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Home range and diel movement pattern of sub-adult lemon sharks in Bimini, Bahamas

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HOME RANGE AND DIEL MOVEMENT PATTERN
OF SUB-ADULT LEMON SHARKS IN BIMINI, BAHAMAS

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ABSTRACT

Home ranges and diel movement patterns were determined using ultrasonic telemetry for 28 sub-adult lemon sharks in Bimini, Bahamas. Individual sharks were tracked intermittently for 11 to 433 days, while remaining within 6.5 km from shore. Mean home range (21.4 km^2) for sub-adults was 30 times larger than that reported for juveniles. Distinct movement patterns were observed for 88% of 43 continuous 24-hour tracks. Daily daytime and nighttime activity areas were not statistically different, but the activity area for all 24-hours tracks combined was 42% larger at nighttime than during daytime. Results indicated that sub-adult lemon sharks foraged at night, close to the mangrove-fringed coastline, deep-water channels, and to a lesser extent, off the western shore of North and South Bimini. During the day, sharks moved further offshore to resting areas where physical and chemical oceanographic conditions were probably more stable and less extreme than in their nighttime activity areas.

DEDICATION

This work is dedicated to my parents, Solange and Gilbert de Marignac, who encourage me to follow my passions and are always supportive; and to my beloved wife Lisa for her inspiration, support and patience.

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INTRODUCTION

A comprehensive understanding of the natural history of any animal must include the pattern of its movements. Movement patterns can be perceived as adaptations to improve an animal's fitness and reproductive success (Matthews 1990). The spatial and temporal distribution of an animal is often a direct response to features of its physical and biological environment (Brown and Orians 1970). Factors, such as food availability, density, reproductive activities, and habitat usage may affect movement patterns (Sanderson 1966). There should be strong selection for animals to move within and among environments that supply needed resources such as food, shelter, and mates (Baker 1978). An animal can gain many advantages by being familiar with its surrounding environment. Familiarity with the area can facilitate foraging by reducing the search time, increasing protection from predators, and improving the ability to find adequate breeding and nursery grounds. Many vertebrates confine their movements to a specific activity space, an area commonly referred to as "home-range" (Baker 1978 and 1982). The location and size of an animal's home range, and the degree of fidelity are important features of its ecology.

Brown (1975) defined home range as "that area in which an animal normally lives, exclusive of migration, emigration, dispersal movements, or unusual erratic wanderings." This definition is incomplete because it fails to provide temporal criteria for defining home range. Time scale is an important component of a definition of home range because measurements of absolute space used by an organism can vary temporally (Spencer et al. 1990). Many species use various habitats during different stages of their life to enhance their fitness. Such shifts between habitats may be responses to many factors such as climate, food availability, or ontogeny. Size of home range may vary with age, sex, and season and within and among species.

Size and shape of an animal's home range should have adaptive significance (Schoener 1981). Maza et al. (1973) proposed that an animal should live in the smallest area that provides its energetic requirements. Body mass influences energy expenditure (McNab 1963). Under similar circumstances, larger organisms require more energy than smaller organisms and may require larger home ranges. In general, herbivores have smaller home ranges than carnivores (Seton 1908, Sanderson 1966) and males have larger activity spaces than females (Sanderson 1966, Maza et al. 1973, Schoener and Schoener 1982). However, it is unlikely that the size of the activity space is affected by body size alone.

Habitat quality is an important factor affecting home range (Sanderson 1966, Laundre and Keller 1984). Typically, animals use some areas within their home range more frequently than others. These core areas are likely to be biologically significant (Hayne 1949, Dice and Clark 1953) and should be identified to understand the ecological factors that affect home range use (Samuel et al. 1985). Home ranges may overlap whereas core areas may not (Ewer 1968).

Comparing home ranges of related species can provide insight into differences in diet, foraging behavior, and social structure among and within species (Braun 1985). The significance of an animal's home range is better appreciated by determining why an animal is at a particular space at a particular time (Bekoff and Mech 1984, White and Garrot 1990).

The study of sharks in their natural environment is difficult because they are swift, elusive, wide-ranging, and live in a concealing medium (Nelson 1977). Because direct observations of sharks under water are limited and often logistically impossible, ultrasonic telemetry is a valuable tool to remotely monitor movements of aquatic animals like sharks. At least 33 species of elasmobranchs have been tracked using this technique. However, most of these studies were of short duration and few provided information on home range and utilization.

Typically, studies of activity space have been restricted to small or young sharks that occupied relatively small areas (Strong 1989, Holland et al. 1993, Morrissey and Gruber 1993 a and b). Studies of activity space for larger sharks are mostly anecdotal and preliminary because of the logistical difficulties associated with tracking larger sharks over long periods of time.

The lemon shark (*Negaprion brevirostris*, Poey 1868) is a stocky, yellow-brown requiem shark (Carcharhinidae) with a short rostrum. It is easily distinguished from other requiem sharks by its second dorsal fin, which is nearly as large as the first dorsal fin, and by its yellowish color from which its name is derived. It is a coastal tropical species occuring from the Gulf of California to Ecuador in the eastern Pacific Ocean, from New Jersey to southern Brazil in the western Atlantic Ocean, and probably wide ranging off West Africa (Compagno 1984). The lemon shark is found from the surface to at least 92 m depth. It occupies hypersaline lagoons and occansionally river mouths; but unlike the bull shark (*Cacharhinus leucas*), it has not been recorded far up tropical rivers (Compagno 1984).

The lemon shark may be an opportunistic piscivore with no apparent pattern of diel feeding, and the young lemon shark consumes about 2% of its body weight daily

(Cortes and Gruber 1990). The lemon shark is viviparous and probably produces litters every other year. After a gestation of 10 to 12 months females enter shallow nursery areas in the spring to give live birth to 4 to 17 pups (Springer 1950, Gruber and Stout 1983, Compagno 1984). Newborns measure 40 to 67 cm in total length (TL; Gruber 1982, unpub. data) and adults may reach 368 cm TL (Hueter and Gruber 1982). The lemon shark grows slowly, an estimated 3.3 to 22 cm/yr (Gruber and Stout 1983, Henningsen and Gruber 1985, Manire and Gruber 1991, Morrissey 1991, unpubl. data). It is long-lived, living to at least 20 years, and matures at about 230 cm TL at an estimated 11 to 13 years (Brown and Gruber 1988). Because it is a typical, large, coastal species that is relatively abundant, easy to capture, and adapts well to captivity, the lemon shark as a species can be used as a heuristic model for tropical coastal sharks (Gruber 1982).

The home range of the juvenile lemon shark is well documented. Morrissey and Gruber (1993 a and b) tracked juvenile lemon sharks (<1 m TL) in the shallow water of Bimini, Bahamas. Juvenile lemon sharks were more active during crepuscular hours than during day and night hours. The sharks were highly site-specific and had small narrow activity spaces (0.23 to 1.26 km^2) along the mangroves, possibly to avoid predation. Activity space was positively correlated with body size in juvenile lemon sharks.

As they grow, lemon sharks gradually expand their home ranges to perhaps 300 km^2, with adults occupying offshore reefs and deep water (Compagno 1984). However, the rate of increase of their home range is unknown. Gruber et al. (1988) estimated activity space areas ranging from 9 to 93 km^2 for three lemon sharks – two sub-adult (150 and 168 cm TL) and one mature individual (230 cm TL). They also reported that nighttime positions of lemon sharks tended to be located westward of their daytime locations for sub-adults, indicating an east-west diel migration. Yet, these area estimates and observations were based on limited tracks.

My objectives were to investigate movement pattern, home range, daily activity space, and diel distribution of the sub-adult lemon shark (150-200 cm TL) in Bimini, Bahamas. This study is part of an ongoing multidisciplinary investigation of the life history, energetics and ecology of the lemon shark to assess its role as an apex predator in a tropical marine ecosystem.

MATERIALS AND METHODS

Study site

The Biminis (25° 42' N, 79° 18' W) are a cluster of low relief subtropical islands on the western edge of the Great Bahama Bank by the eastern edge of the Gulf Stream, located approximately 86 km east of Miami, Florida (Figure 1). Bimini's three major islands - North, East, and South Bimini - are arranged in a triangle that encloses Bimini Lagoon, which is about 24 km^2. The floor of the lagoon contains carbonate sands with overerlying Pleistocene limestone. The upper layer of sand is bound together by gelatinous material that forms sub-tidal mats, a product of low turbulence levels and sediment movements. Large areas of the lagoon's floor are covered by turtle grass *(Thalassia testudinum)* and manatee grass *(Cymodocea manatorum*; Bathurst 1967). The bottom of Alicetown Channel and a few other areas in the lagoon are rocky (Harrison et al. 1970).

Bimini Lagoon is shallow; mean water depth is less than 30 to 100 cm, except for the Alicetown and Bonefish Hole channels that can be as deep as 5 m. Water depths on the Great Bahama Bank east of Bimini rarely exceed 2 m (Bathurst 1967). West of Bimini, however, the sea floor slopes gently to approximately 40 m depth before dropping sharply to about 800 m less than one km off shore at the edge of the Florida Straits. Turekian (1957) described three water masses in Bimini Lagoon: an indigenous water mass that moves in and out of the North Sound with the tide; a mass from the Florida Straits entering Alicetown Channel through the southwestern channel entrance; and a mass entering from the Great Bahama Bank through the waterway of East Bimini and the inlet between East and South Bimini. The rate of mixing of these water masses is low. The salinity of the Gulf Stream west of Bimini, is 35.9‰ and the average salinity of the Great Bahama Bank is 37.7‰ or higher to the east of Bimini. In contrast, the salinity in Bimini Lagoon varies considerably, from 31.0 to 46.5‰, depending on the relative amount of precipitation and evaporation (Turekian 1957). Tides in Bimini are semidiurnal with tidal ranges from 75 to 150 cm (Squires 1958, Harison et al. 1970). Much of the lagoon is exposed during low tides (Bathurst 1967). Although sea level tends to rise and fall together on both sides of the Florida Straits (Wunsch et al. 1969), tidal predictions in Bimini can be difficult to make because of the shallow depth. A tidal lag of three hours may occur between the North Sound and the south side of South Bimini depending on wind velocity and direction. Water temperatures typically oscillate between 23 °C and 30 °C in Bimini but temperatures were recorded as low as 14 °C in the winter of 1991 and as high as 41 °C in June 1998 in the northern part of the lagoon.

The warm northward-moving Gulf Stream enables a tropical West Indian biota to flourish (Bathurst 1967). Most of the islands are undeveloped, except for Alicetown and Baileytown on the western part of North Bimini, and a few scattered houses and a small airport strip on South Bimini. The fringe of the unpopulated area of Bimini Lagoon consists primarily of red mangrove (*Rhizophora mangle*) and black mangrove (*Avicennia germinans*), which acts as a nursery ground for many tropical marine fishes, including lemon sharks. Additional detailed geological, hydrological, and ecological descriptions have been prepared (Newell and Imbrie 1955, Turekian 1957, Squires 1958, Voss and

Voss 1960, Bathurst 1967, Harrison et al. 1970, Wiedenmayer 1977, Jacobsen 1987, and Brattström 1992).

Telemetry equipment

Three models of cylinder shaped ultrasonic transmitters were used for tracking the sharks: a 9 g (in water) crystal controlled XTAL-87 (66x18 mm), a 8 g CHP-87-S (65x18mm), and a 12 g CHP-87-L (10x18 mm; Sonotronics, Tucson, Arizona, USA). The XTAL-87 model had a battery life of 40 d and generated a 10 ms pulse at a frequency of either 76.8 or 78.1 kHz. The interval between pulses varied between 748 and 1053 ms, and provided individual identification codes. The CHP-87-S transmitter had a battery life of 3 mo and CHP-87-L transmitters operated for 3 and 18. Each of these tags transmitted a unique code 18 bits in length. For instance, code "249" was identified by two pulses, rest, four pulses, rest, nine pulses, rest, repeat. All transmitters had frequencies between 75.5 and 78.1 kHz to allow signal detection on one frequency. In ideal conditions, the transmitter range was supposedly 3000 m, but range was much shorter in the field.

Ultrasonic pulses were detected with a directional hydrophone (model DH-2, Sonotronics) with a sensitivity of -84 dBV (re 1 micro Bar at one meter) and a beam width of +/- 6 degrees at half power points, mounted on a 150 cm long by 2.5 cm (1") diameter polyvinylchloride (PVC) pipe. The hydrophone was connected to a compact (16x16x10 cm and 1.5 kg) ultrasonic digital receiver (model USR-4D, Sonotronics) powered by a small 12 V, 20 A·h lead-acid motorcycle battery (model 4L-B, GNB, St. Paul, Minesota, USA). The receiver had 16 positions to enable digital tuning from 65 to

80 kHz in 1 kHz increments. The receiver and battery were placed in a small portable splash-proof plastic box for protection and ease of transport. A small set of headphones was connected to the receiver to monitor the ultrasonic pulses.

Capture and handling

Sub-adult lemon sharks measuring 140 to 200 cm TL (approximately 5 to 10 years old; Brown and Gruber 1988) were captured between November 1992 and April 1995 at three different sites: 1) along the eastern edge of Alicetown Channel, 2) along the east side of Bimini Lagoon, south of Bonefish hole; and 3) approximately 750 m southeast of South Bimini (Figure 1). Sharks were caught with longline gear consisting of two to four 15-hook sections. Each longline section was secured to the bottom with a Danforth anchor and a cinder block at each end. The ends of the longlines were marked with large fluorescent buoys tied to the cinder blocks. Gangions - consisting of a 10/0 or 11/0 stainless steel hook attached to two meters of 7x7 0.8 mm (1/32") diameter stainless steel wire and an additional two meters of 6.2 mm line - were attached to a ground line with tuna clips at 60 m intervals. The four-meter long leader allowed a shark to swim once hooked while the wire end of the leader prevented the shark from biting through the leader and escaping. Longlines were checked every 3 to 4 hours, and rebaited when necessary. Whenever possible, fresh barracuda *(Sphyraena barracuda)* or horse-eye jack (*Caranx latus*) were used for bait, but frozen barracuda and blue runner *(Caranx crysos)* also were used. Buoys were attached half way between each gangion to allow the ground line to be picked up at the proximity of any hooked shark. A small 8-cm diameter float was mounted on the gangion's leader approximately 75 cm from the hook to lift it from the bottom and reduce the chance of crabs taking the bait. Floats and buoys were marked with reflective tape to facilitate night operations. To reduce mortality, fishing operations were conducted from dusk to early morning when air and water temperatures tended to be cooler. Handling procedures were minimized because sub-adult lemon sharks were sensitive to the stress of capture and died easily. When a shark was caught, the gangion was removed from the ground line and tied to a cleat. A tail-rope was placed around the shark's caudal peduncle and also fastened to a cleat. The shark was then secured in the water along the gunwale of the boat. If the shark was poorly hooked, an additional body rope was tied just posterior of the pectoral girdle.

Once secured, the shark's condition was quickly evaluated by examining responsiveness and skin coloration. If deemed unfit, the shark was released immediately. However, if the shark's condition was stable, three length measurements were recorded: precaudal length, fork length, and TL. Gender was determined, and females were examined for evidence of mating scars. All lemon sharks were tagged with passive integrated transponders (PIT, Destron Faring, Inc., Saint Paul, Minesota, USA) using a modified hypodermic needle, whereas other shark species caught, such as bull shark, blacktip shark (*Carcharhinus limbatus*), Caribbean reef shark (*C. perezi*), tiger shark (*Galeocerdo cuvier*), and nurse shark (*Ginglymostoma cirratum*), were tagged with Casey M-Type stainless steel dart tags (National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Narragansett, Rhode Island, USA). A PIT tag is a tiny identification chip, enclosed in a 11x2 mm glass cylinder, which is injected into a specimen for permanent identification. The passive chip provides a unique code (i.e., does not need internal power supply) read by a reader. Both types of tags were positioned below the dorsal fin.

Lemon sharks measuring 140 to 200 cm TL were equipped with an ultrasonic transmitter. The transmitters were attached externally or internally depending on their battery lives. Transmitters with a shorter battery life (XTAL-87) were attached by inserting two steel darts through the skin into the epaxial musculature between the dorsal fins. A 91-kg (200 lb) test monofilament line was attached to the darts, threaded through the ends of the transmitters, which was secured close to the skin with steel press sleeves. Eventually, the dart corroded, and the package detached from the shark. Transmitters with a longer battery life (CHP-87) were surgically implanted in the shark's peritoneal cavity. To avoid respiratory complications for the shark, surgery was performed in the water with the shark's head oriented into the current. The shark was rolled over on its back to induce tonic immobility, a state of stillness or torpor (Chertock 1968, Watsky and Gruber 1990); thus, no anesthetic was required. The transmitter was inserted into the coelom through a 2-cm longitudinal incision on the ventral line 15 to 20 cm above the cloaca. To reduce the risk of lacerating the viscera while making the incision, the scalpel was held in an inverted position and the abdominal wall was raised with forceps (Morrissey 1991). After transmitter insertion, the incision was sutured with two to three stitches through both the skin and the peritoneum. The wound typically healed within 36 to 48 hours (unpubl. data).

Before release, the hook was removed with a pair of vice-grips and a rope, or with a dehooking device (Dehooker, Inc., Palm Coast, Florida, USA) if the shark swallowed the hook. In the cases where the hook could not be removed, it was cut with a pair of bolt cutters, or the wire leader was cut as close as possible to the hook with a pair of wire cutters. Then, the tail rope was removed and the shark set free. Once released, I kept close contact with the shark until its condition was determined stable. Typically, sharks would swim on their own immediately after release. In some cases, however, a shark would sink to the bottom after release. In those cases, to stimulate swimming, it was prodded by a free-diver. When this was not successful, the diver held the shark behind the pectoral girdle and swam with the shark into the prevailing current to increase the flow of water through its gills until it was able to swim on its own. Individual sharks were nicknamed according to their gender and the inspiration of the tagging team, using a different first initial whenever possible.

Tracking Operations

Flat-bottom skiffs (3.3 to 5.2 m long) with small 15 to 50 hp outboard motors were used as tracking boats, because they could be operated in the shallow depths (<30 cm), typical of the Bimini flats. Tracking vessels were crewed by a minimum of two people, a tracker at the bow with the tracking kit who listened for acoustical signals, and a driver responsible for navigation and data recording. In the first phase of tracking, one to three skiffs were sent out at a time following a specific search pattern covering the entire lagoon, with frequent stops to monitor ultrasonic signals. These stops were designed to maximize the chance of locating a tagged shark. Later, search patterns were modified based on time of day, tidal stage, weather conditions, and past experience.

When locating a tagged shark, the tracking vessel carefully approached the shark until the signal was strong in all directions at low gain setting, and latitude and longitude of the skiff were recorded with a hand-held global positioning system (GPS; Ensign, Trimble Navigation, Sunnyvale, California, USA). As GPS accuracy was supposed to be +/- 100 m, the position of the shark was assumed to be the same as the boat's position. In reality, the tracking crew tried to maintain a minimum distance of 30 m from the shark when taking a fix, and a greater distance between fixes, to avoid disturbing the shark's behavior. When the shark swam toward the boat, no effort was made to move away because the abrupt change in throttle would have altered the shark's swimming behavior. When GPS was not available, the position was determined by triangulation using a hand-held compass and known landmarks.

Signal intensity and angular reception was directly proportional to distance but also was affected greatly by bottom topography, current, water depth, sea state, and weather. The signal was detected to 1,000 m distance, or more, in one-meter deep water over a flat sand bottom in calm conditions, but it was reduced to only a few meters by wave action against the mangrove roots and reefs in shallow water habitats. Experienced trackers had a good idea of the shark's distance from the tracking boat depending on location and environmental conditions. Although the actual position of the tracking boat and the shark differed, it was reasonable to assume they were the same for the purposes of this study because of the size of the area covered by the sharks.

Two tracking techniques were used: "search and fix" and "continuous tracking." The search and fix technique was used to gain information on the size of the home range, large-scale movements, and habitat utilization. Once a shark was found, its location was taken and a search for another shark began. During continuous tracking, contact with a shark was maintained and movements were monitored throughout the tracking session. When possible, a continuous tracking session was 24 h duration to cover an entire diel cycle and almost two tidal cycles, because preliminary studies (Gruber et al. 1988) indicated that sub-adult lemon sharks might have diel patterns. During continuous tracking sessions the geographic positions were recorded at typically 15-minute intervals, but also at 5 and 30-minute intervals during some tracking sessions. The 15-minute interval was chosen for convenience, although it carries no biological significance. Other authors conducting this type of study have chosen the same time intervals (McKibben and Nelson 1986, Morrissey 1991, Holland et al. 1993, and Klimley 1993). Environmental data were recorded, including sea conditions, bottom type, water depth, and temperature. When visual contact with the shark was possible, swimming behaviors were recorded. The tracking boat and crew changed every 8 hours to refuel and recharge batteries. The latter technique provided more detailed information on the shark's movements and behavior throughout the diel cycle and tidal cycle.

Data analysis

Tracking data were grouped into four time periods - day, night, dawn and dusk. The day and night periods were 9 hours duration each, day from 0900 to 1800 hours (GMT –4), and night from 2100 to 0600 hours. The dawn and dusk periods were 3 hours each, from 0600 to 0900 hours, and 1800 to 2100 hours. These time periods were chosen to ensure that sunrise and sunset were included within the crepuscular periods throughout the entire year, and that the duration of the day and night periods remained constant throughout the year.

The best available map of Bimini (issued by the Land and Surveys Department, Nassau, Bahamas) was digitized and imported into a Geographic Information System (GIS; PC ArcInfo v 3.2.4, 1995, and ArcView v 3.1, 1998 Environmental Systems Research Institute, Inc., Redlands, California, USA). Geographic positions were translated into Universal Transverse Mercator coordinates using ArcInfo. ArcView was used to query desired sets of location (e.g. individual 24-hour tracks) and to plot shark movements on the Bimini map. Home range parameters were calculated with the Animal Movement Analysis ArcView extension (Hooge and Eichenlaub 1997).

All geographic fixes were used to determine the overall home range of each shark. Individual shark home ranges were estimated using the minimum convex polygon (MCP) method, the smallest possible convex polygon that included all the position fixes of a given shark (Mohr 1947). A polygon is convex if a straight line between any two points in the polygon is entirely included within the polygon. Land areas included within the MCP were removed from the estimates of home range size. The MCP was chosen because it is a non-statistical method that has no *a priori* assumption about the distribution of the animal in the environment and is not biased by autocorrelated data (Swihart and Slade 1985). In addition, MCP is easy to use and has been widely used, facilitating comparison with other studies. The MCP, however, is sensitive to sample size and to movement on the periphery of the home range. Because the MCP does not require independence among fixes, no fixes were removed from the analysis, thus providing the most accurate minimum home range size for individual sub-adult lemon sharks.

To minimize sample size biases and to cover an entire diel period, the remaining analyses were restricted to 24-hour continuous tracks only. Keeping constant contact with a shark could be difficult depending on water depth and weather conditions, and sometimes the signal was lost for short periods during a 24-hour period. To ensure that the entire diel period was equally represented within each track, coordinates for missing fixes were interpolated by averaging the coordinates of the preceding and following fix. However, when more than 21% of the fixes were missing over a 24-hour period, the track was removed from the analysis. Each 24-hour track was plotted over the Bimini map, and these plots were used to determine movement patterns during a diel period (described in the results).

Daily activity areas were estimated with two non-parametric methods: the MCP and the 95% fixed kernel density estimator (Worton 1989, Seaman and Powell 1996). The MCP only provides information on the size, and to a lesser extent, the shape of the home range, whereas the kernel home range estimator also provides information on the relative frequency distribution of the fixes within the home range, thus enabling detection of core areas. Core areas are defined by isopleths representing frequency of use of spatial areas. Day and night activity areas also were estimated with the kernel home range estimator. A parametric paired t-test and a non-parametric Wilcoxon signed rank test were used to compare day and night activity spaces (Systat v 8.0, Chicago, Illinois, USA 1998). For each fix, distance from shore was determined by creating buffers around the islands at 250 m intervals, and a Kolmogorov-Smirnov test for grouped continuous data was used to compare the distances from shore for day and night fixes (Zar 1984; Statview v 4.1, Abacus Concepts, Berkley, California, USA, 1992). Significance level (α) was set at 0.05 for all tests.

I used rate of movement (ROM) as a proxy for shark swimming speed. The ROM was estimated by calculating the distance traveled between two consecutive fixes and dividing it by the time elapsed between the two consecutive fixes. This indirect estimate of swimming speed is conservative, because it implies the sharks swim in a straight line between two consecutive fixes. For consistency, ROM was calculated only for successive positions separated by 13 to 17 minutes. Interpolated fixes were not used to calculate ROM. Mean ROMs of the four time periods for each 24-hour track were compared using a one-way ANOVA (Systat v 8.0).

RESULTS

I captured, tagged, and tracked 28 (13 females and 15 males) sub-adult lemon sharks, between November 1992 and October 1995 (Table 1). Twenty-two of these sharks were captured in Alicetown Channel, five in the eastern part of Bimini Lagoon, and one southeast of South Bimini (Figure 1). Sharks measured 144 to 198 cm TL ($\bar{x}$ =167, s = 15). I attached transmitters with short battery lives of 6 to 18 weeks on the 14 sharks captured before June 1994, and surgically implanted transmitters with a longer battery life of 18 mo in the coelom of the remaining 14 sharks. Individual sharks were tracked for 11 to 433 days ($\bar{x}$ = 94, s = 93) and a total of 11,786 geographic positions were recorded. The actual number of days of contact with individual tagged sharks varied from 5 to 99 days ($\bar{x}$ = 26, s = 22). We completed 43 continuous 24-hour tracks for 15 sharks measuring from 150 to 198 cm TL ($\bar{x}$ = 168, s = 16). The number of 24-hour tracks completed per individual shark ranged from 1 to 6 ($\bar{x}$ = 3, s = 2).

All sub-adult lemon sharks tracked in Bimini remained within 6.5 km from shore (Figure 2). Most of their movements were confined within the lagoon and to a lesser extent off South Point and around North Rock. Occasionally, sub-adult lemon sharks would roam along the shoreline on the west side of North and South Bimini but they remained within 300 m from shore. These excursions were limited to dusk and night. Two sharks (Andromeda and Prince) traveled along a shallow ledge east of Bimini Lagoon. On one occasion, Andromeda wandered 4.5 km off the eastern shores of Bimini. Prince swam east of the lagoon during five different tracking sessions, and was recorded as far as 6.5 km from the nearest shore.

Mean MCP home range area was 21.4 km^2 (s = 9.9), but half of the home ranges were 17 to 22 km^2 (Figure 3). The largest estimated home range was 61.3 km^2 for Prince, a 195 cm TL male. Prince was one of the largest sharks and had the greatest number of fixes. However, there was no statistically significant linear relationship between home range size and total length of sharks, or between home range size and number of fixes per shark. The smallest estimated home range was 2.4 km^2 for Homer, a shark that had only 19 fixes on six different days. Only one of Homer's fixes was recorded at night and 63% of all his fixes were collected within three hours during the middle of the day.

I organized the 24-hour tracks into six categories based on their diel movement patterns: classic East-West, mini East-West, great East-West, South-North and North-South, and no apparent diel patterns described below (Figure 4). These diel movement pattern categories were characterized by distinct day and night activity spaces. Sharks moved from one activity space to the other at crepuscular hours. For all East-West diel patterns, the shark's day positions were eastward of its night positions.

The classic East-West diel movement pattern was observed for eight sharks during fourteen 24-hour tracks (Figure 5). The sharks that followed this pattern occupied the eastern part of Bimini Lagoon during the day. On one occasion, a shark made a jaunt along the east side of East Bimini up to North Rock and returned to the lagoon four hours later (Figure 5 a). The sharks moved westward near dusk and occupied the western part of the lagoon during night. They used Alicetown Channel but spent most of the night on the shallow flat at the eastern edge of the channel, around the western cays. They also swam along the mangrove-fringed shoreline of the west side of East Bimini and the northwestern side of South Bimini. Two sharks entered the North Sound (Figure 5 h and j). Near dawn these sharks moved eastward back to the eastern part of Bimini Lagoon.

The mini East-West diel movement pattern was observed for three sharks during five 24-hour tracks. Akin to the classic East-West diel patterns, nighttime positions during the mini East-West diel movement patterns were restricted to a small area in the southwestern part of Bimini Lagoon – from the entrance of Pirates' Well to Pigeon Cay to the east and the southern part of Alicetown Channel to the west. Daytime positions were eastward of nighttime positions, but in contrast to the classic East-West, sharks remained in the western part of the lagoon throughout the entire diel cycle (Figure 6).

The Great East-West diel movement pattern was observed in only one large shark, Prince, during two 24-hour tracks (Figure 7). As with the two previous East-West diel patterns, nighttime positions were westward from daytime positions. During the first 24-hour track, Prince spent the day northeast of Bimini Lagoon. At dusk, he moved to Southeast Point and to the south side of South Bimini. During nighttime, Prince swam in deeper water (2 to 5 m), around Round Rock and along the coral reef on the southwestern side of South Bimini. By daybreak, Prince moved back eastward and was west of South Point. Nighttime positions during the second track also were in deeper water along the west side of North Bimini.

The South-North diel movement pattern was observed for three sharks during six 24-hour tracks (Figure 8). During these tracks, sharks restricted their movements to the eastern part of Bimini Lagoon. Daytime positions were typically southward from the nighttime positions. During night, they swam along the southern tip of East Bimini, into Bonefish Hole, and on one occasion along the southern shore of Sharkland.

The North-South diel movement pattern was observed for one shark, Dr. Groovy, for only two 24-hour tracks (Figure 9). He restricted his movements to the eastern part of Bimini Lagoon and along the southeastern side of South Bimini. Generally, daytime positions were north of nighttime positions. However, some daytime positions along the shore of South Bimini overlapped nighttime positions. During night, Dr. Groovy restricted his movement along the shoreline of South Bimini, except for one jaunt to Bonefish Hole during the second track.

Ten sharks for fourteen 24-hour tracks demonstrated no apparent diel movement pattern that clearly fitted one of the diel patterns described above (Figure 10). During two tracks, Cappysombadhi used a small area in the western part of Bimini Lagoon, with few or no differences between night and day positions during these two tracks (Figure 10 a and b). During a third track, Cappysombadhi restricted her day movements to the same area from the two previous tracks but moved eastward at dusk. During the night, she swam the northeastern part of the lagoon, then crossed the lagoon to the north side of South Bimini and swam westward along the shoreline to Pirates' Well (Figure 10 c). During two other tracks there were no apparent differences between day and night distribution (Figure 10 i and l). During the nine remaining tracks, however, the sharks swam closer to the shore and Alicetown Channel during the night than during the day (Figure 10 d-h, j, k, m and n).

The described diel movement patterns were observed in 66% of the 24-hour continuous tracks (Table 2). The East-West patterns accounted for 49% all 24-hour tracks and 72% of the tracks that displayed a clear diel movement pattern. Although 34% of the tracks did not fit one of the described diel patterns, in nine out of fourteen tracks, shark positions were closer to shore at nighttime than during daytime. Hence, 88% of the 24-hour tracks indicated a diel movement pattern.

Diel movement varied within and among sharks. More than one movement pattern was observed in nine out of the eleven sharks for which more than one 24-hour track was conducted. Cappysombahdi's tracks exhibited two classic East-West, one mini East-West and three tracks with no apparent patterns (Figure 5 e and f, Figure 6 d; and Figure 10 a-c). Wagamama displayed three classic East-West, one South-North, and one track with no apparent pattern (Figure 5 l-n, Figure 8 f, and Figure 10 n).

Some sharks, however, were more consistent. All four 24-hour tracks for Vera exhibited the South-North pattern (Figure 8) and the two tracks conducted for Ursula were the classic East-West pattern. All six tracks for Baccardi exhibited a East-West diel pattern (Figure 5 b-d, and Figure 6 a-c).

Activity areas for daytime, nighttime, and the entire diel period were highly variable in the 42 continuous 24-hour tracks for which there was a sufficient number of fixes to calculate activity areas (Table 3). During a 24-hour period, sub-adult lemon sharks used 6% to 81% ($\bar{x}$ = 41, s = 21) of their overall home range. The mean daily activity area estimated with the MCP method ($\bar{x}$ = 9.3 km^2, s = 5.4) was smaller than the mean daily activity space area estimated with the kernel method ($\bar{x}$ = 12.0 km^2, s = 7), but the difference was not statistically significant. Daytime activity areas were 0.3 to 23.4 km^2 ($\bar{x}$ = 6.7, s = 5.3), and nighttime activity areas were 0.6 to 25.3 km^2 ($\bar{x}$ = 5.5, s = 5.1). There was no significant size difference between day and night activity space.

Sub-adult lemon sharks remained close to shore: 98% of the 1,506 daytime and 1,505 nighttime position fixes were less than 2,000 m from shore. Sharks were closer to shore at night than during day for 42 continuous 24-hour tracks (Kolmogov-Smirnov goodness of fit, P <0.0001). During night, sharks were located closer to shore more frequently than farther from shore, whereas during daytime they were evenly distributed away from shore (Figure 11). At night, 75% of the fixes were within 500 m from shore, but only 31% of the day positions were less than 500 m from shore. During the day, sharks swam to about 5,500 m from shore, whereas sharks restricted their movements within 2,250 m from shore at night.

Sub-adult lemon sharks did not utilize their activity area uniformly. The kernel method revealed core areas (Figure 12). There were distinct day and night core areas in more than 80% of the 24-hour tracks. Night core areas were typically closer to shore or Alicetown Channel than day core areas for all 24-hour tracks that followed one of the described diel movement patterns (Figure 12 a). This diel core area distribution also was observed in the majority of the fourteen 24-hour tracks for which no apparent diel pattern was described (Figure 12 b). However, geographic differences between day and night core areas were not apparent in all tracks (Figure 12 c).

The night activity area for all 42 continuous 24-hour tracks combined was 32.1 km^2 and the combined day activity space was 18.7 km^2 (Figure 13). All but 3% of the day area was within the night activity area. However, the utilization of the activity space differed throughout the diel cycle. The major daytime core area was located in the northeastern part of Bimini Lagoon south of East Point. A secondary day core area was located east of Pirates' Well. The major nighttime core area was in the southwestern corner of the lagoon in Alicetown Channel and the flats between Pirates' Well and Pigeon Cay. A second core area was located in and around the Bonefish Hole Channel along the southern tip of East Bimini. The nighttime activity space covered most of the lagoon shoreline.

ROM was calculated for 34 continuous 24-hour tracks yielding 2,512 fifteen-minute intervals – 314 dawn, 974 daytime, 318 dusk, and 905 nighttime intervals. The mean ROM for the four time periods ranged from 1.33 km/hr during day to 1.58 km/hr at dawn (Figure 14). Variances were unequal among the diel periods but the difference among them was less than three times, therefore, it probably was appropriate to use a one-way ANOVA (Underwood 1997). Mean ROMs were greater during crepuscular hours than during daytime and nighttime but the differences were not statistically significant ($P < 0.266$).

Occasionally, up to three sharks were tracked simultaneously for short periods of time, and as many as five telemetered sharks were located within the same hour in the southwestern part of the lagoon at night and in the northeastern part of the lagoon during the day. Sub-adult lemon sharks were seen swimming together from the tracking vessel. Four types of aggregations were recorded: 1) two to five sharks were seen at one time swimming in the same general direction, and this swimming pattern behavior was typically observed around crepuscular hours during the classic East-West diel movement pattern; 2) two or three sharks were following each other in a straight-line formation or swimming in a circle; 3) dense aggregations of up to 25 sharks were observed meandering among each other in areas as small as approximately 15 m by 20 m; and 4) loose aggregations of up to 29 sharks were seen meandering in the same general area. Sub-adult lemon sharks also were seen lying on the bottom, their mouths oriented upstream.

Sub-adult lemon sharks also were seen swimming behind two other elasmobranch species – nurse shark and southern stingray (*Dasyatus americana*). These elasmobranchs were of the same size as the sub-adult lemon shark and did not appear to be threatened. Two teleost species were seen associated with sub-adult lemon shark, bar jack (*Caranx ruber*) and sharksucker (*Echeneis nucrates*).

DISCUSSION

Capture and handling methods proved to be safe and effective. Only one telemetered shark died as a result of capture or handling during this study. This was a significant improvement over previous unpublished studies at the Bimini Biological Field Station where handling mortality could exceed 50%. The main reasons for this high survival rate were due in part to: 1) fishing only at night, when water temperature was cooler; 2) fishing in locations where water was well oxygenated (i.e. deeper water and currents); 3) frequently checking the longlines; and 4) strictly reducing handling time to a minimum. The incisions healed rapidly and completely. For example, Queen, a shark tagged on June 16, 1994 got entangled in fishing lines and mangrove roots 53 days after capture. When the fishing line was removed the scar was only a thin dark line and would have gone unnoticed if not specifically checked. Transmitters had no apparent effect on the sharks' swimming behavior. Tagged sharks were observed swimming alone and with other sharks but there appeared to be no differences in the behavior of the tagged and untagged sharks. This supports the assumption that the transmitter did not alter the sharks' movements and behaviors.

movements within defined areas or home ranges. During all 726 days of tracking, tagged sharks remained mostly within the lagoon at Bimini, even though other suitable habitats were available. Presence of additional suitable habitat was supported by visual observations of untagged sub-adult lemon sharks off Turtle Rock and Triangle Rock, from 2.2 to 4.8 km south of Bimini Islands. The home range estimates Sub-adult lemon sharks were not distributed randomly, but rather limited their appeared valid because they were not correlated with the number of position fixes. Only Homer's home range was underestimated because of the limited data recorded for this individual.

The two largest home ranges (63.3 km^2 for Prince and 37.7 km^2 for Andromeda) were recorded for the only two sharks that ventured East of Bimini Lagoon (Figure 3). This eastward movement could have been an exploratory jaunt for Andromeda because she did it on one occasion only. Prince, however, utilized that area more frequently. In both cases, the MCP method increased the total home range of these two sharks disproportionately because that method is sensitive to fixes near the boundary and to remain convex, the home range had to include large areas that had not been used by the shark. For example, the total area added to Andromeda's home range by this one brief excursion was 9.5 km^2, a 25 % increase. However, the MCP area for the jaunt was only 2 km^2, a 5% increase.

The mean home range (21.4 km^2) for all 28 of the sub-adult lemon sharks was 30 times larger than the mean home range (0.7 km^2) for juvenile lemon sharks (Morrissey and Gruber 1993a) and smaller than the 93 km^2 for a 230 cm TL lemon shark tracked in Bimini (Gruber et al. 1988). The home ranges calculated in this study are similar to the preliminary home ranges reported by Gruber et al. (1988) for two sub-adult lemon sharks in Bimini. Home range size was positively related with body size for juvenile lemon sharks (<1m TL, Morrissey and Gruber 1993a), but not for the sub-adult lemon sharks tracked during this study. Morrissey and Gruber (1993a) used the 95% MCP area to estimate home range and this study used the 100% MCP method. Although the two methods differed, the size increase in home range from juveniles to sub-adults was so great that it is reasonable to conclude that range size is positively correlated with body length between the different age groups.

Sub-adult lemon sharks remained in shallow water in contrast to adult lemon sharks that occupied deeper reefs (Gruber et al. 1988). Prince was one of the largest shark tracked during this study and had the largest home range. He swam the farthest east, was the only shark to use both the Alicetown Channel and the south side of South Bimini, and was the only shark tracked off the western side of South Bimini. Also, Prince ventured to the coral reef off the western side of South Bimini, remaining in water less than ten meters at all times. Morrissey and Gruber (1993b) suggested that juvenile lemon sharks limited their home ranges to small shallow areas to avoid predation. The sub-adult lemon sharks tracked during this study were probably large enough to be virtually free of predation, with the possible exception of large tiger sharks. Tiger sharks were caught on the longlines during the night and early morning in the eastern lagoon and off South Bimini.

Currently, there are not enough data to compare size of home ranges of lemon sharks with home ranges of other similar shark species. Evidence of home ranges and site fidelity has been reported for other species of coastal tropical sharks (Nelson and Johnson 1980, McKibben and Nelson 1986, Nelson 1990, Holland et al. 1993, Economakis and Lobel 1998), but few researchers have provided estimates of actual home range. McKibben and Nelson (1986) used the MCP method to calculate activity areas 0.19 to 53 km^2 for the grey reef shark (*Carcharhinus amblyrhynchos*) at Enewetak, Marshall Islands, but sizes of activity space were strongly correlated with the number of position fixes. In addition, they did not report the size of the sharks tagged and the tracking sessions were limited to two to six days of intermittent contact during 2 to 23 days.

Home ranges of sub-adult lemon sharks appeared stable throughout time but resightings during the years were uncommon. Wagamama was the only one of ten sharks tagged during summer 1994 that was relocated the following summer despite intensive search effort. The remaining sharks either; 1) left Bimini; 2) were caught; 3) lost their transmitters; or 4) had transmitter failures. Although tagged sharks may have left Bimini, no shark left the islands while tracked during any of the 726 days of contact. At least two of the 28 sharks were captured by fishermen. A local fisherman caught Prince and Roxanne with hook and line in the southwestern part of Alicetown Channel during fall of 1996. Roxanne was tagged in summer 1994 but was not seen in 1995. Her death in 1996 doesn't explain why she was not located during 1995. Other tagged sharks also may have been fished.

It is unlikely that tagged sharks shed their transmitters because the incision was less than two cm and healed within a few days after surgery. If a shark rejected its transmitter, it probably would have occurred soon after surgery. In addition, the trackers probably would have located the transmitters if they were shed in Bimini, as they did for some of the transmitters that had been attached externally and were shed. Transmitter failures may have been the main reason sharks were not relocated. At least two of the transmitters with a battery life of 18 months were defective.

The transmitter code for Wagamama was originally 2-4-9 but the following summer it switched to 3-8 before the signal intensity faded. The transmitter code for Vera was initially 3-8-4 when the shark was tagged in January 1995. By the end of June 1995, the code was replaced by a continuous series of pulses. These two sharks were recaptured with dip nets and their PIT tag confirmed their identity. If the missing sharks left Bimini, at least two returned. Roxanne and Iago were both recaptured in Bimini 911 and 714 days after they were tagged in 1994, respectively (Table 1).

The diel distribution observed in many sharks indicated that sub-adult lemon sharks may forage more actively at night than during the day. Based on species diversity, vegetation abundance, and hydrographic conditions, their nocturnal habitats are thought to be more productive than the habitats utilized during the day. The shoreline of Bimini, the Alicetown Channel and the Bonefish Hole Channel appear to be more productive areas than the center of Bimini Lagoon (Turekian 1957, Voss and Voss 1960, Wiedenmayer 1977). The mangrove-fringed coastlines and the patchy coral reef on the west side of North and South Bimini have a diverse and abundant fauna and flora. The channels are dynamic areas that are bordered by turtle grass beds, which must be highly productive compared with the sandy bottom of the lagoon. Gulf Stream water flushes in and out of Alicetown Channel with the tides, and the floor of the lagoon is covered by turtle grass. Other areas like the Sharkland and Bonefish Hole areas may also be productive, but these areas are inaccessible to sub-adult lemon sharks during low tides. These night areas are potential feeding grounds for sub-adult lemon sharks. Cortes and Gruber (1990) did not find any diel feeding patterns in young and sub-adult lemon sharks and feeding was intermittent and asynchronous. In addition, night ROMs were not significantly greater than day ROMs during this during this study. However, Nixon and Gruber (1988) reported greater oxygen consumption and swimming speed at night than during the day for lemon sharks in a laboratory experiment. Increased night activity and nocturnal feeding occur in other shark species including the horn shark (*Heterodontus francisci*; Nelson and Johnson 1970, Strong 1989), the swell shark (*Cephallocsylium ventriosum*; Nelson and Johnson 1970), the angel shark (*Squatina californica*; Standora and Nelson 1977), the blue shark (*Prionace glaucae*; Sciarrotta and Nelson 1977, Pittenger 1984), the whitetip reef shark (*Triaenodon obesus*; Nelson and Johnson 1980), and the grey reef shark (McKibben and Nelson 1986).

There is no direct evidence that the sub-adult lemon sharks were feeding at night, but their sensory anatomy and their diel habitat utilization support nocturnal feeding. Lemon sharks may feed at night when they can approach their prey without being detected. Their eyes are well adapted for low light conditions because they have a high rod-to-cone cell ratio and a large *tapedum lucidum* (Hueter and Gruber 1982). Combined with their electroreception abilities, lemon sharks are well adapted for nocturnal activity. Stomach contents of 14 sub-adult lemon sharks (>140 cm TL) contained approximately 59% of teleost, 20% of elasmobranch, 6% of crustacean and 15% of turtle grass (Cortes and Gruber 1990). Turtle grass beds were more abundant in sub-adult lemon sharks' night activity space than in day activity space also suggesting benthic feeding.

Fish prey availability may have been greater at night than during the day because of diurnal-nocturnal changeover of fish prey activity pattern (Colette and Talbot 1972).

Yellowfin mojarras (*Gerres cinereus*) are common in Bimini Lagoon. Anecdotal observations made while snorkeling suggest that the mojarras are easier to approach at night while they hover over the bottom than during the day when they are more active. Larger prey such as snappers (Lutjanidae), and grunts (Haemulidae), and spiny lobster (*Pamulirus argus*) feed at night over turtle grass and near the mangroves, but are not available during the day because they are under ledges or within the mangrove roots.

The diurnal core areas may be interpreted as resting areas. Although these areas do not appear as productive as nocturnal core areas, their physical oceanographic conditions (i.e. deeper water, faster current, and perhaps more stable salinity, water temperature, and oxygen concentration) may have been more favorable to sub-adult lemon sharks than the night areas' physical oceanographic conditions. Also, as a result of tidal circulation and shallow depths, conditions near the shore and the center of Bimini Lagoon may not be optimal for sub-adult lemon sharks because large areas of the lagoon were exposed at low tide. The shallow depths resulted in extreme ranges of water temperature, salinity and oxygen concentration. On a windless summer day, water temperature in the Bimini Lagoon could exceed 40 °C, evaporation could have increased the salinity, and low mixing might have reduced oxygen concentrations. Fishing for juvenile and sub-adult lemon sharks under such conditions during previous studies in Bimini resulted in a high mortality rate, thus suggesting that sharks that remained within the lagoon during these extreme conditions could not tolerate any additional stress. However, conditions were not as drastic in the diurnal core areas because of their proximity to deeper open water and increased water circulation.

Sub-adult lemon sharks rarely used the Alicetown Channel during the daytime, although water was deep and tidal currents were stronger than in the lagoon. It is possible that the sharks avoided this area during the day because of boat traffic. Early tracking sessions during this study revealed that shark swimming behavior was affected by powerboats, particularly at high speed and during abrupt changes of throttle. Alicetown is the major human settlement in Bimini with numerous marinas on the west side of the channel. Boat traffic near the diurnal core areas was minimal compared to the Alicetown Channel traffic.

The nocturnal activity space possibly used for feeding was larger than the diurnal activity space possibly used for resting. Although there were no statistical differences between day and night activity spaces for individual 24-hour tracks, the night activity spaces for all 24-hour tracks for 15 sharks combined was 42% larger than the combined daytime activity areas. The requirements of the day resting areas should not be dependent on size of the activity space, whereas feeding areas where sharks depend on prey abundance and availability may need to be larger areas.

Although the 24-hour tracks were grouped into six categories, 88% of them displayed the same general movement pattern. During day tagged sharks remained mostly off the shoreline, and at night they moved closer to shore, to Alicetown Channel or to Bonefish Hole Channel. Although they are described using cardinal axes (East-West and North-South), there is no evidence that electromagnetic forces directed these movements. Rather, it appears more related to habitat types. This general diel pattern was predominant but there was a high degree of variation within it. This natural variation was noted within and among individual sharks.

The variation within diel patterns provided mixed evidence for resource partitioning. Sub-adult lemon sharks in Bimini might forage over different feeding grounds to reduce intraspecific competition. None of the 22 sharks tagged in Alicetown Channel swam on the south or west side of South Bimini and only two of the six sharks that were not tagged in Alicetwon Channel were tracked in the southwestern part Bimini Lagoon: Lady X and Prince. However, it was not unusual to observe up to five tagged sharks in the southwestern part of the lagoon during the same night.

Greater rates of movement during crepuscular periods, compared with daytime and nighttime ROMs, may reflect the more directional movement during crepuscular hours. Sharks typically moved from day to night activity spaces during crepuscular hours. Estimating swimming speed accurately for sub-adult lemon sharks without a speed-sensing transmitter was difficult. Shark positions needed to be as accurate as possible but the tracking boat had to stay far enough from the sharks to prevent altering their swimming behavior. Additionally, the GPS used during the study had an accuracy of +/- 100 m. Furthermore, the method used to calculate ROM assumed that the shark swam in a straight line during each interval. This assumption was regularly violated. Because of these difficulties, ROMs must be interpreted with caution. A shark that swims slowly in a straight line may have a greater ROM than a shark that swims quickly but changed its swimming direction frequently, and yet remained in the same area. The first estimate would be close to the true swimming speed of the shark, whereas the later would underestimate the true swimming speed of the shark.

The sub-adult lemon shark aggregations observed in the assumed resting area in the northeastern part of the lagoon suggest some degree of social interactions. The swimming formations and the dense aggregation were evidence that the sub-adult lemon sharks' movements were not always random. There was no evidence of aggressive behavior within the aggregations. Aggregations or schools have been reported for other coastal tropical shark species, including grey reef shark (McKibben and Nelson 1986, Economakis and Lobel 1998) and scalloped hammerhead (*Sphyrna lewini*; Klimley 1985, Holland et al. 1993). The purposes for loose aggregations in core areas could be reproduction, predator avoidance, or energy conservation as proposed in other shark studies (Klimley 1985, McKibben and Nelson 1986, Carrier et al. 1994, Economakis and Lobel 1998). The lemon sharks tracked during this study were still immature and large enough to be free from predation. Hence the purpose of these social interactions is unknown but is consistent with the aerial observations of Gruber et al. (1988).

The intraspecific relationships between sub-adult lemon sharks and nurse sharks and southern stingrays are unknown. The associations with remoras and bar jacks may be commensalism or mutualistic symbiotic relationships. The remora and the bar jack may gain protection, food, and hydrodynamic advantage from their association. Gruber et al. (1988) proposed that the jack also could use their host as a scratching surface and that the shark would benefit from the jack's sensory system. The remora and jack also may clean their host.

To better understand the sub-adult lemon shark's movement in Bimini, future studies should focus on its feeding habits and its habitats (biologically and physically). The tracking methods used during this study did not allow detection of feeding events. On a few occasions, a splash was recorded but it could not be associated with certainty with a feeding event. A transmitter that could detect pH change in the shark stomach may be a valuable tool to investigate feeding frequency and locations. Mapping habitat, prey diversity, and abundance would provide insight into available resources for lemon sharks in Bimini.

A better knowledge of the physical and chemical oceanography would also assist in describing areas preferred by sub-adult lemon sharks. Water circulation may influence sub-adult lemon shark movement. The role of tides may be of particular importance because the tidal range in Bimini Lagoon is often greater than the mean water depth. Movements of the dusky shark (*Carcharhinus obscurus*; Huish and Benedict 1978) in the Cape fear River, North Carolina, USA; the sandbar shark (*Carcharhinus plumbeus*; Medved and Marshall 1983) in Chincoteague Bay, Virginia, USA; and the grey reef shark (Nelson 1990) in Rangiroa, French Polynesia were correlated to tide.

A combination of ultrasonic and satellite tracking would allow monitoring of larger sub-adult and mature lemon sharks to determine when lemon sharks move to deeper water, how far to they go and whether they return to their place of birth to mate and give birth.

The data presented here are the most extensive tracking records of any coastal sharks. The 43 continuous 24-hour tracks demonstrated the occurrence of a clear diel movement pattern for sub-adult lemon sharks in Bimini. Results indicated that sub-adult lemon sharks foraged at night, close to the mangrove-fringed coastline, deep-water channels and to a lesser extent, the western shore of North and South Bimini. During daytime, tagged sharks moved further off shore to resting areas where physical and chemical oceanographic conditions were more stable and less extreme than in their nighttime activity spaces.

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Table 1. Tracking summary for the sub-adult lemon sharks captured in Bimini between November 1992 and April 1995. Sex is female (F) or male (M), and size is total length (TL, cm). Capture location is Alicetown Channel (AC), East Lagoon (EL) or South Bimini (SB). Duration is the number of days elapsed between the first and last day of contact. Days of contact are the actual number of days a shark was located. Number of fixes is the number of times that a shark position was recorded, and 24 h track is the number of times a shark was continuously tracked for a 24-hour period.

Shark	Sex	TL (cm)	Capture Location	Capture Date	Duration (day)	Days of contact	# of fixes	24 hr track
Andromeda	F	182	AC	03-Nov-92	122	20	226	1
Baccardi	M	151	AC	19-Jan-94	59	16	658	6
Cappysombahdi	F	160	AC	20-Feb-93	53	26	481	6
Damian	M	162	AC	17-Jun-94	128	51	492	
Dr.Groovy	M	156	EL	22-Jan-95	276	59	1465	3
Ennio	M	183	AC	13-Nov-92	11	7	50	
Foxy	F	150	AC	03-Aug-94	33	9	132	1
Gonzo	M	150	AC	22-Feb-93	32	11	50	
Homer	M	167	EL	28-Aug-94	20	6	19	
Iago	M	158	AC	21-Jun-94	59	29	397	1
Junkanoo	M	169	AC	24-Jan-94	19	6	80	
Krusty	M	196	SB	25-Aug-94	107	26	379	
Lisette	F	156	AC	13-Nov-92	70	24	180	
Matthias	M	190	AC	03-Nov-92	45	14	83	
Nanuk	M	156	AC	21-Feb-93	44	20	265	2
OJ	M	198	AC	21-Jun-94	59	28	286	1
Piccolino	M	144	AC	12-Nov-92	83	15	89	
Prince	M	195	EL	17-Apr-95	190	30	1328	4
Queen	F	176	AC	16-Jun-94	131	41	736	2
Roxanne	F	155	AC	18-Jun-94	157	50	600	2
Sebastian	M	164	AC	22-Feb-93	28	9	33	
Tootsie	F	186	AC	25-Jan-94	59	17	529	3
Ursula	F	173	AC	21-Jan-94	64	12	396	2
Vera	F	166	EL	22-Jan-95	219	63	1160	4
Wagamama	F	161	AC	19-Jun-94	433	99	1172	5
X (Lady)	F	161	EL	29-Aug-94	67	27	409	
Yolande	F	153	AC	13-Nov-92	56	5	43	
Zelma	F	166	AC	21-Feb-93	16	6	47	

Table 2. Diel movement patterns recorded during 24-hour continuous tracks for sub-adult lemon sharks in Bimini: Classic, Mini and Great East-West; South-North (S-N); and North-South (N-S). Capture location is Alicetown Channel (AC) or East Lagoon (EL).

			Diel movement patterns					
			East-West					
Shark	TL (cm)	Location	Classic	Mini	Great	S-N	N-S	Other
Andromeda	182	AC	1					
Baccardi	151	AC	3	3				
Cappysombahdi	160	AC	2	1				3
Dr.Groovy	156	EL					2	1
Foxy	150	AC						1
Iago	158	AC				1		
Nanuk	156	AC		1				1
OJ	198	AC						1
Prince	195	EL			2			2
Queen	176	AC	1					1
Roxanne	155	AC	1					1
Tootsie	186	AC	1					2
Ursula	173	AC	2					
Vera	166	EL				4		
Wagamama	161	AC	3			1		1
All sharks			14	5	2	6	2	14

Table 3. Home range and activity space areas estimated with the minimum convex polygon (MCP) and the 95% fixed kernel method for 24-hour continuous tracks of sub-adult lemon sharks in Bimini. Areas were calculated for daytime positions (day), nighttime positions (night) and the entire 24-hour track (24-hour). Percent HR is the ratio of an MCP area (based on a 24-hour track) divided by the entire home range of a shark (all fixes).

		MCP (km^2)			95% Kernel (km^2)		
Shark	Track code	All fixes	24-hour	% HR	24-hour	Day	Night
Andromeda	A-24h-1	37.7	22.5	60	26.2	23.6	3.8
Baccardi	B-24h-1	17.1	10.2	60	14.9	8.0	1.0
	B-24h-2		8.2	48	10.7	5.6	1.2
	B-24h-3		7.8	46	12.6	3.3	2.4
	B-24h-4		1.0	6	0.7	0.3	1.0
	B-24h-5		1.8	11	2.0	1.0	0.6
	B-24h-6		2.9	17	2.9	1.7	0.6
Cappysombahdi	C-24h-1	15.9	3.1	20	3.0	0.4	2.2
	C-24h-2		1.8	12	1.9	1.0	1.5
	C-24h-3		3.3	20	4.0	2.8	3.2
	C-24h-4		11.8	74	18.7	3.0	15.5
	C-24h-5		7.6	48	12.7	8.3	2.6
	C-24h-6		11.1	70	16.7	11.6	4.2
Dr. Groovy	DG-24h-1	21.9	10.8	49	13.0	6.7	9.3
	DG-24h-2		6.3	29	10.5	14.0	5.1
	DG-24h-3		10.2	47	13.9	5.2	8.5
Foxy	F-24h-1	12.5	6.7	54	7.9	10.7	3.1
Iago	I-24h-1	27.2	11.7	43	17.8	11.1	8.9
Nanuk	N-24h-1	23.1	6.2	27	9.1	10.9	2.0
	N-24h-2		2.7	12	4.4	1.8	1.4
OJ	O-24h-1	17.4	7.0	40	7.5	6.3	6.3
Prince	Pr-24h-1	61.3	8.9	15	7.2	6.5	5.5
	Pr-24h-2		26.0	42	27.8	21.9	4.8
	Pr-24h-3		15.6	25	10.2	1.1	25.3
	Pr-24hr-4		10.1	16	17.1	9.3	16.4
Queen	Q-24-1	20.4	14.8	72	20.3	3.5	3.7
	Q-24h-2		4.5	22	5.2	3.2	4.5
Roxanne	R-24h-1	27.0	5.8	21	6.7	4.4	4.7
	R-24h-2		17.0	63	26.3	6.1	7.8
Tootsie	T-24h-1	23.4	7.7	33	8.8	5.0	7.5
	T-24h-2		7.6	32	11.2	5.4	8.7
	T-24h-3		13.0	56	18.1	3.7	6.5

Table 3 continued

Shark	Track code	MCP (km^2) All fixes	MCP (km^2) 24-hour	% HR	95% Kernel (km^2) 24-hour	95% Kernel (km^2) Day	95% Kernel (km^2) Night
Ursula	U-24h-1	20.8	16.8	81	23.0	7.4	7.4
	U-24h-2		11.8	57	15.4	2.3	2.3
Vera	V-24h-1	20.0	6.1	31	8.0	8.3	3.0
	V-24h-2		6.7	34	8.9	7.3	1.8
	V-24h-3		10.4	52	9.8	8.7	4.8
	V-24h-4		5.3	27	5.3	7.7	3.7
Wagamama	W-24h-2	18.8	13.7	73	19.9	12.5	16.7
	W-24h-3		7.2	38	9.8	9.6	2.9
	W-24h-4		13.0	69	15.9	5.2	1.9
	W-24h-5		11.4	60	18.0	6.5	6.2

Figure 1

Sub-adult lemon sharks were tracked in the waters of Bimini, Bahamas – a cluster of tropical islands on the Great Bahama Bank on the eastern edge of the Gulf Stream. Alicetown Channel and Bonefish Hole Channel are two narrow channels with a maximum depth of 5 m. Water depth in Bimini Lagoon rarely exceeds 2 m and much of the lagoon may be exposed at low tide. Sharks were captured at three locations: Alicetown Channel, East Lagoon (EL) and off South Bimini (SB).

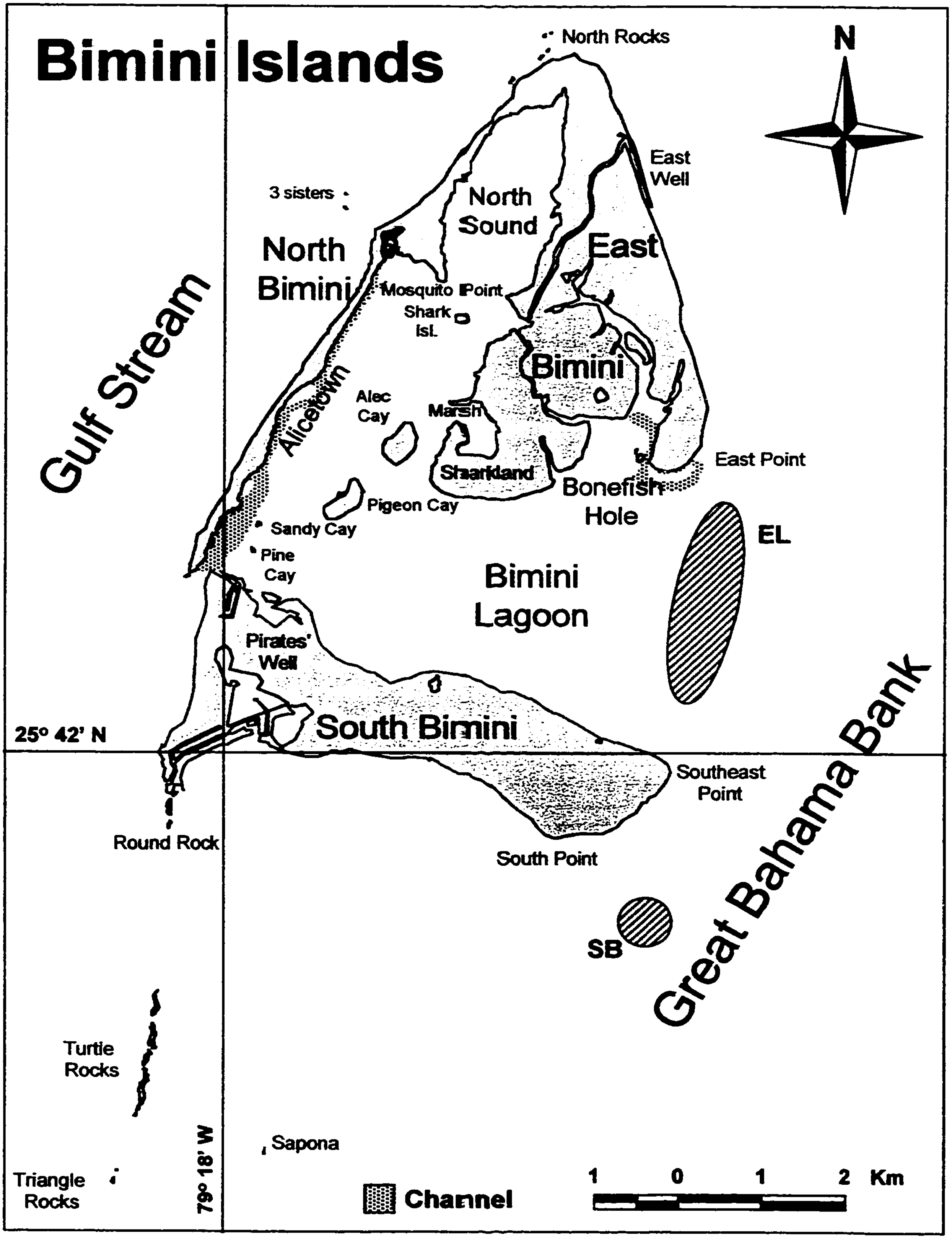
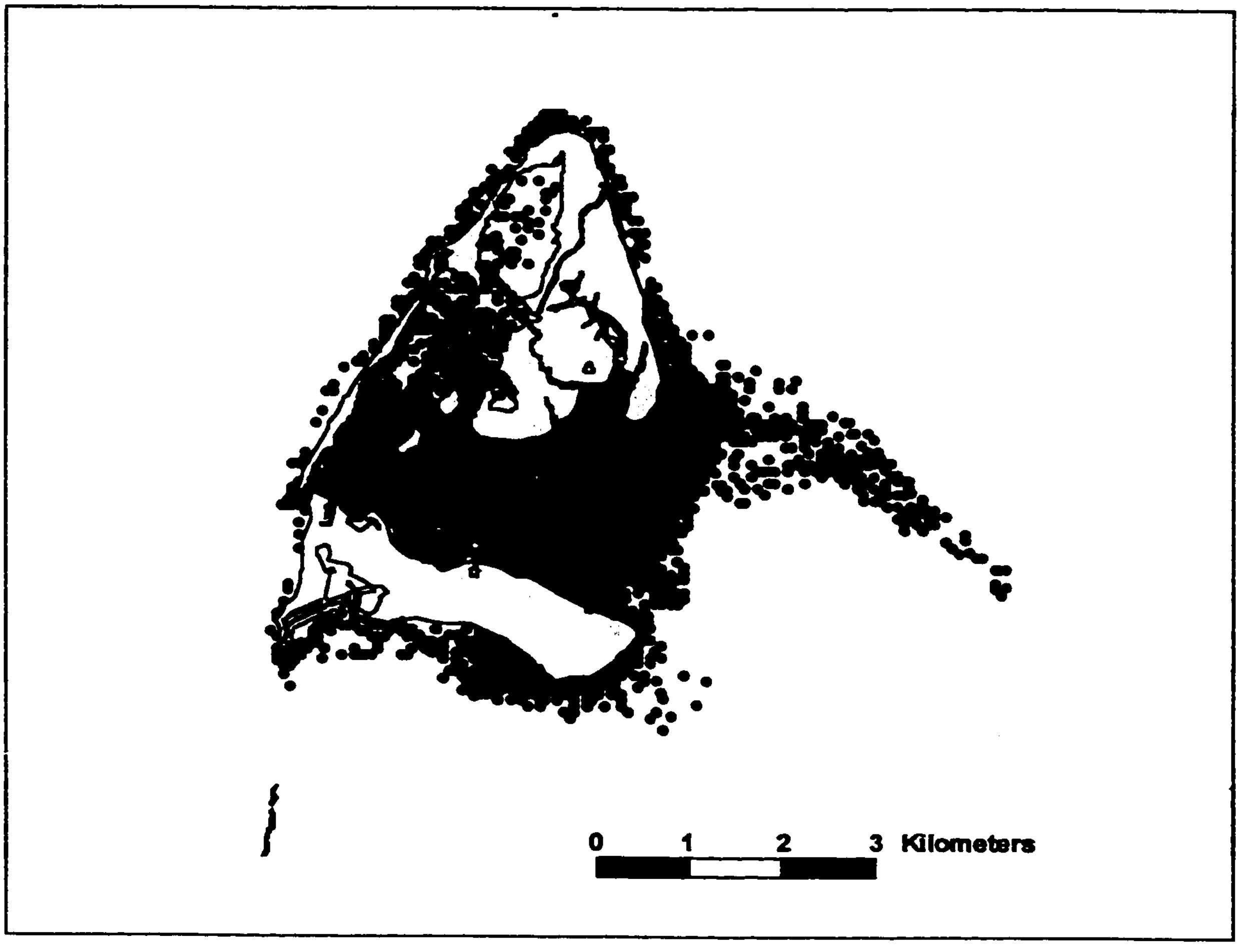

Bimini Islands
North Rocks
N
East Well
3 sisters
North Sound
East
North Bimini
Mosquito Point
Shark Isl.
Gulf Stream
Bimini
Alicetown
Alec Cay
Marsh
East Point
Sharkland
Bonefish Hole
Pigeon Cay
Sandy Cay
EL
Pine Cay
Bimini Lagoon
Pirates' Well
South Bimini
25° 42' N
Southeast Point
Great Bahama Bank
Round Rock
South Point
SB
Turtle Rocks
79° 18' W
Sapona
Triangle Rocks
Channel
1 0 1 2 Km

Figure 2

Distribution of all 11,786 positions (●) recorded for the sub-adult lemon sharks tracked in Bimini between November 1992 and October 1995.



0 1 2 3 Kilometers

Figure 3

Frequency histogram of home range (minimum convex polygon method) for 28 sub-adult lemon sharks tracked in Bimini.

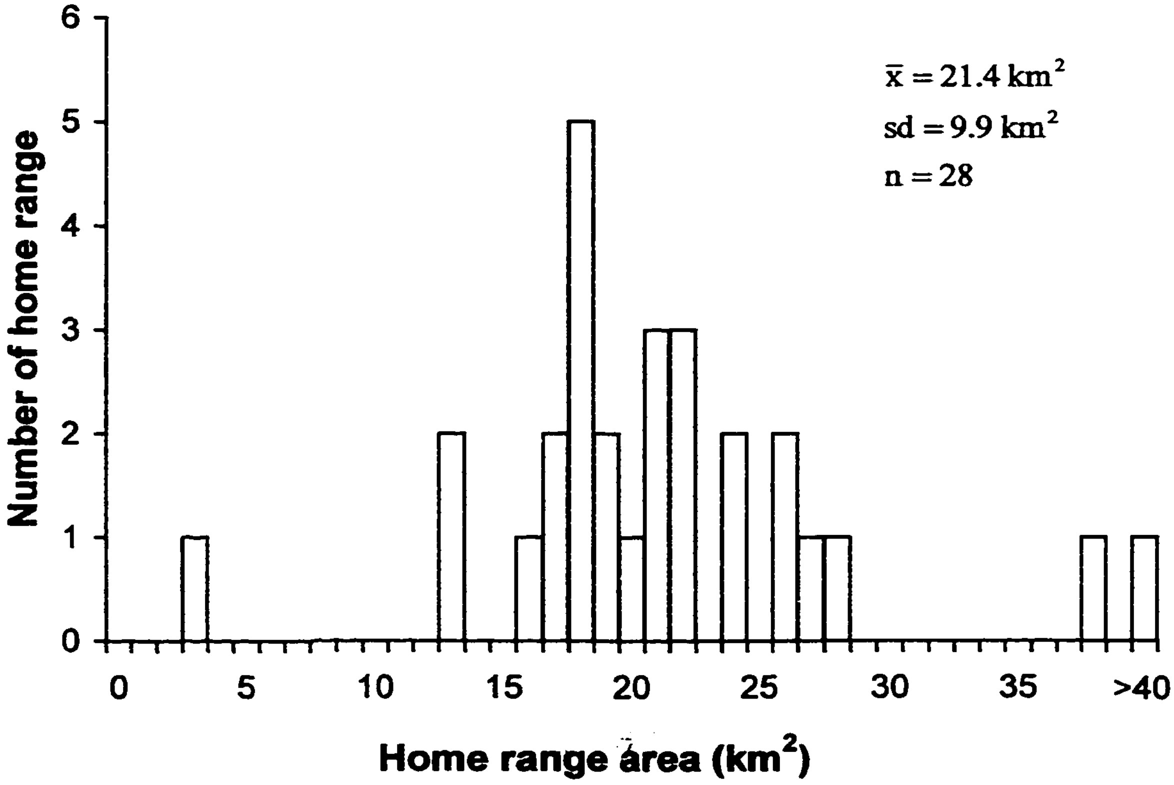

6
5
4
3
2
1
0
Number of home range
0
5
10
15
20
25
30
35
>40
Home range area (km2)
x̄ = 21.4 km2
sd = 9.9 km2
n = 28

Figure 4

Generalized diagram of five diel movement patterns described for sub-adult lemon sharks in Bimini: Classic, Mini and Great East–West (E-W); South–North (S-N); and North–South (N-S).

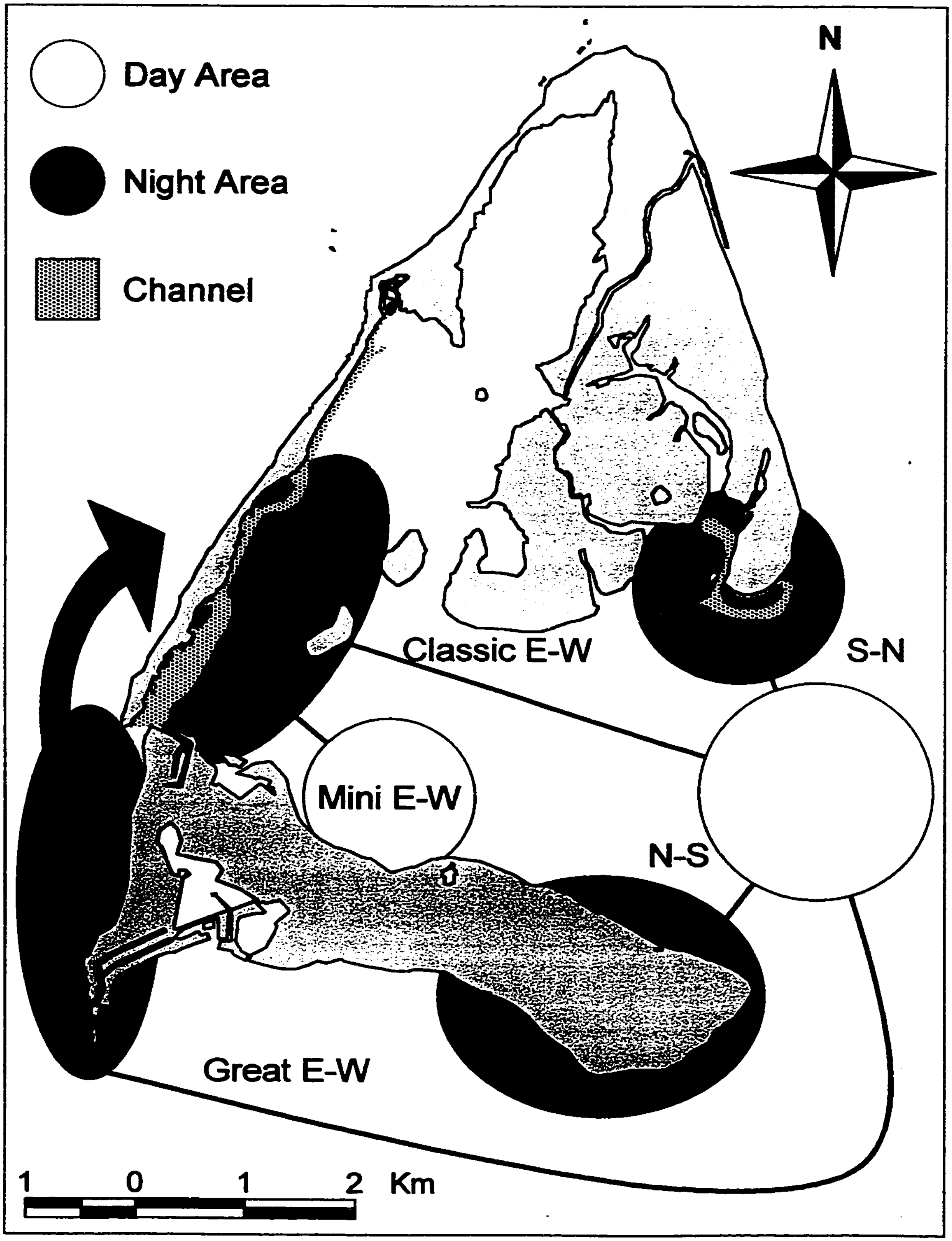
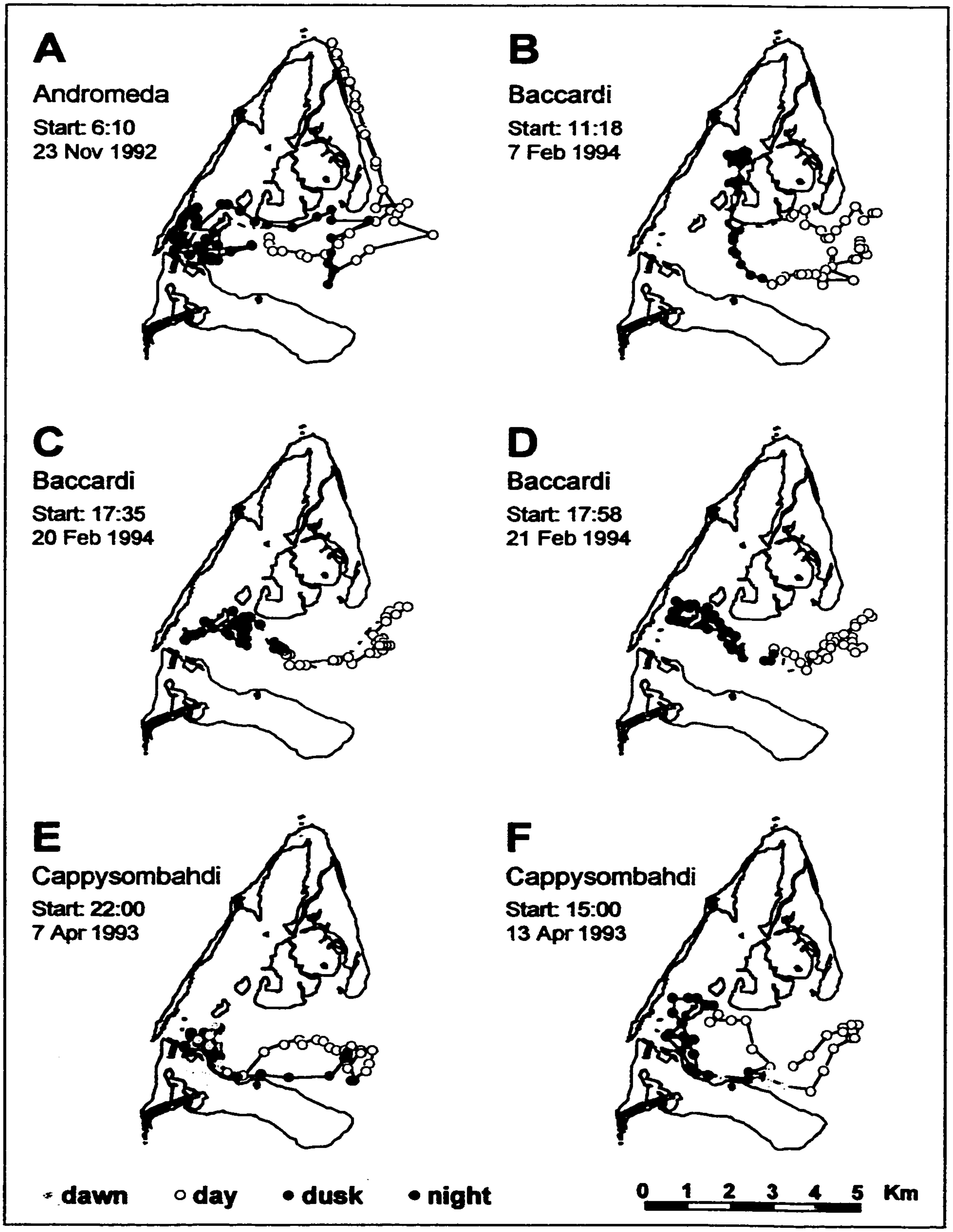
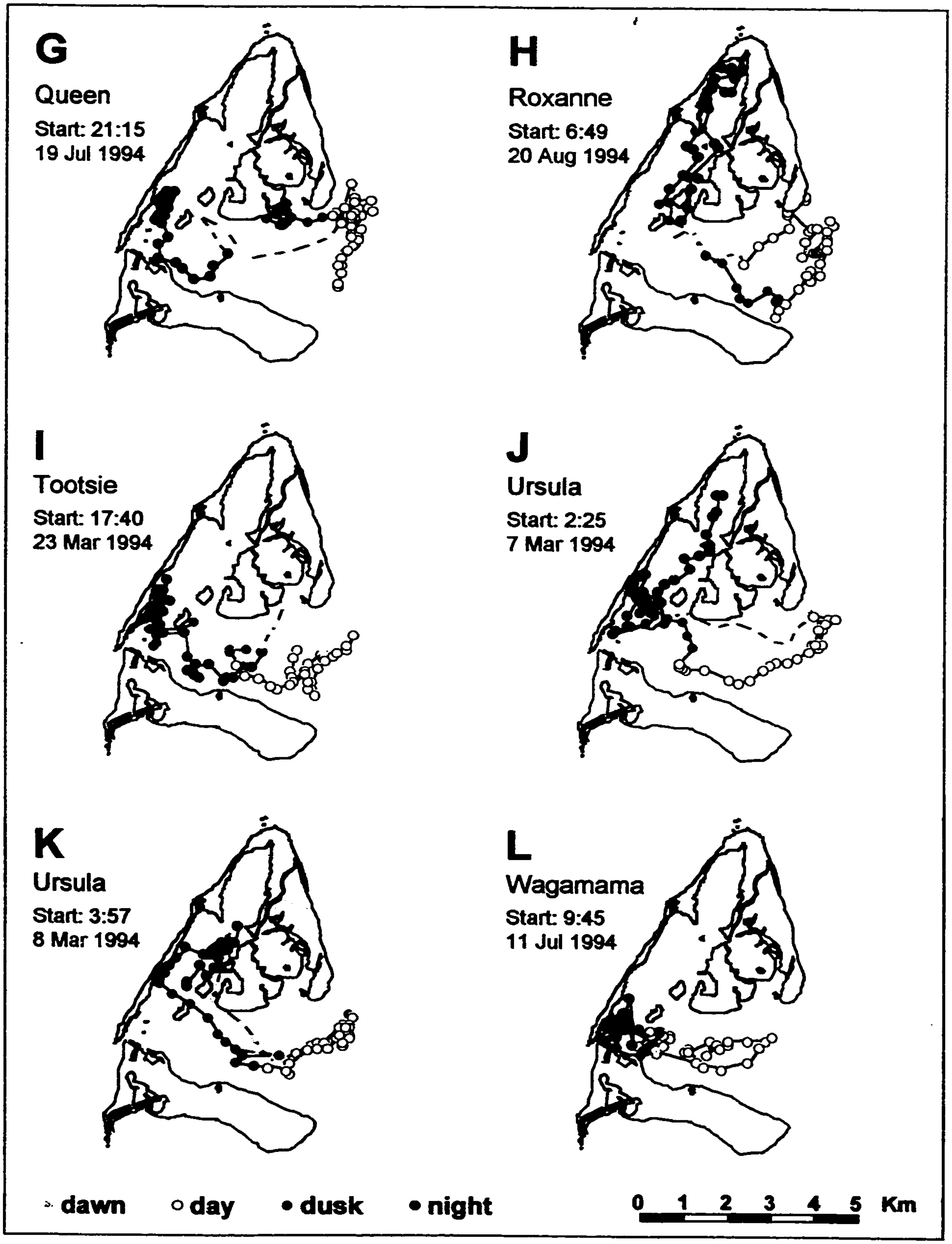

Day Area
Night Area
Channel
N
Classic E-W
S-N
Mini E-W
N-S
Great E-W
1 0 1 2 Km

Figure 5

Classic East-West diel movement patterns observed for eight individual sharks during fourteen 24-hour periods. Each plot represents one 24-hour continuous track with the time and date of the start of the track.


A
Andromeda
Start: 6:10
23 Nov 1992
B
Baccardi
Start: 11:18
7 Feb 1994
C
Baccardi
Start: 17:35
20 Feb 1994
D
Baccardi
Start: 17:58
21 Feb 1994
E
Cappysombahdi
Start: 22:00
7 Apr 1993
F
Cappysombahdi
Start: 15:00
13 Apr 1993
dawn
day
dusk
night
0 1 2 3 4 5 Km


G
Queen
Start: 21:15
19 Jul 1994
H
Roxanne
Start: 6:49
20 Aug 1994
I
Tootsie
Start: 17:40
23 Mar 1994
J
Ursula
Start: 2:25
7 Mar 1994
K
Ursula
Start: 3:57
8 Mar 1994
L
Wagamama
Start: 9:45
11 Jul 1994
dawn
day
dusk
night
0 1 2 3 4 5 Km

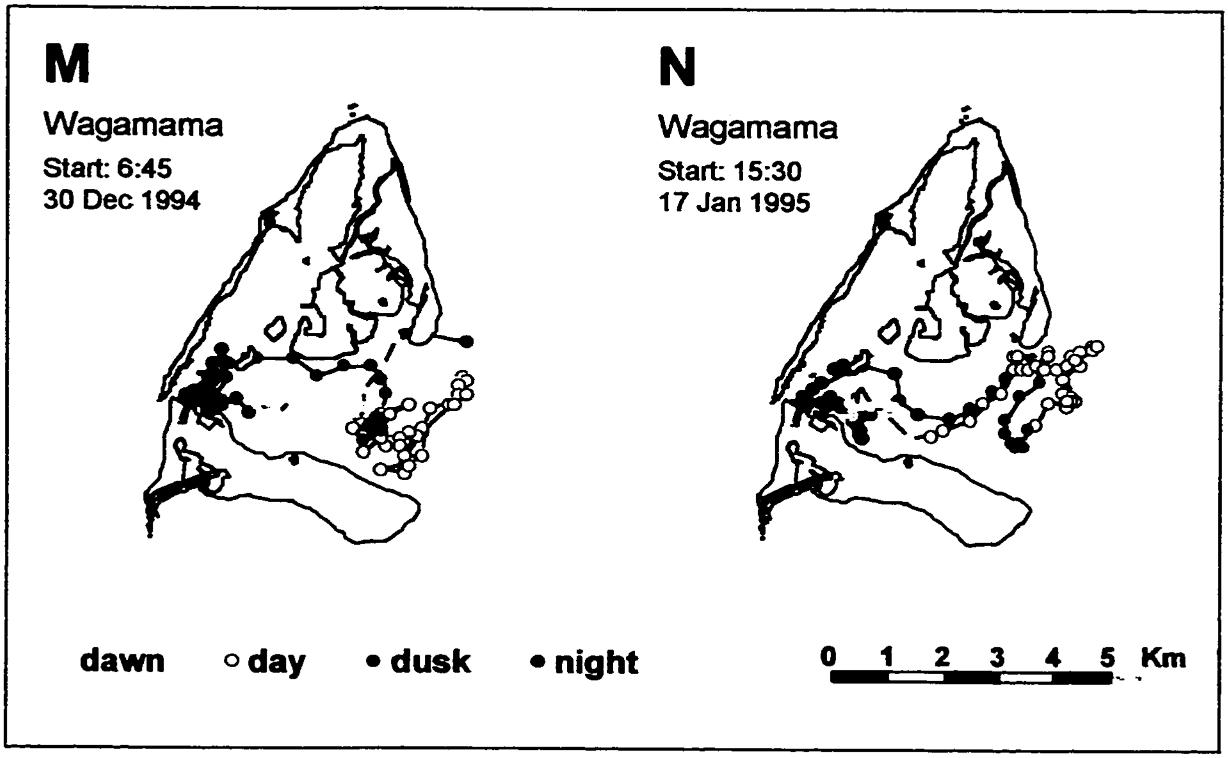

M
Wagamama
Start: 6:45
30 Dec 1994
N
Wagamama
Start: 15:30
17 Jan 1995
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 6

Mini East-West diel movement patterns observed for three individual sharks during five 24-hour periods. Each plot represents one 24-hour continuous track with the time and date of the start of the track.

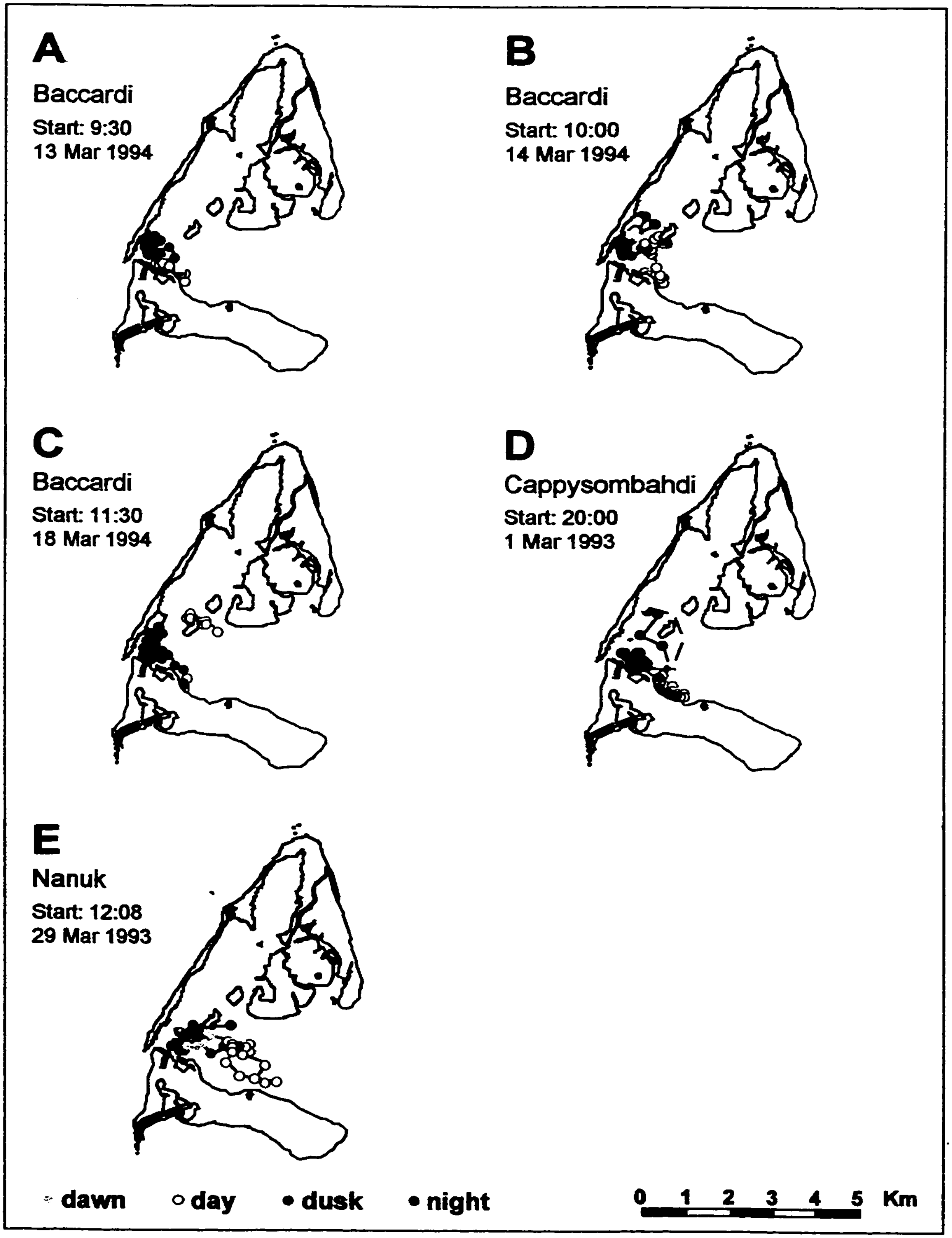

A
Baccardi
Start: 9:30
13 Mar 1994
B
Baccardi
Start: 10:00
14 Mar 1994
C
Baccardi
Start: 11:30
18 Mar 1994
D
Cappysombahdi
Start: 20:00
1 Mar 1993
E
Nanuk
Start: 12:08
29 Mar 1993
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 7

Great East-West diel movement patterns seen in one shark, Prince, during two 24-hour periods. Each plot represents one 24-hour continuous track with the time and date of the start of the track.

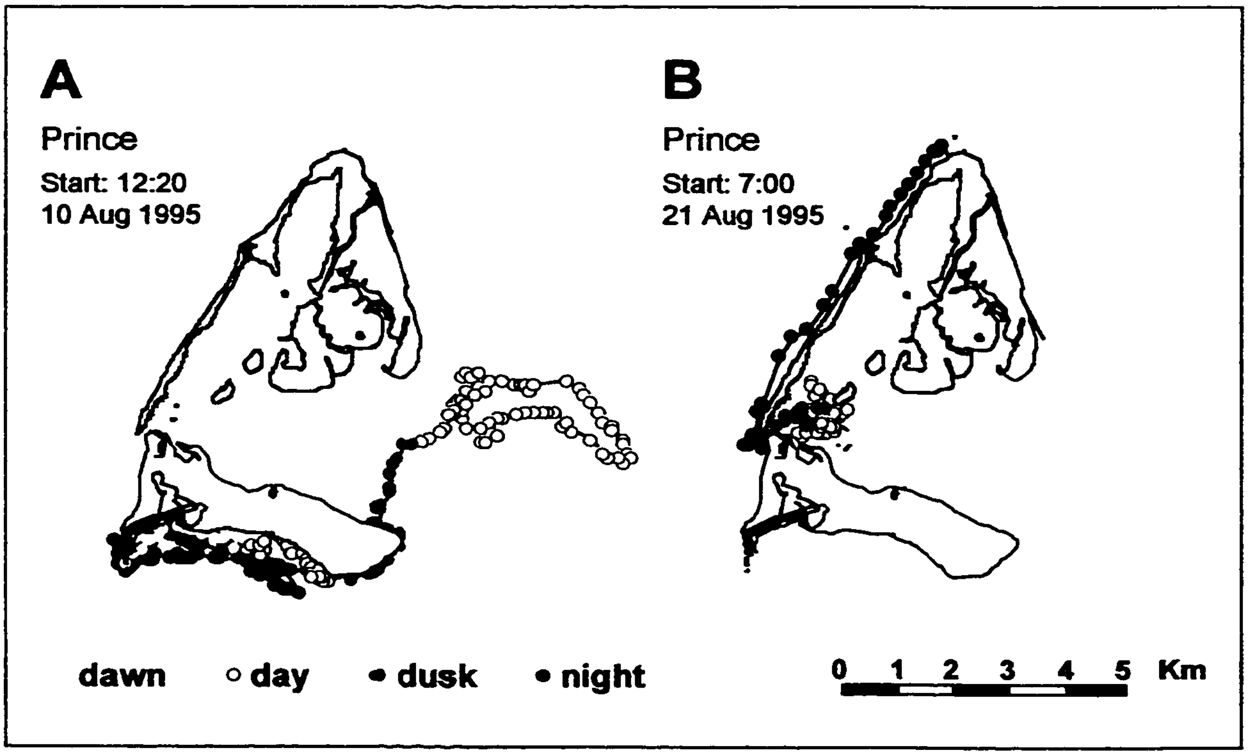

A
Prince
Start: 12:20
10 Aug 1995
B
Prince
Start: 7:00
21 Aug 1995
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 8

South-North diel movement patterns as determined for three individual sharks during six 24-hour periods. Each plot represents one 24-hour continuous track with the time and date of the start of the track.

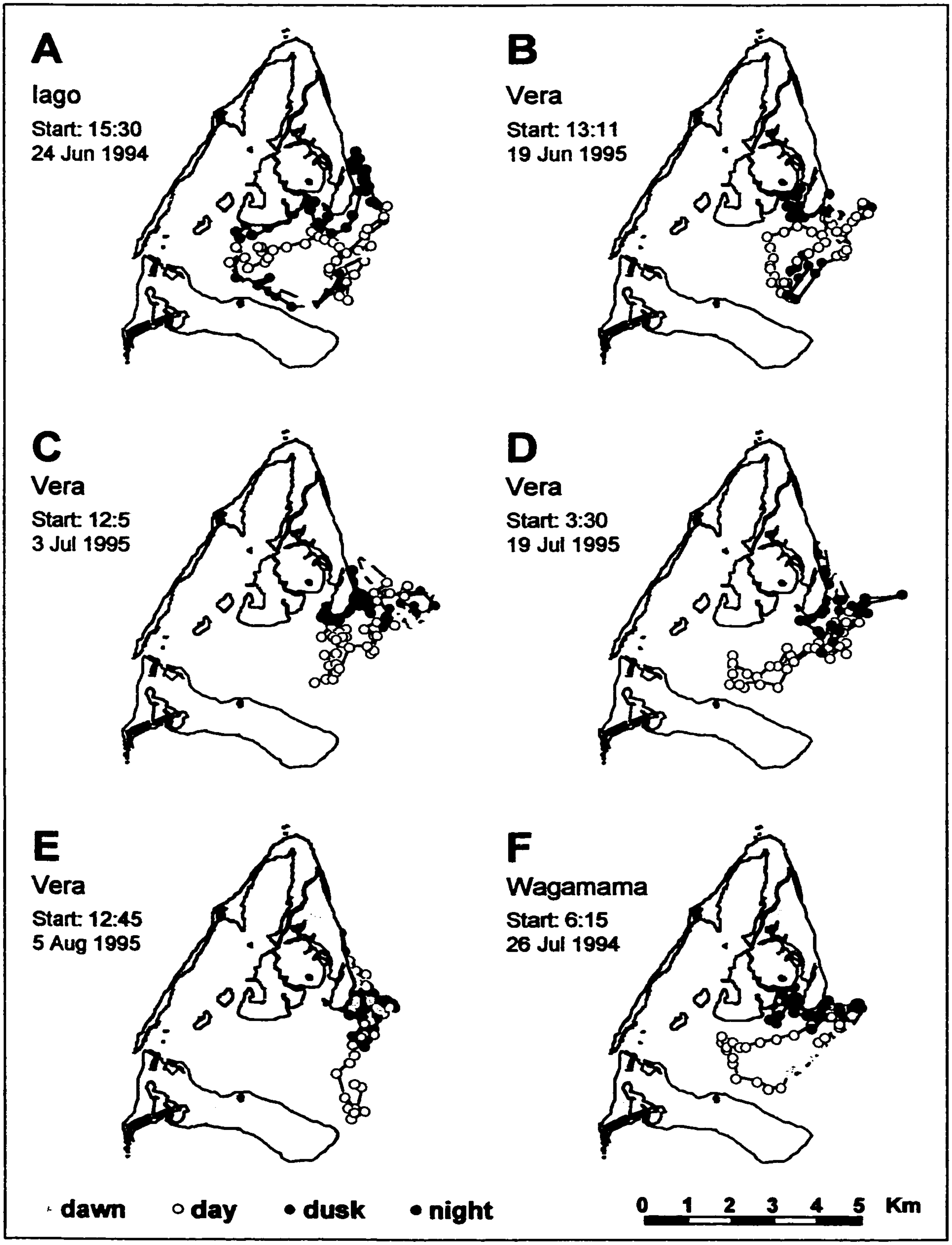

A
Iago
Start: 15:30
24 Jun 1994
B
Vera
Start: 13:11
19 Jun 1995
C
Vera
Start: 12:5
3 Jul 1995
D
Vera
Start: 3:30
19 Jul 1995
E
Vera
Start: 12:45
5 Aug 1995
F
Wagamama
Start: 6:15
26 Jul 1994
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 9

North-South diel movement patterns seen in one shark, Dr. Groovy, during two 24-hour periods. Each plot represents one 24-hour continuous track with the time and date of the start of the track.

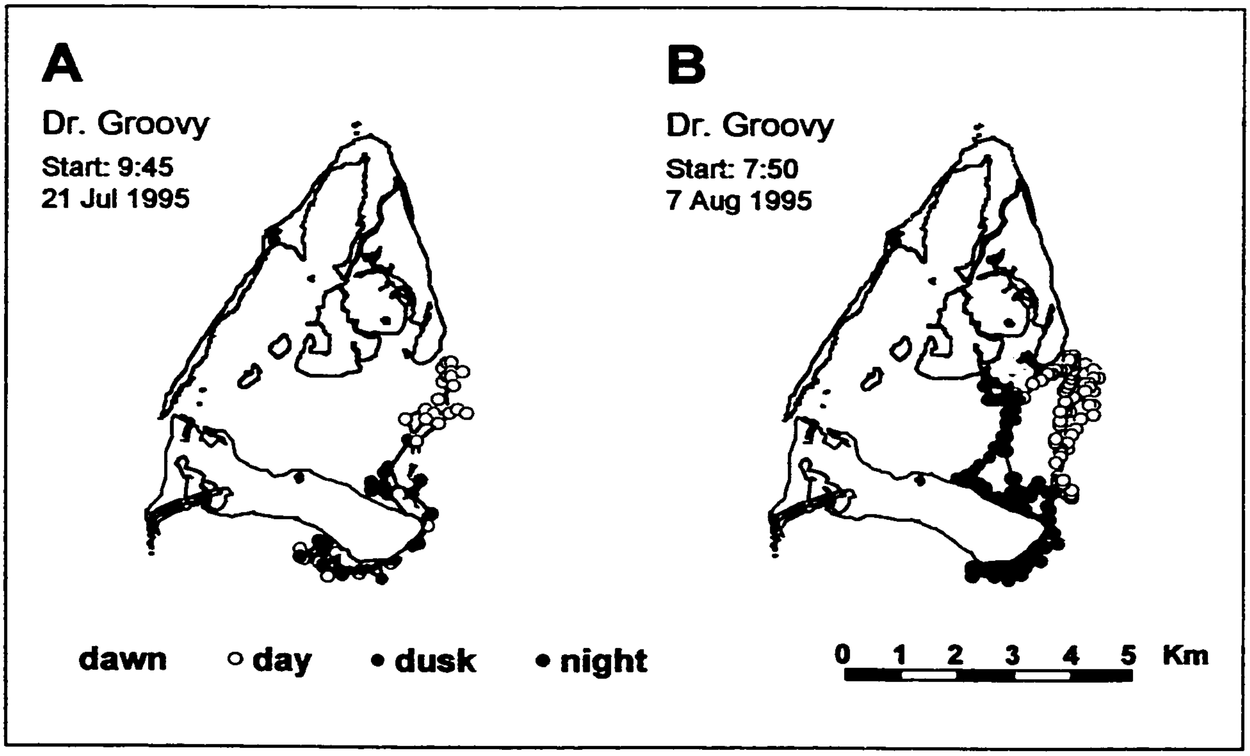
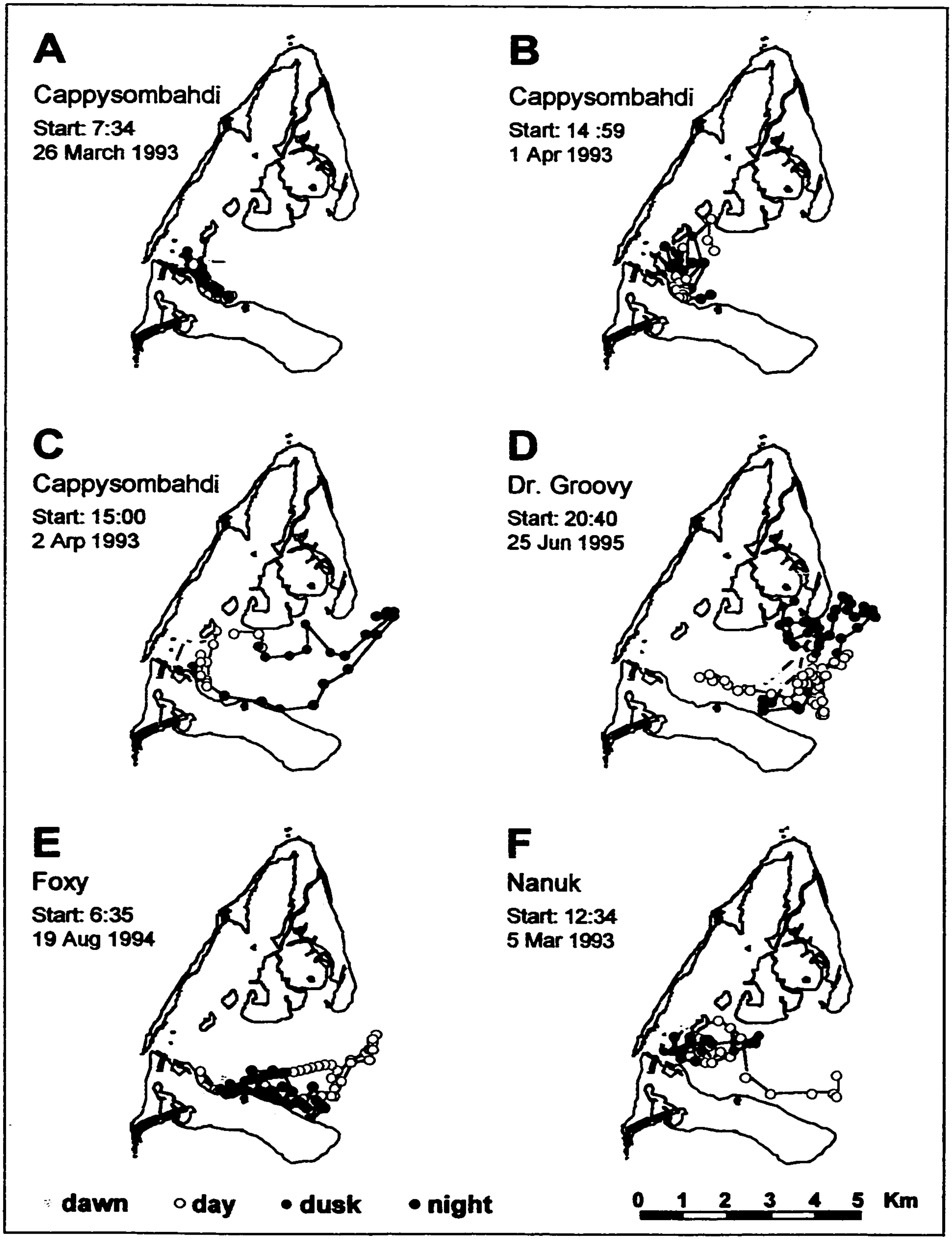
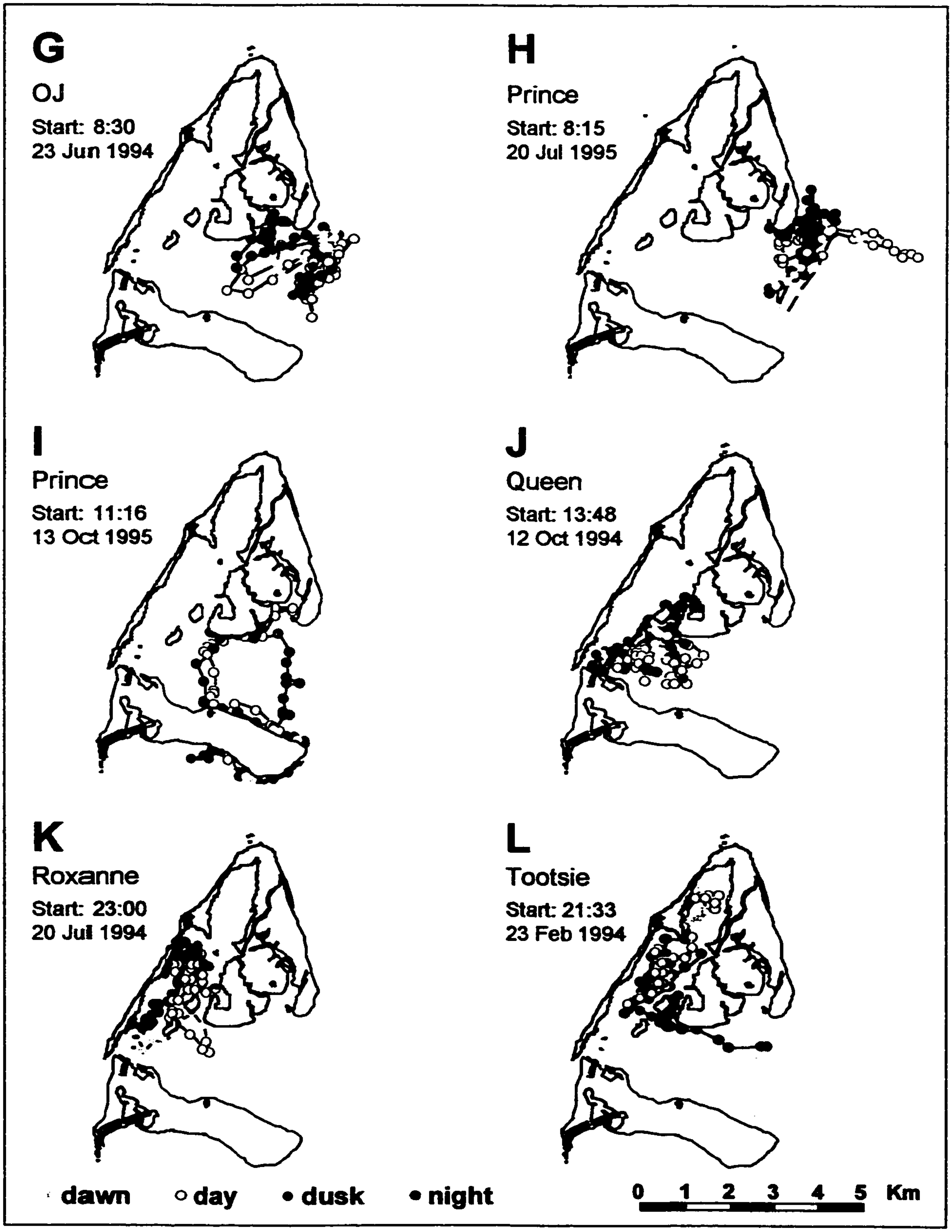

A
Dr. Groovy
Start: 9:45
21 Jul 1995
B
Dr. Groovy
Start: 7:50
7 Aug 1995
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 10

Plots for ten sharks that displayed no apparent diel movement patterns during fourteen continuous 24-hour tracks. Each plot represents one 24-hour continuous track with the time and date of the start of the track.


A
Cappysombahdi
Start: 7:34
26 March 1993
B
Cappysombahdi
Start: 14 :59
1 Apr 1993
C
Cappysombahdi
Start: 15:00
2 Arp 1993
D
Dr. Groovy
Start: 20:40
25 Jun 1995
E
Foxy
Start: 6:35
19 Aug 1994
F
Nanuk
Start: 12:34
5 Mar 1993
dawn
day
dusk
night
0 1 2 3 4 5 Km


G
OJ
Start: 8:30
23 Jun 1994
H
Prince
Start: 8:15
20 Jul 1995
I
Prince
Start: 11:16
13 Oct 1995
J
Queen
Start: 13:48
12 Oct 1994
K
Roxanne
Start: 23:00
20 Jul 1994
L
Tootsie
Start: 21:33
23 Feb 1994
dawn
day
dusk
night
0 1 2 3 4 5 Km

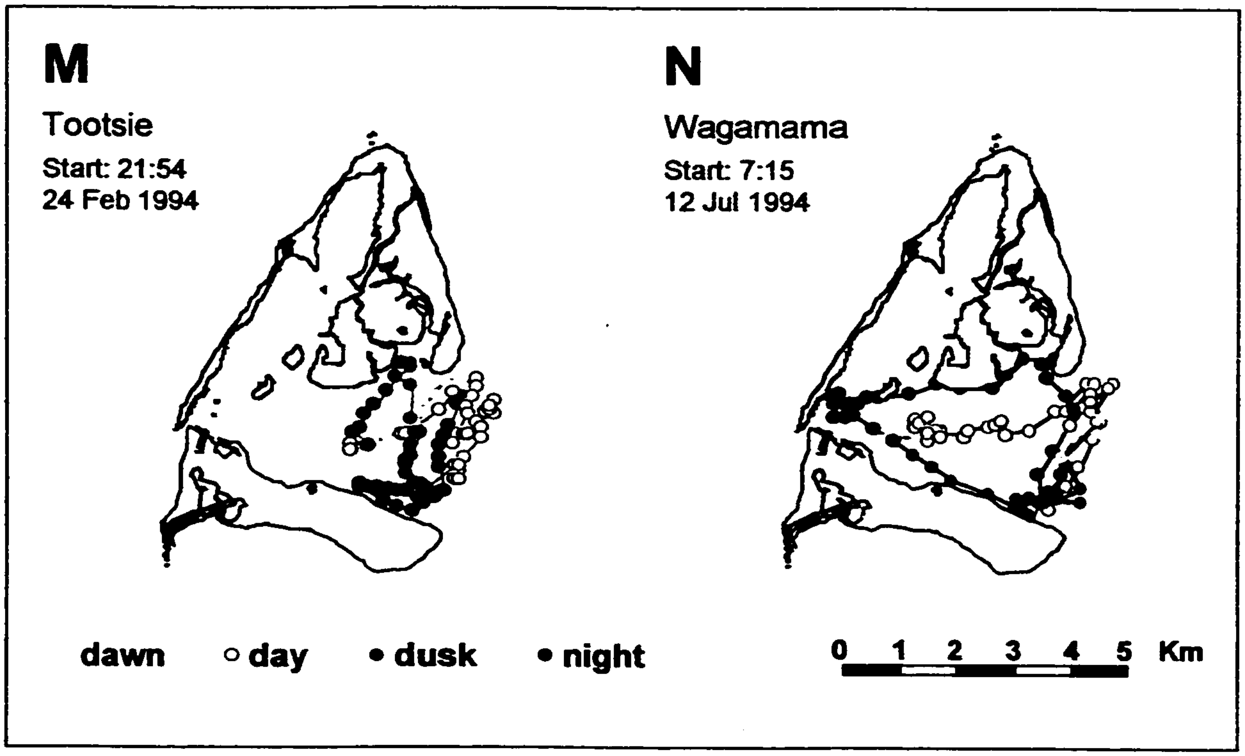
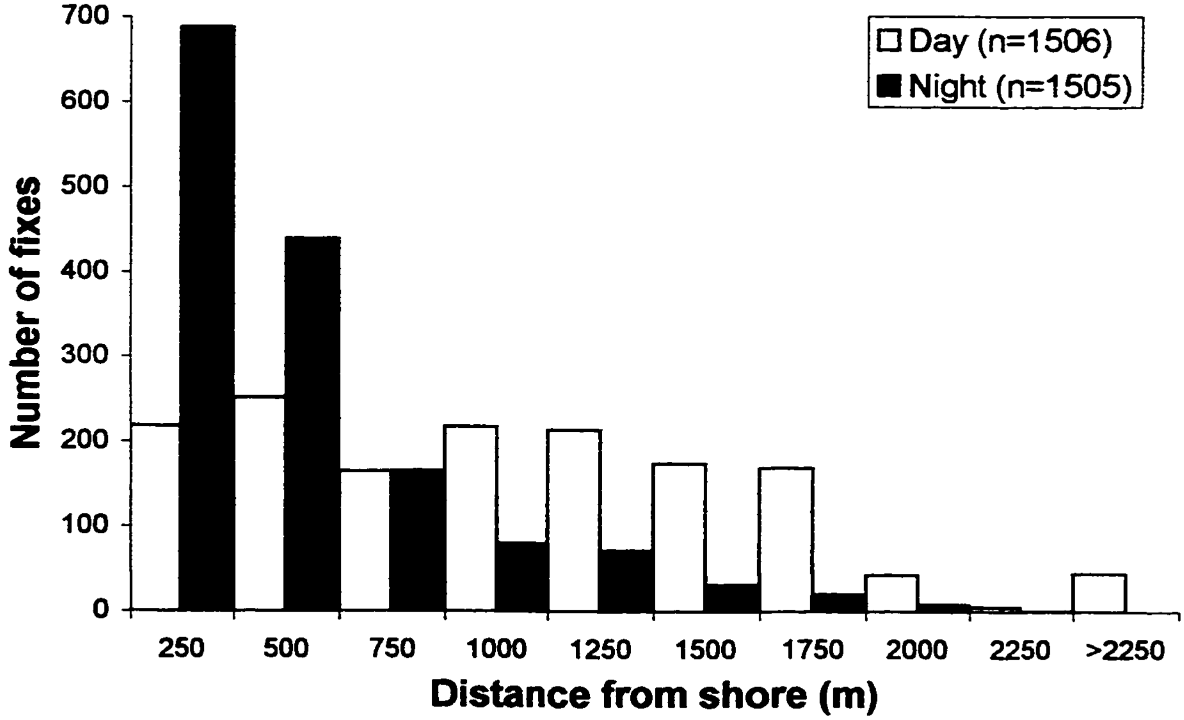

M
Tootsie
Start: 21:54
24 Feb 1994
N
Wagamama
Start: 7:15
12 Jul 1994
dawn
day
dusk
night
0 1 2 3 4 5 Km

Figure 11

Histogram of number of fixes at different distances from shore for day versus night positions.



Day (n=1506)
Night (n=1505)
Number of fixes
700
600
500
400
300
200
100
0
250
500
750
1000
1250
1500
1750
2000
2250
>2250
Distance from shore (m)

Figure 12

Representative diel kernel density distributions of sub-adult lemon sharks' 24-hour tracks showing day and night core areas. The track for Queen (a) is typical of tracks that displayed diel movement patterns – with distinct day and night core areas. The track for Wagamama (b) is representative of the nine tracks where there was no defined diel pattern but for which night core areas were closer to shore or channels than day core areas. The track for OJ (c) is one of the five tracks for which there were no clear differences between day and night core areas. Contour lines are 95%, 90%, 75%, 50% and 25% estimate area determined by the kernel method. Light regions are areas of high density, i.e. core areas.

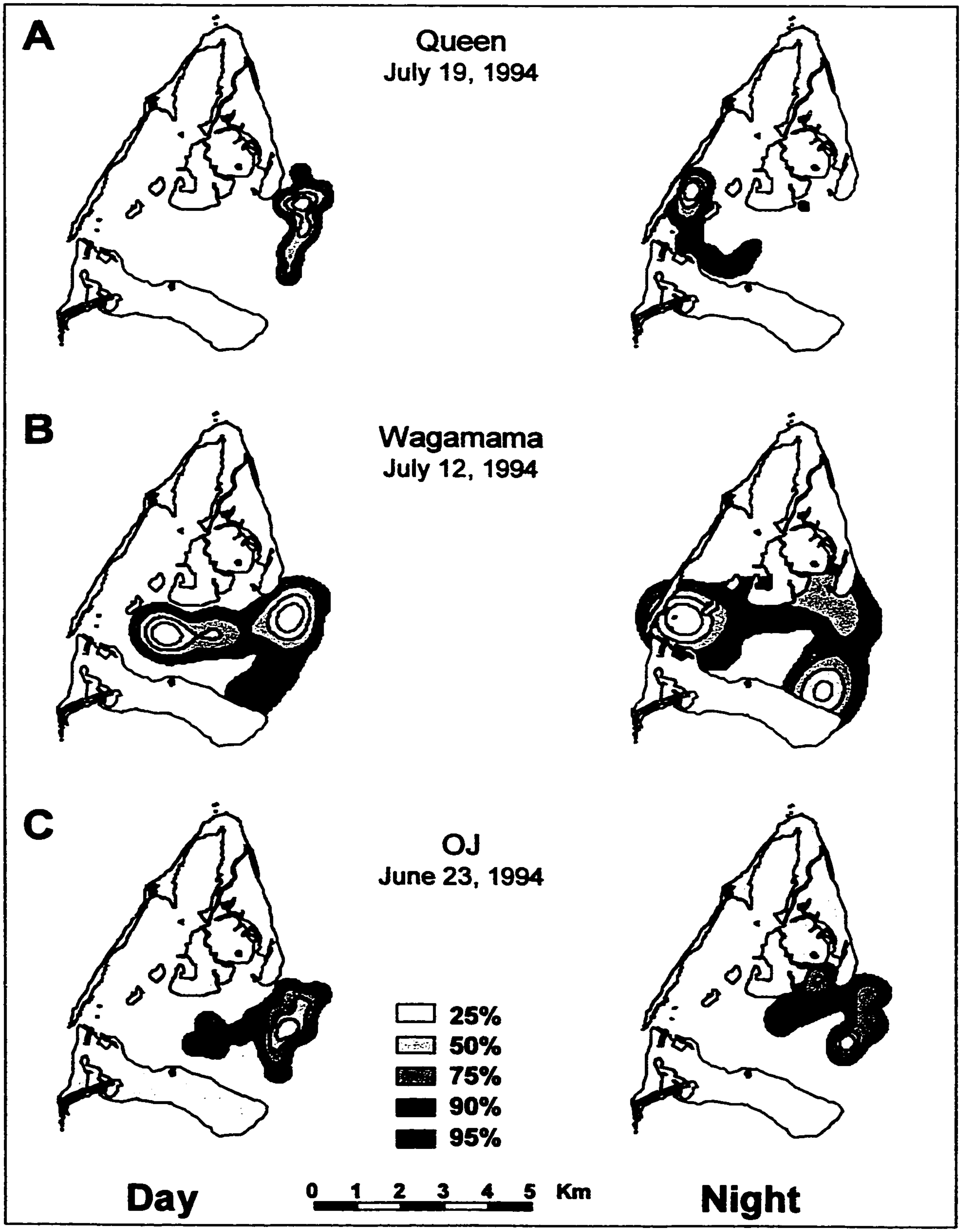

A
Queen
July 19, 1994
B
Wagamama
July 12, 1994
C
OJ
June 23, 1994
25%
50%
75%
90%
95%
Day
0 1 2 3 4 5 Km
Night

Figure 13

Day and night activity space areas of all 42 continuous 24-hour tracks combined for 15 sharks. Contour lines are 95%, 90%, 75%, 50% and 25% estimate area determined by the kernel method. Light regions are areas of high density, i.e. core areas.

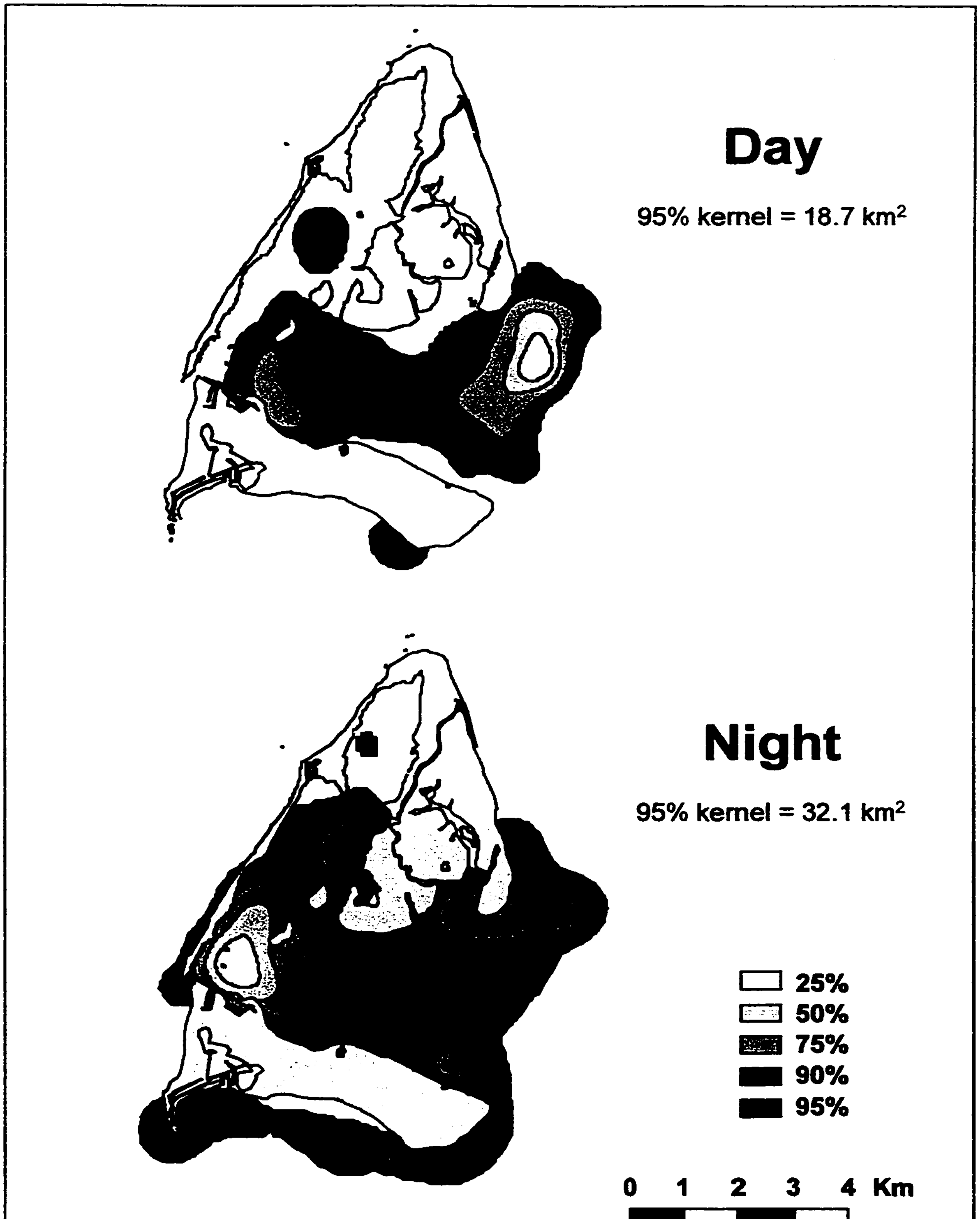
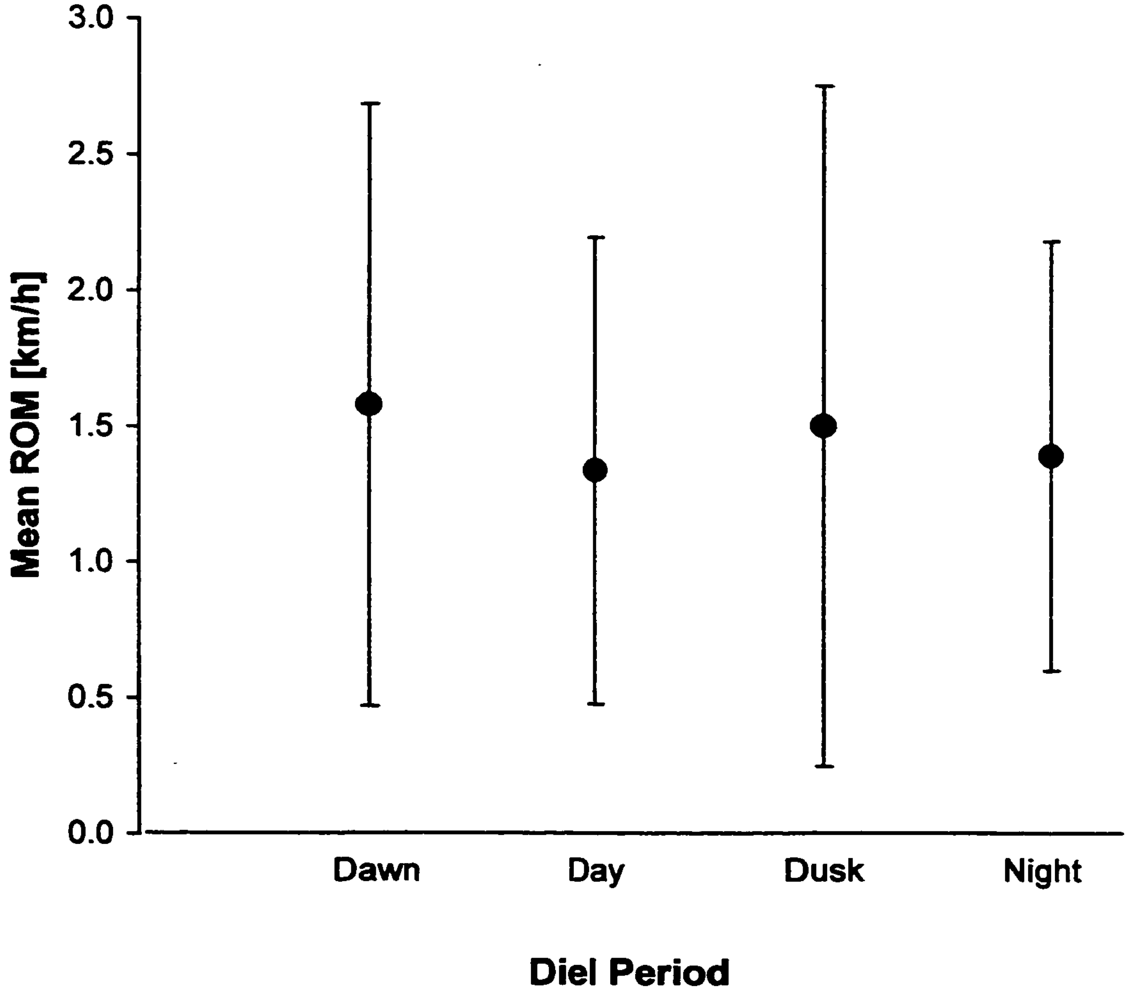

Day
95% kernel = 18.7 km²
Night
95% kernel = 32.1 km²
25%
50%
75%
90%
95%
0 1 2 3 4 Km

Figure 14

Mean rates of movement (●) comparing four time periods (dawn, day, dusk, and night) based on 42 continuous 24-hour tracks for 15 sub-adult lemon sharks in Bimini. Error bars are 95% confidence intervals.


3.0
2.5
2.0
1.5
1.0
0.5
0.0
Mean ROM [km/h]
Dawn
Day
Dusk
Night
Diel Period