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Seasonal occurrence of male Antillean manatees (*Trichechus manatus manatus*) on the Belize Barrier Reef

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Abstract

A fragment of manatee habitat that crosses the border of Belize and Mexico includes both activity centres and travel routes linking rivers, lagoons, seagrass beds and mangrove islands near Chetumal Bay. Little is known about how geophysical features like coral reefs may influence manatee movements within and between habitat fragments like this. In this inductive study (1995–2001), we documented the seasonal occurrence of Antillean manatees at breaks in the northern Belize Barrier Reef. Survey locations were at: (1) Bacalar Chico National Park and Marine Reserve on Ambergris Caye (Basil Jones Cut) and (2) breaks in the reef 70 km south near the Drowned Cayes (Gallows Reef). The probability of sighting at least one manatee on a 20-min point scan survey was 40% (n=382). Sighting probability was significantly higher during the summer season (May–August) compared to winter months (December–March). Group size ranged from one to five manatees, peaking earlier (May) at the northern than southern site (August). Seventeen identifiable individuals accounted for 87% of the sightings at Basil Jones Cut, with re-sightings within and between years. One individual from Basil Jones Cut was re-sighted at Gallows Reef. Of the manatees for which sex was determined, 100% were males. No calves were sighted. To better understand manatee activity centres and travel routes, we identified potential hypotheses relating seasonal influences, stopover sites for travelling males, and habitat connectivity. To protect this highly vulnerable species, we recommend inclusion of the Belize Barrier Reef as an important component of manatee habitat within the coastal zone of Belize.

Key words: Antillean manatee, *Trichechus manatus manatus*, Caribbean, Belize, habitat connectivity, stopover sites, coastal zone management, Belize Barrier Reef, fragmented populations, seasonal habitat use.

Introduction

A sub-species of the West Indian manatee, the Antillean manatee (*Trichechus manatus manatus*) occurs in rivers and coastal marine systems of at least 19 countries in the Wider Caribbean Region, including the Greater Antilles, Mexico, Central America, and South America (CEP/UNEP, 1995; Lefebvre *et al*., 2001). It is listed by the IUCN (Hilton-Taylor, 2001) as vulnerable, in continuing decline, with severely fragmented populations (VU A1cd, C2a), and has been identified as one of the 'priority protected species of regional concern' (CEP/UNEP, 1995 pp. 1).

One population of this focal species spans the border of Belize and Mexico, a diverse habitat including Chetumal Bay and the northern Belize Barrier Reef Lagoon System (Fig. 1). With a relatively short coastline extending from the Gulf of Honduras in the south to Chetumal Bay in the north, Belize reports the largest number of Antillean manatees in the Caribbean region (O'Shea & Salisbury, 1991). The contiguous Chetumal Bay is one of the most important areas for manatees in Mexico (Morales *et al*., 2000) and Northern Belize (Auil, 1998). Primary habitat consists of rivers, coastal lagoons and bays, and mangrove islands between the Belize Barrier Reef and the mainland (Bengtson & Magor, 1979; O'Shea & Salisbury 1991; Gibson, 1995; Auil, 1998; Morales-Vela *et al*., 2000). Offshore atoll systems, such as Turneffe Atoll, are considered secondary habitat for manatees (Gibson, 1995; Auil, 1998; Morales-Vela *et al*., 2000).

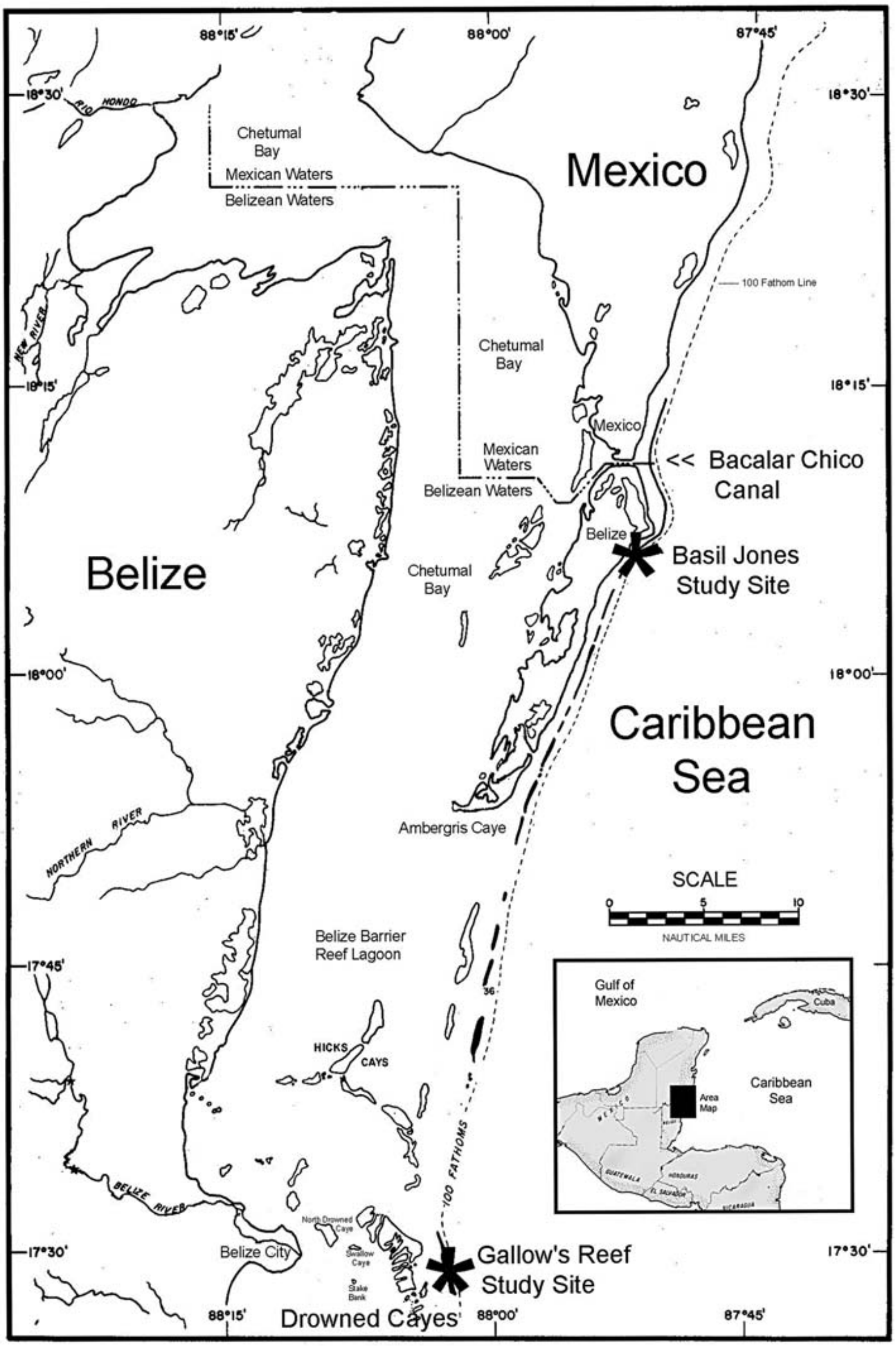

Figure 1. Northern Belize Barrier Reef Lagoon System and Southern Chetumal Bay showing survey locations and the 100-fathom line (100 fathoms = 183 m, map modified from Purdy *et al.*, 1975).

As identified by Packard & Wetterqvist (1986) in Florida, the components of manatee habitat systems include activity centres, travel routes, resources for expansion (potential feeding areas for recovering populations), essential areas (necessary to survive seasonal extremes), and the supporting ecosystem. For the purpose of the present study, we focused on the former two. We defined activity centres as areas where manatees were frequently observed using resources such as vegetation and freshwater, in all seasons. For Belize, previous studies (Gibson, 1995; Lefebvre *et al*., 2001) indicated activity centres were located in silty substrates at 1–3 m depth. Activity centres could have attracted both residents and travellers (Reid *et al*., 1991; Koelsch, 1997). We defined travel routes as connections between activity centres used by individual manatees for daily, seasonal, or migratory movements (Sanderson, 1966). We were interested in whether geophysical characteristics such as a reef could have been used as landmarks by traveling manatees.

Traditional knowledge in local communities indicated manatees were often sighted on the Belize Barrier Reef in the summer. However, the reef had not been included in descriptions of manatee habitat in Belize, possibly due to a bias from research done in Florida where reefs were not present in areas where manatees had been studied. Only one section of Belize Barrier Reef was included in national standardized surveys i.e., in the north where it lies within several 100 m of Ambergris Caye and has been classified as the caye habitat type (Auil, 1998). As recommended by Weeks & Packard (1997), we listened to local residents and chose to document in a systematic manner the patterns of manatee occurrence that they perceived. Using an inductive approach, we examined whether the seasonal trend was robust, and explored the reasons that this component of the habitat system would be most attractive to manatees in the summer.

In this paper, we describe the seasonal occurrence of predominately male manatees at two locations along the Belize Barrier Reef: (1) Basil Jones Cut, which was isolated by Ambergris Caye from a manatee activity centre in Chetumal Bay, and (2) Gallows Reef, which was adjacent to a manatee activity centre in the Belize Barrier Reef lagoon system (the Drowned Cayes) and exposed to frequent boat traffic. The study was initiated at Basil Jones Cut and extended to Gallows Reef. If manatee presence on the reef was influenced by access to warm or fresh water during the winter, we expected to find manatees at Gallows Reef when they were not at Basil Jones. Similarly, if the predominance of males was influenced by isolation from an activity centre, we expected to find female manatees and calves at Gallows Reef when they were not at Basil Jones.

Materials and Methods

Study site

The Belize Barrier Reef extends from the Mexican border, where it is only a few meters from the coast, to the Gulf of Honduras where it is 50 km offshore (Purdy *et al*., 1975). It forms an important geophysical barrier between the shallow coastal lagoon system and the deep Caribbean Sea. The Belize Barrier Reef, an extensive fringing and barrier reef, developed along an escarpment that abruptly terminates the 250 km-long Belize continental shelf; the seafloor plunges to over 183 m (100 fathoms) just beyond the reef crest (Fig. 1).

In this tropical area of the Caribbean, seasons are less defined by temperature and more by rainfall. The average air temperature ranges from 24°C in November–January, to 27°C in May–September (Purdy *et al*., 1975). The dry season extends from February through May; the rainy season extends from June through November (corresponding to the peak probability of hurricanes in July–October); December and January are referred to as the transition season (Auil, 1998). Average annual rainfall increases in a north to south direction, with 124 cm near Chetumal Bay, 178 cm at Belize City, and 380 cm near the Gulf of Honduras (Purdy *et al*., 1975).

The two sampling locations are approximately 70 km apart (Fig. 1). These locations differ substantially in both geophysical characteristics and human activity, as described in more detail below. The northern location, Basil Jones, is relatively far from boat traffic centres and manatee resources (abundant seagrass beds, freshwater, deep channels). Both locations could provide shelter from surf surge, with areas suitable for resting and socializing with other manatees. Compared to Gallows Reef, seagrass beds appear sparser near Basil Jones.

Northern location

Basil Jones Cut (Fig. 2a), is a few hundred metres east of Ambergris Caye (18°5′38″N, 87°52′12″W). Inside the Bacalar Chico National Park and Marine Reserve, this cut is one of several dozen small breaks in a 50 km, continuous section of Belize Barrier Reef that hugs the windward shore (Purdy *et al*., 1975). Basil Jones Cut (>3 m) is used by powerboats travelling to a shrimp hatchery, about a dozen local residents, and a few fishermen or tour operators. The reef lagoon is narrow (<500 m) and shallow (0–2 m), with seagrass rooted in hard calcareous sediments. Travel inside the lagoon appears to be hindered by a maze of back reef coral patches and shallow water. Ambergris

(a)

(b)

Figure 2. Aerial photographs of (a) the northern survey location at Basil Jones Cut (manatees were observed resting in the deep water channel, i.e. the darker water in the photo), and (b) the southern survey location east of the Drowned Cayes (Gallows Reef is located along the right margin of photograph; mainland Belize is approximately 15 km to the west). Photographs by Jimmie C. Smith.

Caye is a solid landmass that blocks manatee travel from Belize Barrier Reef to Chetumal Bay, a core centre of manatee activity (Morales-Vela *et al.*, 2000). Manatees at Basil Jones Cut could travel to activity centres via two routes (Fig. 1): (1) about 7 km north via Bacalar Chico, a secluded narrow canal that connects Chetumal Bay to the Caribbean Sea along the border between Belize and Mexico, or (2) about 30 km south, around the southern tip of Ambergris Caye where San Pedro Town is located (a highly developed tourist destination).

Southern location

Gallows Reef (Fig. 2b), is a section of Belize Barrier Reef with two breaks: North Gallows Cut (17°30′32″N, 88°3′4″W) and South Gallows Cut (17°27′25″N, 88°2′17″W). This central section of the Belize Barrier Reef is discontinuous, with large breaks in the reef crest, which provide many connections between deep water and the Belize Barrier Reef lagoon. Gallows Reef is about 2 km east of the Drowned Cayes (Fig. 1), an area of mangrove islands and associated seagrass beds used by manatees in both winter and summer (Auil, 1998; Sullivan *et al.*, 1999; LaCommare *et al.*, 2001). About 15 km due east of Belize City, this string of islands provides potential navigational 'stepping stones' from the reef to the Belize River, a long-term manatee activity centre identified from modern aerial survey data (Auil, 1998) and pre-historic archaeological data (McKillop, 1984). Throughout this shallow coastal zone, boat traffic is frequent, including fishing boats, tugboats pulling sugar barges, recreational boats, tour boats, and water taxis. English Channel, a deep-water shipping route into the major port at Belize City, is used by cargo ships, tankers, and cruise ships. Cruise ships and sugar ships, which are too large for the port, have berths within the barrier reef lagoon. Small fast boats transport tourists in all directions from the cruise ships and Belize City, including well-travelled routes through the cuts at Gallows Reef to Turneffe Atoll. Tugboats tow barges of sugar from points north to temporary sites within the Drowned Cayes and then to the sugar ship.

Sampling methods

Based on year-round effort at Basil Jones Cut, seasonal periods representing winter (December through March) and summer (June through August) were chosen for efficient allocation of sampling effort at Gallows Reef. At Basil Jones Cut, opportunistic observations of manatees by a local resident (the second author) began prior to 1995 and extended beyond 1997 (Smith, 2000). A 2-year period (April 1995–March 1997) of consistent effort was selected for the purpose of the present analysis (Fig. 3). Preliminary studies indicated that manatees were not present in December-February; hence, more effort was allocated to summer months. To determine whether manatees from Basil Jones Cut were re-sighted further south, surveys were extended to Gallows Reef during a study of the Drowned Cayes by the primary author (Sullivan *et al.*, 1999). Sampling effort was limited to winter (December–March) and summer (June–August) at Gallows Reef (1999–2001).

Observation and recording procedures were similar at both locations, following a protocol that minimized disturbance by in-water observers (Smith, 2000). Each sample consisted of a 20-min continuous scan (Lehner, 1996) around a fixed survey point. One to two snorkellers continuously scanned 360° around the survey point, while floating at the water's surface. All samples were collected between 0800 and 1600 h local time. Only one sample was taken at each survey point on any given day at Gallows Reef; no more than two samples (one in the morning about 1000 h and one in the afternoon about 1600 h) were taken at the survey point at Basil Jones Cut.

To determine sighting probability, any manatee observed during the scan, was recorded as a 'sighting'. If a manatee approached after the end of the scan, it was not recorded as a sighting although it could have been photographed, if feasible. 'Group size' was recorded as the total number of individual manatees present in a scan. In other words the number of sightings within a 20-min scan was limited (0, 1); group size was unlimited (0, 1, 2, 3, . . ., N). Group sizes greater than 1 were recorded only if more than one manatee was observed simultaneously or if sequential observations were of uniquely marked individuals. Sketches and photographs were used to record individual identities at Basil Jones Cut; photographs and video tapes were used to record individual identities at Gallows Reef. When visibility was too poor for positive identification of an individual, it was recorded as an 'unknown'.

Behaviours (resting, feeding, socializing, milling, and travelling), body size (calf, adult) and gender (male, female) were recorded when possible. Definitions of behavioural activities were: (a) when 'resting', the manatee was stationary, either in contact with the sea floor or at mid-water, occasionally rising in the vertical direction for breaths, but with no horizontal movement, no rooting or chewing, and no reaction to observer, (b) when 'feeding', the manatee was rooting or chewing in a seagrass bed or had seagrass parts trailing from it's mouth when it rose above the bottom, (c) when 'socializing', one manatee touched or followed another, (d) when 'milling', the direction of movement changed both vertically and horizontally with no consistent orientation to other manatees, to food, or in any one

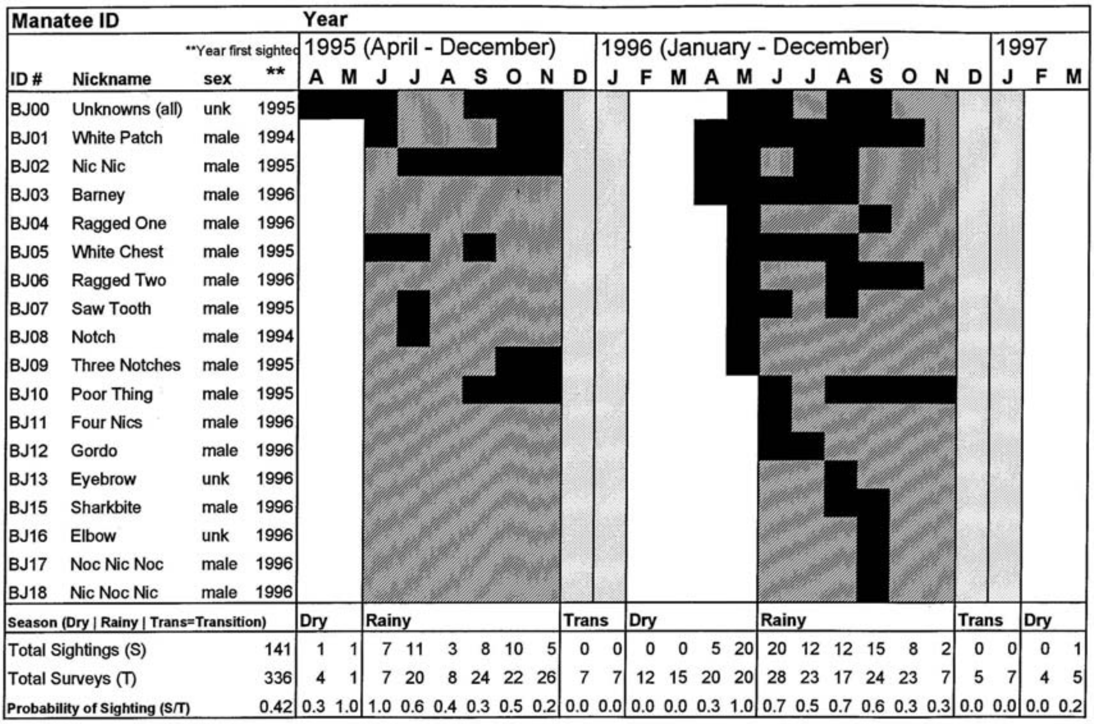

Figure 3. Individual manatee sightings at Basil Jones (April 1995–March 1997). Black boxes indicate the manatee was sighted at least once during the month; seasonal code indicates dry (white), rainy (dark grey), and transitional (light grey) months. Monthly probability of sighting (S/T) is defined as the number of surveys that manatees were present, divided by the total number of surveys for each month. Note: BJ14 (an unmarked male) is included with unknowns in this figure.

direction, and (e) when 'travelling', the manatee was moving horizontally in one consistent direction, either towards or away from the survey point.

To aid in interpretation of results at Gallows Reef, additional data were collected regarding the context of samples. As a check on visibility bias, assistants on a boat (anchored at the survey point) recorded surface behaviours of manatees relative to the in-water observer(s). Environmental measurements collected immediately following the sample included: (1) sea-surface water temperature using a thermometer (analogue or digital), (2) sea-surface salinity using a refractometer, and (3) vertical visibility using an eight-inch Secchi disk. In no instance was a manatee sighted by above-water assistants that was not also sighted by the in-water observer(s).

The analyses were designed to account for differences in sampling effort at Basil Jones (n=336) and Gallows Reef (n=45). Independent variables were season (winter, summer) at Gallows Reef and month (January through December) at Basil Jones. Dependent variables at both locations included: (a) group size, (b) frequency of surveys with manatees present or absent. Environmental measures of sea surface temperature, salinity, and visibility were also analysed at Gallows Reef. Non-parametric statistical tests of continuous variables included the Mann–Whitney U, and the Kruskal–Wallis (Lehner, 1996). Contingencies were tested using the Fisher's exact test and the Freeman–Tukey deviate (Bishop *et al.*, 1975).

Results

Manatees were documented at both locations on the Belize Barrier Reef during the summer months, but not during the winter months. On 40% of all surveys, at least one manatee was sighted. As follows, analyses were specific to each location.

Basil Jones Cut

At least one manatee was sighted on 42% of the 336 surveys at Basil Jones Cut (Fig. 3), and mean group size varied significantly among survey months (Kruskal–Wallis H=119, df=6, $P<0.0001$). Group size ranged from 1 to 5, with a distinctive peak in May (Fig. 4). Only single manatees were observed during most sightings (64%), and groups larger than three manatees were infrequent (5%). Manatees

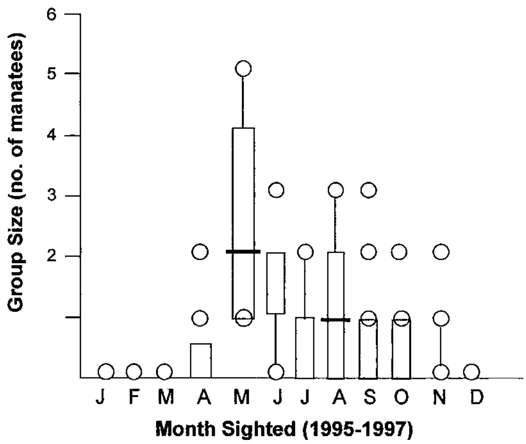

Figure 4. At Basil Jones, group size varied significantly by month (1995–1997). Horizontal bars indicate means and circles indicate the range of values.

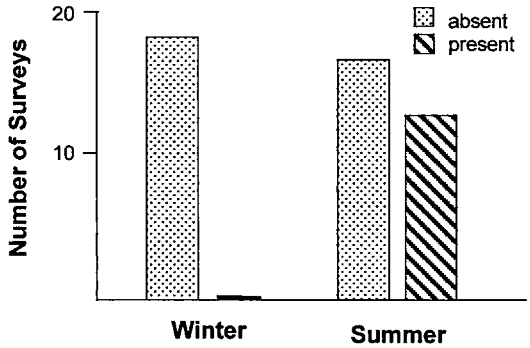

Figure 5. At Gallows Reef, manatees were absent on all 18 winter surveys and present on 12 of 27 summer surveys.

were present at Basil Jones during the rainy season (June through November) and absent from December through March (Fig. 3). They returned at the end of the dry season (April/May).

Manatees stayed in the calm, deep water of the channel inside the reef crest. The primary activity was resting, with occasional socializing. During one sighting two manatees were observed with seagrass trailing from their mouths. During another sighting, two manatees were observed rooting in an area of sparse seagrass approximately 20 m east of the resting area. On one occasion, a bull shark was observed with the manatees, with no interaction. Travel into the shallower areas of the lagoon system was rare. Trends in direction of travel by manatees outside the reef crest could not be determined.

For 87% of the manatees sighted, identity was determined (Fig. 3). Seventeen individual manatees had unique markings and were documented by sketches; most were photographed at least once. Fifteen of these individuals were observed to be males. No calves or females were sighted; the sex of only two identifiable individuals was undetermined. The sex of unknowns (13% of the sightings for which individual identity could not be determined) was undetermined in most cases.

Group composition was fluid, with no detectable long-term associations among individuals (Fig. 3). Two males (BJ01 and BJ08) were re-sighted in each of 3 years sampled. All seven males that were first identified in 1995 were re-sighted the next year. Ten individuals, eight males and two undetermined, were newly identified in 1996. The pattern of re-sightings within each year was variable; some individuals were present only one month each season, others departed and returned after a break of 1–3 months. One individual 'White Patch' (BJ01) came and went regularly (1994–1997), being sighted 17 times over seven consecutive months in 1996. The most frequently sighted individual (BJ03) was present in 41 surveys between April and August 1996; however, he was not re-sighted again until June of 1998.

Gallows Reef

At least one manatee was sighted on 27% of the 45 surveys at Gallows Reef (Fig. 5). Presence differed significantly between seasons (Fisher's exact phi=0.492, df=1, P=0.001). Manatees were absent on 100% of surveys during the winter season (Freeman–Tukey deviate z= − 3.494) and present during 44% of the surveys in the summer season (Freeman–Tukey deviate z=1.611). Group size ranged from one to three, with the larger groups occurring only in late July and August. 'White Patch' (BJ01) who was frequently re-sighted at Basil Jones, was re-sighted at Gallows Reef in 1999. Sex was determined to be male for 10 of the 17 manatees observed during all sightings. No calves or females were sighted, although the sex of seven manatees was undetermined.

In general, manatees approached the in-water observer, paused momentarily and then retreated beyond visible range, remaining within view of assistants in the boat. On several occasions, the same manatee approached the in-water observer and retreated multiple times during a 20-min scan. On two occasions, more than one identifiable manatee approached the in-water observer, both simultaneously and sequentially. Only once did a second individual approach the in-water observer after the end of the scan. The primary activity was milling, with occasional socializing. Rarely manatees were observed with seagrass trailing from their mouths; however, they were not observed rooting into the substrate for rhizomes.

Season significantly affected mean sea surface temperature (Mann–Whitney U=33, n=18, 27, P<0.001) and salinity (Mann–Whitney U=84, n=18, 27, P=0.008), but not visibility (Mann–Whitney U=241, n=18,27, P=0.97). Mean sea surface temperature was higher in summer (29.7 ± SD 0.7 °C) than winter (27.6 ± SD 1.2 °C). Mean salinity was higher in the hot summer rainy season (36.6 ± SD 0.8 ppt) than during the cooler winter dry season (35.7 ± SD 0.9 ppt).

Discussion

These site specific studies at Basil Jones Cut and Gallows Reef showed that manatees use breaks in the reef, at least 9 months of the year. Frequent manatee sightings during the summer indicate that the reef should be included in the delineation of primary coastal habitat for manatees.

Contrary to our expectations based on movements in Florida, manatees did not appear to be moving from the northern survey location to the southern location in the winter. They were absent from both locations on the Belize Barrier Reef during winter samples. However, we documented that north-south travel on the reef was possible, because one individual that was re-sighted frequently in the north, was re-sighted 3 years later at the southern survey location.

Based on a model of potential east-west movements between the Drowned Cayes activity centre, where females and calves were frequently sighted during the same study period (Self-Sullivan, unpublished data), and the reef, we expected to see females at Gallows Reef. Observations of only males at both locations were inconsistent with this expectation. However, our sampling effort and techniques may have been inadequate to detect female presence.

Consistent with an inductive approach, we caution against interpretation of these results in a manner broader than the specific locations, months and years of this study. To generalize from the specific to the broad, we have identified alternative hypotheses related to the function of reefs as travel routes and breaks in reefs as stopover points during travel, as described in more detail below. Multiple factors are likely to influence manatee use of the reef and we encourage further research as to why some individuals stayed longer than others at breaks in the reef. On a larger scale, both seasonal residency and travel routes would have important implications for expanding populations and genetic exchange between demes in fragmented habitats.

We hypothesized that variation in seasonal distribution and/or movement along the Belize Barrier Reef could be related to: (a) seasonal changes in water temperature, salinity, depth and surge, or (b) sex-specific differences in reproductive activity. Most likely, these factors are not independent, rather are correlated as discussed below.

Seasonal use of activity centres relative to physical factors

Our observations are not consistent with the hypothesis that southern breaks in the reef serve as essential areas important for winter survival of northern residents. Areas defined as essential within north/central Florida habitat include warm water effluents (>20 °C) such as natural springs and human-made attractions such as the warm-water effluents of power plants (Packard & Wetterqvist 1986). However, the concept of an essential area is open to critique based on more recent studies of individual manatee movements using satellite telemetry. Individual manatees from the Florida population vary widely in seasonal movements (Deutsch *et al*., 2000). Some travel long distances along the east coast of the USA, others travel short distances within Florida or between Florida and Georgia, and still others appear to be year-round residents remaining in one activity centre. Since some southern-most ranges overlap with other northern-most ranges of Florida manatees (*T. m. latirostris*), factors other than ambient water temperature appear to interact in determining seasonal movements. Perhaps ‘seasonal activity centre’ would be a better term for resident manatees.

We hypothesize that access to freshwater is more of a directive factor than temperature in influencing seasonal manatee use of the reef in the Belize coastal zone. Alternatively, individual manatee movements may be determined by a complex interaction of many factors experienced during a lifetime, including learning processes influencing how travel routes are stored and retrieved from memory. Our reasoning is as follows.

Even though manatee presence/absence on the reef was associated with water temperature, the same variation in seasonal water temperature was found in the adjacent Drowned Cayes where manatees were observed year-round during the same sampling period (Sullivan *et al*., 1999; LaCommare *et al*., 2001). Water temperature in the study area ranged between 25 °C in the winter and 31 °C in the summer, well above the incipient lethal level (as defined by Fry, 1947) of cold tolerance for manatees (20 °C *c.f.* Irvine, 1983). Temperature may have been correlated with another, undetermined, directive factor or gradient.

An alternative hypothesis might be that manatees move further from estuaries during the summer rainy season when freshwater plumes from rivers are more likely to penetrate further into the coastal zone, meaning that manatees are more likely to be at the reef in the summer. Annual salinity range at Gallows Reef was 34.5–38.0 ppt. Osmoregulation experiments on Florida manatees indicate that: (1) they are good osmoregulators in both fresh (0‰) and marine (34‰) environments (Ortiz *et al.*, 1998); and (2) although they drink large amounts of freshwater when available, they do not drink marine water, but possibly oxidize fat to meet their water needs when restricted to eating seagrass in the marine environment (Ortiz *et al.*, 1999). Manatees are considered to be dependent on freshwater in Florida (Hartman, 1979), and periodic access to freshwater is thought to be important to manatees in Belize (Gibson, 1995). However, it is not known whether nor how often manatees might move from the offshore activity centres to mainland sources of freshwater in Belize. Although this distance is all well within 1-day's travel range, manatees within the Drowned Cayes area are often sighted with dozens of salt-water barnacles covering their bodies (Self-Sullivan, unpublished data), an indication of long periods of time spent in the marine environment (Husar, 1997).

Alternatively, underwater springs near our study locations may dry up or become unpalatable during winter. One manatee, sighted three times at Basil Jones in January and February 2001, was near a spring adjacent to the channel (G. Smith, unpublished data). Whether the manatee was drinking from the underwater spring could not be determined; the water was sulphurous as determined by smell and colour. Since we documented higher surface salinity in the summer compared to the winter at Gallows Reef, we do not believe that rainfall provides a lens of fresh surface water at the reef. Possibly the higher salinity was related to evaporation during summer months.

Another hypothesis might be that the breaks in the reef could serve as a stopover site for manatees travelling in search of fresh water, in an east–west direction to and from offshore atolls. Gallows Reef is midway between the Belize River (a fresh water source) and Turneffe Atoll, located further offshore. Manatees have been opportunistically sighted at Turneffe Atoll, a large complex mangrove island-seagrass-coral reef system similar to the Drowned Cayes (Auil, 1998; Barbara Bilgre, pers. comm.).

Seasonal distribution also might be related to winter storms from the northwest. Cold air masses from North America frequently affect both temperature and wind strength during October through January (Purdy *et al.*, 1975). 'Northers', as the local people call these events, may lower the sea surface by as much as 0.8 m. These events have a greater effect than spring tides (0.5 m) on water depth in shallow northern lagoons. If manatees move away from shallow areas inside the reef, then absence would be more likely after storm events in the winter.

Alternatively, manatees may have learned that the reef provides shelter from high surf during the summer hurricane season. For example, three manatees were at Gallows Reef 2 days after Tropical Storm Chantal hit the coast of Belize in 2001 (Self-Sullivan, unpublished data). This is the largest group sighted at Gallows Reef. If manatees that move into the protected lagoon system sense protection from strong currents created by storm surge, breaks in the reef might serve as stopover sites for individuals moving back out to the atolls or continuing their north-south travel outside the reef. For obvious logistical reasons, such movements during hurricanes would be better studied by satellite telemetry than boat-based surveys.

Clearly, there are several physical factors that are correlated with seasonal changes in the habitat used by manatees in Belize. To tease out the relative importance of these factors, we would recommend a combination of regional studies of individual manatee movements using satellite telemetry as well as simultaneous site-specific studies at breaks in the reef. This type of approach would also provide a better understanding of how external environmental conditions interact with physiological states, as outlined below.

Relation between travel and seasonal male reproductive activity

Noting the distinctive absence of females at the breaks in the reef that we studied, a hypothesis emerged related to potential seasonal changes in reproductive activity of males. The evidence that manatees show seasonal patterns in reproductive behaviour is still ambiguous. Early reports by Hartman (1979) and Marsh *et al.* (1978) found no evidence for strong seasonality in Sirenian reproductive behaviour. However, Best (1982) reported seasonal breeding in the Amazonian manatee (*T. inunguis*). More recently, seasonal spermatogenesis has been reported in both Florida manatees (Hernandez *et al.*, 1995) and dugongs (*Dugong dugon*) (Marsh, 1995). Similarly, seasonal variation in female reproductive hormones has been shown in captive Florida manatees (Larkin, 2000). However, seasonal reproductive activities were not tightly coordinated within populations (Larkin, 2000; Best, 1982; Marsh *et al.*, 1984; Marsh, pers. comm.).

By tracking manatees using VHF radio and satellite tags since 1997, Powell *et al.* (2001) found more variation in male than female movement patterns in coastal lagoons south of Belize City. For example, females and some males remained inside the enclosed estuary year-round. However, a few males wandered outside the lagoon system, north and south along the mainland coast of Belize; one male travelled at least as far as Belize City, 33 km north (Powell, pers. comm.).

Based on published literature and our observations of only males on the reef with seasonal peaks and absences, we hypothesized that male manatees use the reef as a landmark during searches for oestrous females throughout the coastal lagoon system. If there is a winter low in spermatogenesis, then movement rates might decline. If there is a peak in both oestrous females and searching behaviour of males in summer, then male movement rates may increase. Variations in seasonal reproductive activity within a population might explain the difference in sighting peaks between Basil Jones (May–June) and Gallows Reef (July–August). Alternatively, sighting peaks could indicate clustered movements by males along the reef.

To test these alternate hypotheses, we would recommend satellite-telemetry studies of both males and females in activity centres adjacent to the reef (Drowned Cayes and Chetumal Bay), combined with simultaneous site-specific studies of individually identifiable manatees. Such studies could answer the critical question of the degree to which there is a seasonal peak in reproductive activity of manatees in Belize and the degree to which male manatees move along the reef during peak reproductive periods.

Implications for expanding populations in fragmented habitat

Based on our sightings of 'White Patch' (BJ01) at both the northern (1994–1997) and southern (1999) sampling locations, we hypothesized manatees move along the reef in a north-south direction. However, we were not able to monitor both locations simultaneously. Extensive studies based on re-sightings of individually marked manatees have been successful in Florida (Reid *et al.*, 1991) and should be continued in Belize. Over the long-term, these studies can be combined with satellite-tagging studies to determine variation in movement patterns during the lifetimes of individuals within a population (Beck & Reid, 1995; Reid *et al.*, 1995). By comparing records at Turneffe Atoll (Bilgre, unpublished data), the Drowned Cayes, Gallows Reef (Smith, 2000; Self-Sullivan, unpublished data), and Basil Jones (Smith, 2000), a more accurate model of what influences manatee movements in the centre of the species' range may emerge for comparison with what is known from the northern extreme of the range, as studied in Florida.

Long distance movements influence gene flow among subpopulations, as reflected in complex patterns of genetic variation among manatees in the greater Caribbean area (Garcia-Rodriguez *et al.*, 1998). Movements of individual Florida manatees along the Atlantic coast of North America range from 44 km to 2360 km (median = 309 km) at rates of 25 km to 87 km per day (Deutsch *et al.*, 2000). In comparison, the Belize Barrier Reef extends only about 220 km, with many breaks that could be used as stopover sites or for ingress to manatee activity centres such as Chetumal Bay, Cayes off Belize City, Southern Lagoon, the Gulf of Honduras, and numerous coastal rivers and bays (Auil, 1998). Considering the long travel range of Florida manatees, Antillean manatees could move among population centres along the Yucatan Peninsula from Mexico through Belize to Guatemala and Honduras (Auil, 1998). During population expansion following historical exploitation, manatees from Belize may colonize unoccupied habitat between population centres in a wider region, with positive influences on gene flow.

The reef may also influence connectivity within the Belize Barrier Reef lagoon system, decreasing the probability of inbreeding by increasing movements between southern areas and Chetumal Bay. The deep water just east of the barrier reef offers an unobstructed north-south travel corridor and the reef offers a physical feature that could be used for navigation. Use of this travel route by manatees could be an alternative to movement through the complex labyrinth created by the mangrove-seagrass-coral lagoon system inside the barrier reef. An analogy might be a loop highway around a metropolitan maze of small roads.

Consistent with knowledge of 'bachelor males' in other marine mammals species, we hypothesize that the turnover of individuals using stopover sites on the reef could be related to turnover in male access to breeding females. In 2001, local tour guides and staff at Bacalar Chico Reserve reported that they 'regularly' observed manatees in a side lagoon adjacent to Bacalar Chico and at another cut in the reef between Bacalar Chico and Basil Jones (Smith, unpublished data). Another local tour guide reported that he observed a group of five manatees inside the reef crest at Goff's Caye (a sand caye on the Belize Barrier Reef just south of Gallows Reef) in November 2001 (Self-Sullivan, unpublished data). And a third tour guide reported seeing a manatee outside the reef crest at South Water Caye (a sand caye on the Belize Barrier Reef still further south) in June 2002 (Self-Sullivan, unpublished data). We recommend studies to determine if these are young dispersing males, prime males between periods of breeding activity, or old males unlikely to breed again. Answering these questions will provide insight to how genetic heterogeneity may be maintained in relatively isolated subpopulations of manatees.

We recommend that the broader implications of this highly specific study should be considered in the context of efforts to design marine reserve systems within the Caribbean. The concept of 'connectivity' was used by Roberts (1997:1454) to draw attention to how 'local populations may depend on processes occurring elsewhere'. Although Roberts referred to patterns of larval transport among coral reefs, the concept also should be applied to large-bodied vulnerable species that use the lagoon systems protected by reefs e.g., manatees. We use the concept of 'stopover sites' in a manner similar to its use in studies of migratory bird species. For example, Higuchi *et al*. (1996) identified stopover sites where migratory cranes paused for less than 10 days during travel between breeding and non-breeding locations. Although Antillean manatees clearly are not migratory as a species, the concept of a stopover site may be applied to a relatively short interruption of travel by individuals. Protecting stopover sites within local lagoon systems could be as important for conserving genetic heterogeneity, as protecting long-distance travel routes connecting fragmented populations on a regional scale.

Conclusions

Developing effective strategies for conservation of manatee habitat requires knowledge of activity centres and movements among them. We documented manatee presence at breaks in the Belize Barrier Reef, with significantly more sightings in the summer (rainy) season than in the winter (transition/dry) season. Groups were small (average of two manatees), some individuals were repeatedly sighted and others were not. At least one individual moved between the northern and southern breaks that we monitored. All of the manatees for which sex was determined were male and no calves were sighted. However, we are cautious about interpretation of these data, due to the inductive nature of this study. We proposed several hypotheses related to physical (temperature, salinity, depth, storm surge) and physiological (thermoregulation, osmoregulation, reproductive status) factors potentially affecting manatee use of breaks in the reef. To test these hypotheses, we recommend simultaneous studies of identifiable manatees at several locations on the reef. In addition, satellite-tagging techniques would be appropriate for determining the seasonality and extent of individual manatee movements among activity centres and stopover sites along travel routes associated with geophysical characteristics of the Belize Barrier Reef. Based on results of this study, we propose that reefs should be considered part of the network of travel routes and stopover sites identified as important components maintaining connectivity within manatee habitat in Belize and between fragmented populations of Antillean manatees in the Caribbean.

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