone was uniform (±3 dB) from 2 to 30 kHz. The sensitivity was measured by the manufacturer at 170 dB re 1 µPa per volt from the output of the preamp. The sampling rate of the DAT was 44.1 kHz, resulting in a frequency range of 20 to 22 kHz (±1 dB). The hydrophone was placed 1.5 m off the side of the boat and, following Gannon (2002), was lowered to half-depth, between the surface and the lagoon floor. Recordings were then analyzed for sound production by fish using CoolEdit Pro (Syntrillium Software Corporation 1992–2000).

RESULTS

Dolphin behavior and microhabitats

In 2003, we conducted 132 surveys (410.6 h) of which 95 surveys (72%) yielded a total of 116 sightings of 1 or more dolphins. A total of 427 dolphins were sighted. Seventy-five animals (17.6%) were identified as calves. The mean group size was 2.8 ± 3.2 (± SD) dolphins. In 2004, we conducted 39 surveys (103.2 h), of these 29 surveys (74.3%) yielded a total of 39 sightings of 1 or more dolphins. A total of 129 dolphins were sighted, of these 15 (11.6%) were calves. The mean group size was 3.2 ± 3.0 dolphins. A total of 150 microhabitat characterizations were completed over 73 surveys and 81 sightings.

Of the 6 defined microhabitat classes, 5 were frequented by dolphins, with the majority of sightings in seagrass (58%) and boundary microhabitats (17%) (Table 1). Thirty-eight percent of foraging activity occurred in seagrass areas, 40% occurred in bound-

Table 1. *Tursiops truncatus*. Percentage of dolphin sightings (sight.) within each microhabitat class

Microhabitat	Dolphin sight. (n)	All sight. (%)	All foraging sight. (%)	% foraging of all sight. in a habitat
Grass	87	58	38	46
Boundary	25	17	40	72
Sand	18	12	2	0
Mixed	13	9	13	54
Coral	7	5	7	43

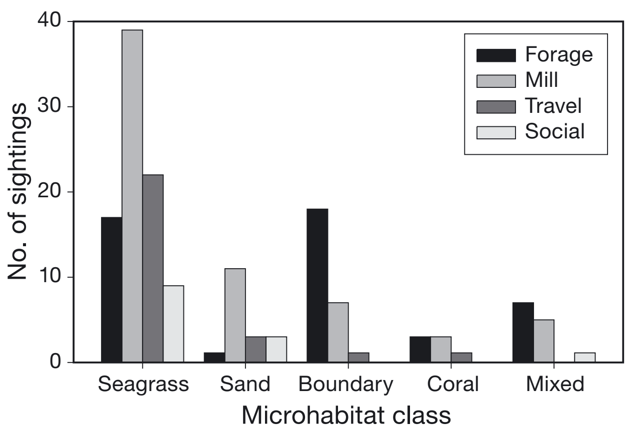

Fig. 2. *Tursiops truncatus.* Number of observations of dolphin behavior within each microhabitat class. The majority of sightings occurred in seagrass microhabitats, where the dominant behavior type was milling. In the boundary microhabitat, the dominant behavior was foraging

ary areas, and 2% was in sand areas. Of the total sightings within the seagrass, 46% were of foraging activities, while 72% of sightings within the boundary were foraging.

Foraging was observed in 31% of the 150 microhabitats that were measured, while milling was observed in 42% (Fig. 2). Observed predominant group activity differed significantly with microhabitat compared to a random distribution of activity across microhabitat ($\chi^2 = 36.4$, df = 12, $p < 0.001$) (Fig. 2). Foraging activity occurred significantly more often in boundary microhabitats than in seagrass microhabitats when compared to non-foraging use ($\chi^2 = 29.8$, df = 1, $p < 0.001$) (Fig. 3).

Visual census and acoustical transect

With a mean of 57 ± 46 fish line^{-1}, Long Bogue had the highest fish density compared to Fishing Bogue (ANOVA post hoc LSD, $\alpha = 0.05$, $p = 0.001$) and Harry Jones Cut ($p = 0.001$). Fishing Bogue, with a mean of 38 ± 21 fish line^{-1}, had more fish than did Harry Jones Cut ($p = 0.001$), which had a mean of 19 ± 20 fish line^{-1}. Overall, grunts (family Haemulidae) were the most abundant fish, with French grunts *Haemulon flavolineatum* (20.2%) and bluestriped grunts *Haemulon sciurus* (18.6%) being the most abundant species in total counts (Table 2).

For fish community distribution, a fifth-degree polynomial, with location as the predictor, was the best-fitting linear mixed-effect model, with the lowest Akaike information criterion (AIC). Comparing the location model to the null model resulted in 7 of

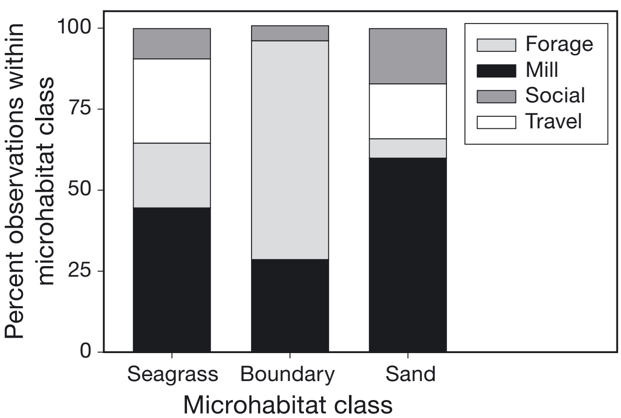

Fig. 3. *Tursiops truncatus*. Percent occurrence of each behavior type within seagrass, boundary, and sand microhabitats. Milling was the dominant dolphin behavior within seagrass and sand microhabitats, whereas foraging was the dominant behavior within boundary microhabitats

the 9 lines showing a significant correlation between the fish abundance and the location along the transect line (Table 3). Peaks in average fish abundance occurred in the boundary area of each line, regardless of depth or slope (Fig. 4). Inclusion of depth in the linear mixed-effect model did not significantly improve the model, with no decrease in the AIC.

Schools of grunts were frequently sighted at Fishing Bogue and Long Bogue but were less common at Harry Jones Cut. Their distribution was also related to microhabitat, with more grunts observed in the boundary area than in the grass or sand. A fifth-degree polynomial was the best-fitting linear model for the distribution of grunts along every transect line. Grunt abundance was significantly correlated to the location along the transect line for all 9 lines, with the highest abundance occurring in the transition region (Table 3).

Out of 271 acoustic 2 min samples (542 min), a total of 23 fish calls were heard in 12 samples: 8 samples at Long Bogue, 3 samples at Harry Jones Cut, and 1 sample at Fishing Bogue. Overall calling rate for the 271 samples was 0.0425 calls min^{-1} (1 call/11.76 min). Call length ranged from 0.03 to 0.43 s, with a mean of 0.15 ± 0.14 s.

DISCUSSION

The location of foraging activity by bottlenose dolphins *Tursiops truncatus* at Turneffe Atoll and the distribution of the fish community within boundary microhabitats were both related to benthic habitat type. The dolphins foraged proportionally more in boundary microhabitats than in any other, despite fewer observations of dolphins in these locations.

Visual fish census in boundary microhabitats demonstrated that fish congregate at the transition between seagrass and sand areas. Dolphins, as opportunistic predators, may feed whenever prey is present and accessible (e.g. Cockcroft & Ross 1990, Corkeron et al. 1990, Connor et al. 2000). Boundary microhabitats may play a large role in providing a reliable food source in an ecosystem with a relatively low fish density. Because the boundary zone is a border area between sand and grass, the fish in the area may be more visually exposed there than in seagrass areas. Additionally, the area may reduce acoustic clutter during echolocation or signal attenuation during passive listening. In many areas, the boundary microhabitat occurred on or by a slope that may provide a physical boundary the dolphins can use in capturing prey.

Table 2. Percent of all observed fish species at Fishing Bogue, Long Bogue, and Harry Jones Cut, and totaled across all counts. Ordered from most abundant to least abundant in terms of total counts. The 3 most abundant from total counts are in **bold**

Latin name	Common name	Fishing Bogue	Long Bogue	Harry Jones Cut	Total
Haemulon flavolineatum	**French grunt**	**30.3**	**11.1**	**16.0**	**20.2**
Haemulon sciurus	**Bluestriped grunt**	**11.1**	**28.6**	**12.7**	**18.6**
Haemulon chrysargyreum	**Smallmouth grunt**	**17.8**	**0.0**	**0.0**	**7.8**
Gerres cinereus	Yellow mojarra	17.5	0.0	0.2	7.7
Lutjanus apodus	Schoolmaster snapper	1.5	13.1	6.2	7.0
Acanthurus bahianus	Ocean surgeonfish	0.4	14.3	0.0	6.1
Sparisoma aurafrenatum	Redband parrot	6.8	1.9	14.8	5.9
Sparisoma sp.	Parrot sp.	1.8	7.6	1.3	4.2
Halichoeres sp.	Wrasse sp.	0.7	4.3	9.4	3.5
Scarus croicensis	Striped parrot	3.7	0.7	8.5	3.2
Thalassoma bifasciatum	Blue wrasse	0.9	4.3	4.5	2.9
Scarus taeniopterus	Princess parrot	2.6	0.3	8.0	2.4
Lutjanis mahogoni	Mahogany snapper	0.3	3.1	4.1	2.0
Caranx ruber	Bar jack	1.0	3.4	0.0	1.9
Acanthurus coeruleus	Blue tang	<0.1	3.3	0.0	1.4
Sparisoma radians	Bucktooth parrot	0.4	0.0	5.0	0.9
Pomacentrus sp.	Damselfish sp.	1.5	0.0	1.4	0.9
Mulloidichthys martinicus	Yellow goatfish	0.1	1.3	0.1	0.6
Gobiosoma sp.	Goby sp.	0.0	0.0	3.0	0.4
Sparisoma viride	Stoplight parrotfish	0.3	0.1	1.7	0.4
Halichoeres garnoti	Yellowhead wrasse	0.2	0.4	0.2	0.3
Acanthurus chirugus	Doctorfish	0.0	0.6	0.0	0.2
Ocyurus chrysurus	Yellowtail snapper	0.0	0.5	0.0	0.2
Pseudupeneus maculates	Spotted goatfish	<0.1	0.2	0.6	0.2
Dasyatis americana	Southern Stingray	0.0	0.3	0.7	0.2
Calamus calamuc	Saucer-eyed porgy	<0.1	0.4	0.0	0.2
Hypoplectrus sp.	Hamlet sp.	0.3	0.0	0.3	0.2
Sphoeroides testudineus	Checkered puffer	0.3	0.0	0.1	0.1
Cantherhines pullus	Orangespotted filefish	0.1	0.0	0.6	0.1
Caranx batholomaei	Yellow jack	0.1	0.1	0.0	0.1
Bothus lunatus	Peacock Flounder	0.0	0.0	0.6	0.1
Lactophyrs polygonia	Honeycomb cowfish	0.0	<0.1	0.1	0.1
Lactophyrs triqueter	Smooth trunkfish	<0.1	0.0	0.0	<0.1
Lachnolaimus maximus	Hogfish	0.0	<0.1	0.0	<0.1
Corythoichthys sp.	Pipefish sp.	0.0	<0.1	0.0	<0.1

Table 3. For transect lines at Fishing Bogue, Long Bogue, and Harry Jones Cut, likelihood ratio results from ANOVA (α = 0.0028 with Bonferroni correction) comparison of null linear mixed-effects model to linear mixed-effects model, with location as the predictor value. *$p < 0.0028$, **$p < 0.0001$

Distribution	Fishing Bogue			Long Bogue			Harry Jones Cut		
	Line 1	Line 2	Line 3	Line 1	Line 2	Line 3	Line 1	Line 2	Line 3
Total fish	14.84	7.78	21.95*	66.77**	49.73**	58.39**	36.12**	47.02**	42.75**
Haemulidae	38.64**	18.57*	47.67**	80.29**	65.42**	62.28**	75.81**	75.05**	93.72**

The greater abundance of fish at the transition between sand and seagrass may be the result of a positive edge effect often seen in terrestrial systems (reviewed in Ries et al. 2004). Other studies have found that certain groups of fish, particularly predatory fish, are found at higher densities at the edge of seagrass and sand than within seagrass patches (Dorenbosch et al. 2005, Smith et al. 2011). A positive edge effect has been proposed as the explanation for the higher faunal density found in smaller seagrass patches compared to in larger patches (Macreadie et al. 2009). The abundance of fish at these edges may be due to a high abundance of the fishes' prey species found in this area, as demonstrated for pipefish (Macreadie et al. 2010). Haemulidae (grunts) and Lutjanidae (snappers) species prey on small crustaceans (Cocheret de la

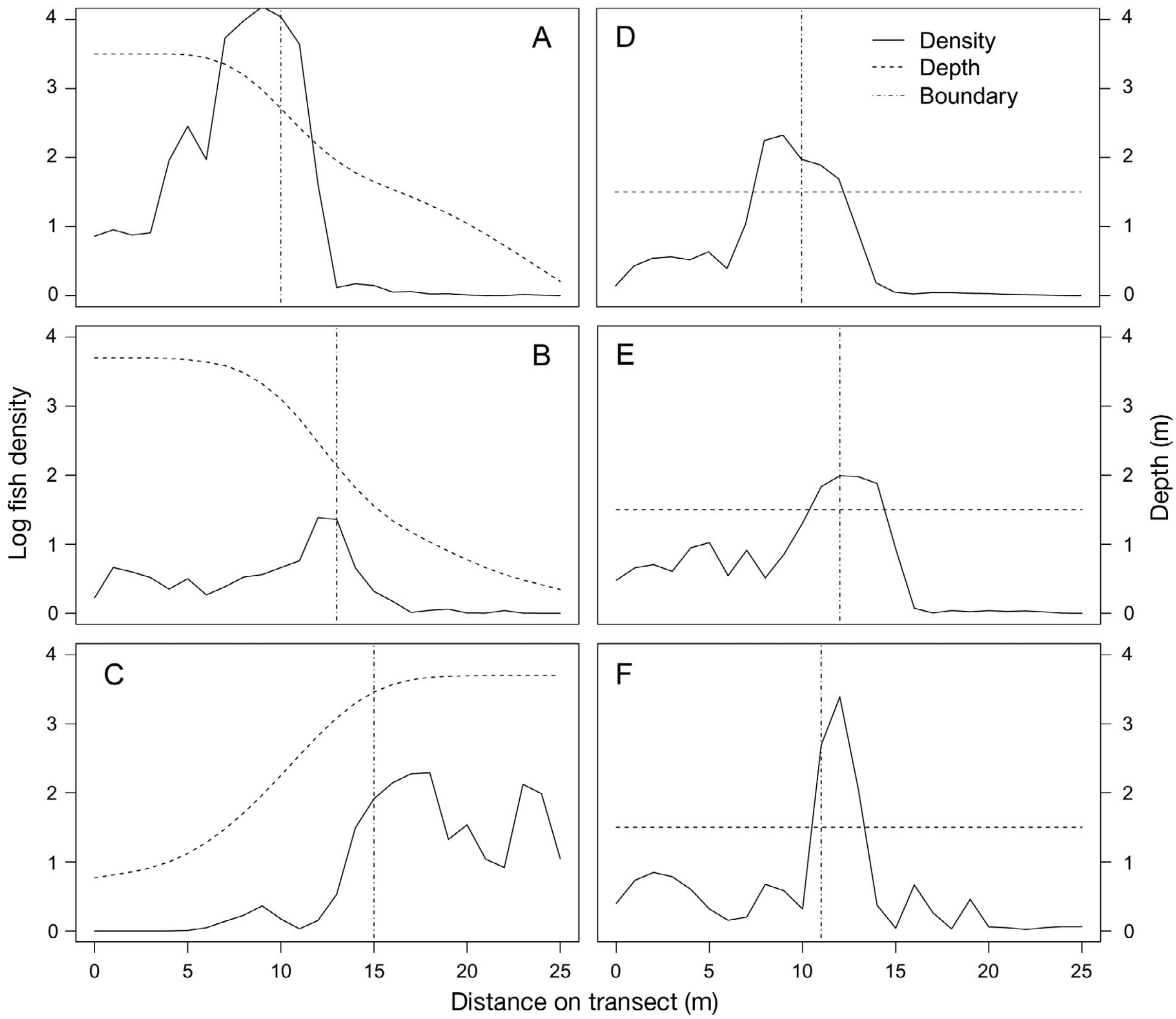

Fig. 4. Comparison of slope and log fish density (no. of fish m^{-2}, species listed in Table 2) for the fish transect lines at Fishing Bogue and Harry Jones Cut: (A) Fishing Bogue Line 1, (B) Fishing Bogue Line 2, (C) Fishing Bogue Line 3, (D) Harry Jones Cut Line 1, (E) Harry Jones Cut Line 2, and (F) Harry Jones Cut Line 3. Fish density is highest within 3 m of the boundary line, independent of the presence of slope

Morinière et al. 2003), particularly penaeid and caridean shrimps (Austin & Austin 1971, Carr & Adams 1973, Harrigan et al. 1989, Heck & Weinstein 1989, Rooker 1995). Many crustaceans and several polychaete taxa are more abundant at the boundary between seagrass and sand than in either sand or seagrass (Barberá-Cebrián et al. 2002, Bologna & Heck 2002, Tanner 2005, Warry et al. 2009). This increase in invertebrate density is similar to the edge effect seen in certain terrestrial arthropod taxa (Samways et al. 1997, Didham et al. 1998, Kotze & Samways 2001, Major et al. 2003).

The limited recordings of fish sounds suggest the fish community is not acoustically active diurnally. Many of the species common in Belize and observed during visual census are known to be soniferous. However, sound production of fish, particularly scaenid and haemulid fish, is crepuscular or nocturnal, particularly during spawning (Rountree et al. 2006). Because surveys were completed between 8:30 and 17:30 h, peak calling times were most likely missed. Dolphin observations and fish counts were also made during the same diurnal range, allowing the acoustic and visual data to be correlated. Therefore, passive listening for fish calls is highly unlikely to be the primary mechanism for diurnal prey detection in this population. The tropical waters of Turneffe Atoll are less turbid than the coastal waters of North Carolina and Florida, USA, where passive listening has been suggested to be an important means of finding prey

(Barros & Wells 1998, Gannon 2002, Gannon & Waples 2004, Gannon et al. 2005). Clearer waters may allow for easier visual detection of fish and other prey species. Echolocation and passive listening for other prey cues, such as motion and feeding noises, are also likely means of prey detection.

The selection of specific microhabitats for different activities and the variation of fish density by substrate have important conservation implications. Until the November 2012 signing of legislation to establish the Turneffe Atoll Marine Reserve, Turneffe Atoll, was the only atoll off the coast of Belize lacking government protection. With a diverse habitat of >200 mangrove cayes, the presence of endangered species, including West Indian manatees and American saltwater crocodiles, and relatively pristine coral reefs, it is obvious that the need for protection is high. In terms of management decisions for the new reserve, microhabitat selection by dolphins and the effect of substrate on fish density demonstrate the necessity of habitat heterogeneity. Recent increases in island development, mangrove burning, and dredging may have large, negative impacts on the lagoon environment and the dolphin population, particularly dolphin foraging areas and prey populations. Increased sedimentation in the water may also impact the dolphins' ability to detect prey if visual detection is their primary means of finding food. With the new Turneffe Atoll Marine Reserve, information on dolphin microhabitat use and fish community distribution can now inform management planning and the zonation of use within the reserve.

We envision 2 future studies what would further enhance our understanding of the dolphins' role in the Turneffe Atoll ecosystem. High-resolution imaging (not available in 2003 to 2004) could be used to incorporate habitat availability. We caution that such an exercise would also need to ascertain which areas within the study site are actually available to dolphins (e.g. are deep enough for access) and how habitat availability scales with dolphin density. Second, studies could explore the possibility of a relationship between patch size and behavior.

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