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Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary

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Abstract Acoustic telemetry was used to examine the size of daily activity space, small-scale movement patterns, and water quality preferences of juvenile bull sharks in the Caloosahatchee River, Florida. Movement pattern analysis included rate of movement, swimming depth, linearity, direction, tidal influence, diel pattern, and correlation with environmental variables. Manual tacking occurred before and after a large freshwater influx which divided the sharks into two groups based on movement patterns. The first group displayed increased rate of movement, distance traveled, and space utilization at night, and movements correlated with salinity, temperature, and dissolved oxygen. The second group had an increased rate of movement, distance traveled, and space utilization during the day, and movements correlated with temperature, dissolved oxygen, turbidity and pH. These juvenile bull sharks displayed distinct diel movement patterns that were influenced by physical factors, which may account for the distribution of this top-level predator in the Caloosahatchee River.

Keywords *Carcharhinus leucas* · Habitat use · Activity space · Movement patterns · Acoustic telemetry · Manual tracking

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Introduction

The life history and ecology of euryhaline elasmobranchs is poorly understood, as is the extent of their ecological role in freshwater and brackish systems (Martin 2005; Curtis 2008). Understanding behavior, especially movement patterns, will help define the ecological role of species within these systems. Movement enables fishes to fulfill their resource requirements in spatially and temporally changing environments (Schlosser and Angermeier 1995) and choose suitable habitats to optimize survival and growth (Gowan and Fausch 2002). Environmental factors influencing movement have received little attention and increased modification of aquatic systems requires the study of this relationship to help predict how mobile residents will respond. Several environmental factors may interact to define elasmobranch movement patterns, including water temperature (Morrissey and Gruber 1993a; Matern et al. 2000), oxygen levels (Parsons and Carlson 1998), diel periodicity (Tricas et al. 1981; McKibben and Nelson 1986; Klimley et al. 1988; Holland et al. 1992), tides (Medved and Marshall 1983; Ackerman et al. 2000) and salinity (Curtis 2008; Heupel and Simpfendorfer 2008). Due to the close proximity of freshwater systems to human development, elasmobranchs that utilize reduced salinity environments may be especially vulnerable to anthropogenic habitat modification, making it essential to gain a better understanding of their habitat utilization and environmental preferences.

Bull sharks, *Carcharhinus leucas*, are found worldwide in warm subtropical and tropical coastal, estuarine, and riverine waters (Bass et al. 1973; Compagno 1984), and are one of the few elasmobranch species known to be physiologically capable of tolerating freshwater for extended periods of time (Thorson et al. 1973). The bull shark is well known for its ability to travel long distances in freshwater systems (Thorson et al. 1966; Sadowsky 1968; Branstetter 1981; Pillans et al. 2006) and is one of the most common large shark species in Florida's coastal waters (Snelson et al. 1984; Wiley and Simpfendorfer 2007). Despite its broad distribution and known use of freshwater systems, habitat utilization by this species has received limited scientific attention. The Caloosahatchee River and San Carlos Bay in southwest Florida is a nursery area for bull sharks during their first year of life (Simpfendorfer et al. 2005). Although it is known that young bull sharks utilize this system, there is a lack of information regarding the relationship between environmental factors and habitat utilization. The goal of this research was to investigate short-term detailed space utilization, movement patterns, and to determine whether environmental variables influence short-term movement patterns of juvenile *C. leucas*.

Materials and methods

Study site

The Caloosahatchee River extends 105 km and links Lake Okeechobee to San Carlos Bay on Florida's southwest coast (Barnes 2005). Sharks were tracked in the Caloosahatchee Estuary which consists of approximately 32 km of river habitat (Fig. 1). Due to the long and narrow configuration of the river, the estuary can experience large water quality fluctuations generated by wind, tide, runoff, and precipitation. These changes are compounded by the artificial release of freshwater from Lake Okeechobee, with variable discharge rates that have reached as high as 1,278 m^3s^{-1} (South Florida Water Management District 2008). The unnatural, rapid flow of freshwater may cause severe damage to estuarine organisms and communities (Barnes 2005). Due to these abrupt alterations, this system provided an ideal location to examine *C. leucas* movement patterns in relation to environmental fluctuations.

Field methods

Eight juvenile sharks were collected from June to August of 2006 via rod and reel fishing using circle hooks and frozen mullet, *Mugil cephalis,* or fresh catfish, *Arius felis* and *Bagre marinus*. Captured individuals were weighed, measured by stretched total length (STL), sexed, and tagged with a single-barb plastic dart tag inserted into the dorsal musculature adjacent to the first dorsal fin. In addition, a V13P (Vemco Ltd) acoustic depth sensing transmitter was attached to the dorsal fin via a rototag. Transmitters (13×84 mm) pulsed continuously on one of four acoustic frequencies (75, 78, 81, or 84 kHz). Two transmitters of each frequency were used. Each shark was tracked for one 24 h period and one shark was tracked at a time, with transmitters on the same frequency spaced out during the course of the research to avoid signal overlap.

A Vemco VR100 acoustic receiver and directional hydrophone mounted on the boat were used to manually track shark movements. To eliminate possible influence on shark movement, an estimated distance of 100 m between the shark and the boat was maintained. Shark location was recorded every 15 min for up to 24-hours using a global positioning system. Water quality samples were collected at the surface and bottom every 15 min using a Niskin bottle and tested for several parameters including salinity, temperature, dissolved oxygen, turbidity, and pH using a water quality meter, pH meter and turbidimeter.

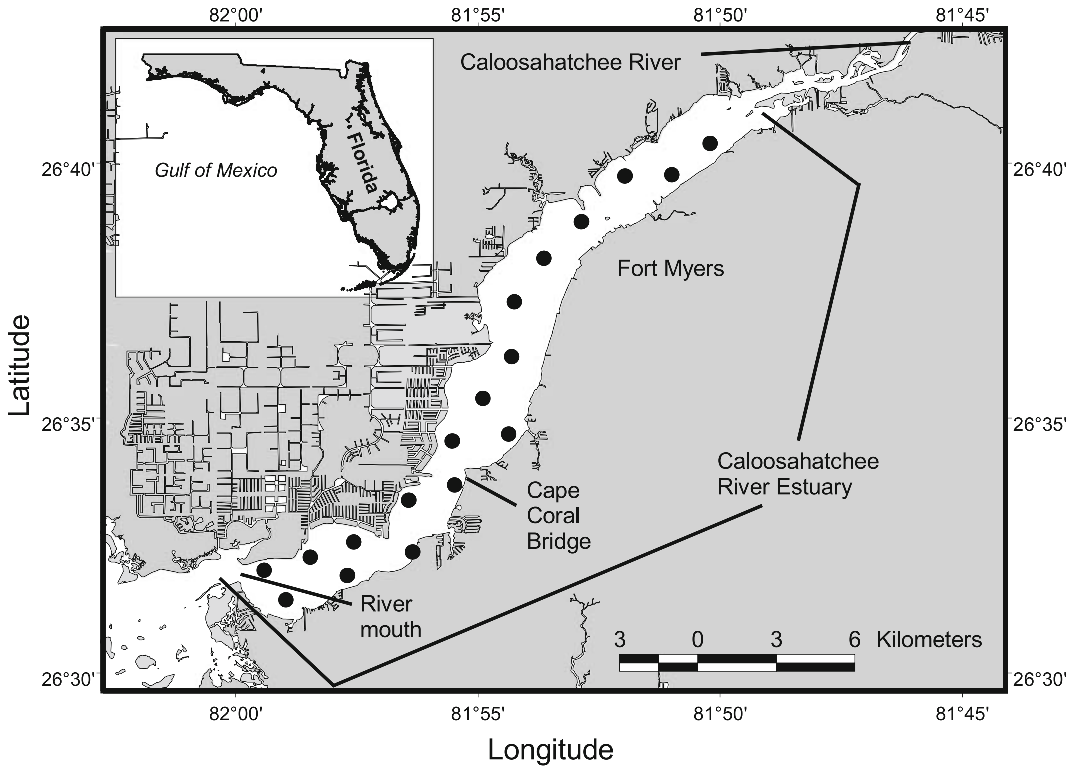

Fig. 1 The Caloosahatchee estuary. Inset: Location of the study site in Florida showing and connections to Lake Okeechobee and the Gulf of Mexico

Data analysis

From June to August of 2006, 509 positional fixes were obtained for eight juvenile *C. leucas* that were actively tracked for periods of up to 24 h. Six of these tracks were considered to be full tracks (i.e. >21 h) and were used in all statistical analyses (individuals 3 and 8 were omitted), data are shown in Table 1 and Fig. 2. Animals 1–3 were caught in the same section in the northern portion of the estuary in salinities of 7.6–11.1‰. Following a large freshwater influx, the salinity in that location dropped to approximately 2.6‰, after which no additional sharks were captured despite extensive fishing efforts. After moving closer to the mouth of the river, an individual was caught in 6.5‰ within 45 min. All subsequent individuals were captured in this lower portion of the estuary in salinities ranging between 6.5 and 12.5‰ at time of

Table 1 Summary data for eight juvenile *C. leucas* tracked using acoustic telemetry within the Caloosahatchee River, FL in 2006

Track	Sex	Size–STL	Date	Latitude of capture	Longitude of capture	Duration (h)	Total positional fixes
1	M	80	14-Jun-07	26.64392	−81.89285	24	75
2	F	77	28-Jun-07	26.64474	−81.88980	24	62
3	F	78	06-Jul-07	26.64983	−81.88493	7	13
4	M	80	18-Jul-07	26.64942	−81.86473	21	74
5	M	84	01-Aug-07	26.55795	−81.92523	24	79
6	M	77	03-Aug-07	26.55847	−81.92476	24	82
7	F	82	08-Aug-07	26.55818	−81.92437	24	74
8	M	104	23-Aug-07	26.52864	−81.96098	6	20

Size is indicated as stretch total length (STL) in centimeters

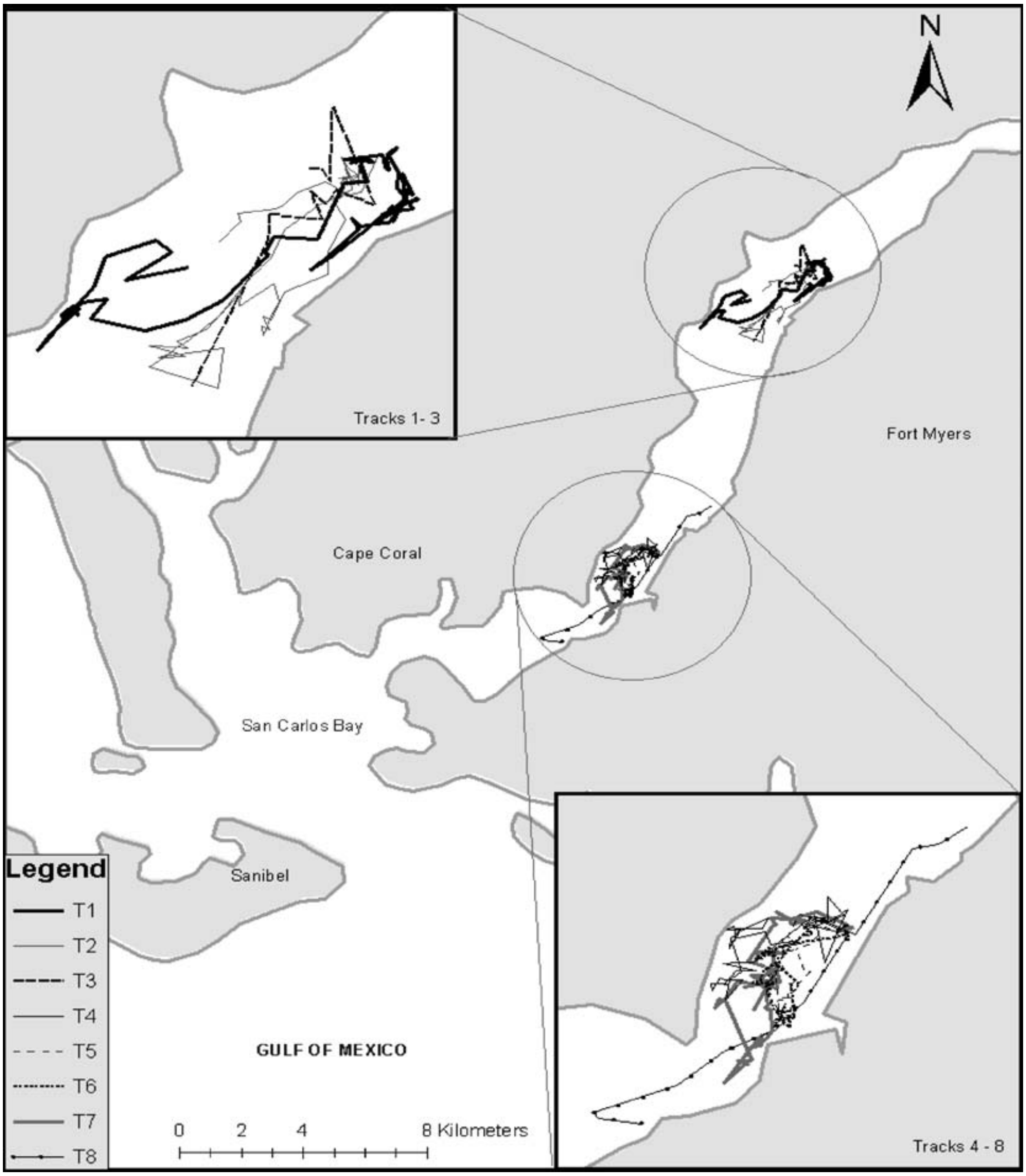

Fig. 2 Movement of eight actively tracked bull sharks within the Caloosahatchee River. Inset maps provide closer detail of the movements within the two clusters

capture. Results were reported as pooled data for all tests where a uniform trend was observed. However, when uniformity between the six individuals was not the result, animal behavior patterns clustered by tracks 1-2 and 4–7, and results were reported by cluster. Clustered results were reported for activity space, distance traveled, rate of movement, and water quality analyses.

Activity space

Positional fixes derived from active tracking were plotted and analyzed using ESRI ArcView 3.3 geographic information systems software. The total activity space used by each animal was determined for day, night, and 24 h (total) periods using minimum convex polygon analysis in the Animal Movement

Extension for ArcView (Hooge and Eichenlaub 2000). Movements between positions recorded from 07:00 to 19:00 were categorized as daytime and movements between 19:00 and 07:00 were categorized as nighttime to coincide with local sunrise and sunset times. A Brainerd-Robinson Similarity Coefficient Analysis, which measures the similarity of assemblages by comparing the proportional representation of each category within the assemblage, was used to determine whether there was a difference in day and night activity space size between tracks. Hierarchical cluster analysis using the average linkage method and squared euclidean distance measure was conducted to support those results. A Wilcoxon signed rank test based on groupings from the cluster analysis was used because the data were paired and non-normal. The test was performed to determine if there was a significant diel difference in the size of activity space, however, only one cluster (n=4) was used because the second cluster was too small (n=2) for statistical analysis.

Movement

Six variables were used to describe movement patterns: swimming depth, rate of movement (ROM), linearity of movement, direction of travel (upriver, downriver, shoreline), tidal stage, and diel period. The rate of movement was calculated using the distance traveled between successive positional fixes divided by the sampling interval. To achieve normality, ROM data were normalized using a log transformation. A linearity index was calculated to determine if there was a linear or random trend to shark movement. The linearity index values were determined using the formula from Bell and Kramer (1979):

$$LI = (F_n - F_1)/D$$

Where F_n was the last fixed location of the animal, F_1 was the first fixed location, and D was the total distance traveled by the shark. Values of linearity ranged from 0 to 1, with values near zero representing random movements and values approaching 1 indicating linear travel. Direction of travel in degrees (a_i), or the angle of movement between fixes, was calculated between successive fixes using the formula described in Kernohan et al. (2001).

These results were used to determine if an individual was moving upriver, downriver, or towards the shoreline. If movement was between 330° and 120°, movement was categorized as upriver, between 120° and 150° or 300° and 330° was considered towards the shoreline, and between 150° and 300° was considered downriver. These chosen angles most closely reflected the northeast to southwest trajectory of the river where the tracks occurred.

A multivariate analysis of variance (MANOVA) was conducted to assess whether there was a difference in shark depth, ROM, or linearity in relation to directional travel. A Tukey's post-hoc test was used to identify if ROM changed upriver, downriver, or perpendicular to the shoreline. A univariate general linear model (GLM) determined if there were significant changes in ROM, shark depth, and linearity among the tracks. A univariate GLM was also conducted to elucidate if swimming depth, ROM, linearity, or directional travel displayed diel differences within tracks. Spearman correlation analysis was used to determine relationships between depth and ROM, linearity, or direction of travel. Spearman analysis was also used to determine if there was a tidal influence on ROM, depth, linear movement, or direction of travel.

Water quality

To understand how water quality changed over time, a univariate GLM was used to determine if top and bottom values for salinity, temperature, dissolved oxygen (DO), turbidity, and pH were different among tracks (i.e. over time) and if there were significant diel differences within each track for each variable. A correlation analysis was conducted to ensure that water quality variables were independent, with results between 0.3 and 0.8 considered correlated. Since the largest correlation was 0.32, variables were analyzed independently. Preference for each water quality variable was analyzed using multiple linear regression comparing average habitat condition with latitudinal shark position. Latitude was chosen as the position variable due to the north-south orientation of the river and the higher degree of latitudinal heterogeneity in habitat characteristics. Based on an analysis of the residual error, multiple regressions were again performed with the tracks separated into two groups, as determined via cluster analysis. Both groups of data were analyzed using Cook's and Mahalanobis distance and two outliers were removed per group because they fell outside two standard deviations from the mean. Statistical tests were performed with Statistica (1999) and SPSS (15.0), and a rejection level of 0.05 was employed.

Results

Activity space

Activity space for the six complete tracks varied from 1.2 to 4.3 km^2 (mean=2.5 km^2, median=2.4 km^2). Results from the Brainerd-Robinson Similarity Coefficient Analysis showed tracks 1 and 2 were highly related in regards to activity space with a correlation value of 0.92, and tracks 4 though 7 were highly related, with all correlation values above 0.90. Hierarchical cluster analysis supported a cluster of two groups, with the upriver tracks, 1 and 2, completed in June (*n*=2) grouping and the downriver tracks, 4–7, conducted in July and August (*n*=4) forming the second cluster. With data separated according to cluster membership, it was shown that tracks 1 and 2 had a larger nighttime activity space and tracks 4 through 7 had a significantly (Wilcoxon, $p<0.0001$) larger daytime activity space (Fig. 3).

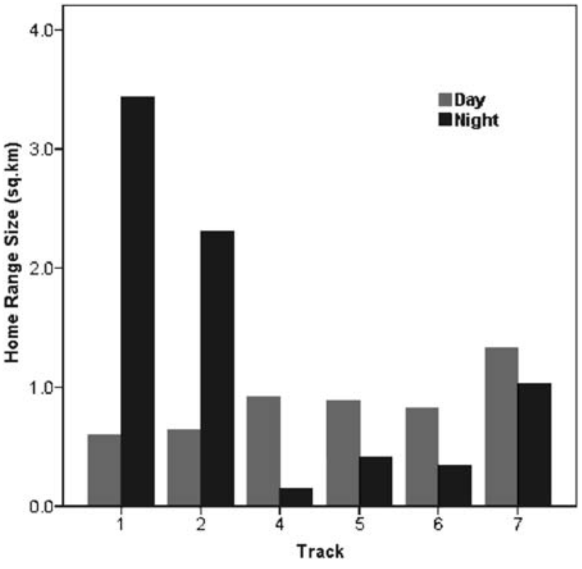

Fig. 3 Estimates of diel spatial usage of six actively tracked individuals as measured by minimum convex polygon

Total distance traveled by all individuals per 24 h period ranged from 9.7 to 20.6 km, with a mean of 14.9 km. When examined individually, sharks 1 and 2 traveled 4.32 and 7.22 km farther at night than during the day. Shark 4 had a slightly higher total distance traveled during the night, but the difference was small (1.65 km). Sharks 5 through 7 had small diel variation (1.28—1.69 km) but generally displayed increased daytime travel distances, corresponding with diel spatial usage patterns, as shown in Table 2.

Movement patterns

There was a significant difference in the mean rate of movement (ROM) among all six individuals (GLM, df=5, F=12.991, $p<0.0001$). When examined by cluster, the first two tracks showed an overall higher ROM (mean=15.1 $m \cdot min^{-1}$, SE=0.93) than the second cluster of individuals (mean=9.3 $m \cdot min^{-1}$, SE=0.62). These two individuals also moved faster during the night (mean=18.8 $m \cdot min^{-1}$, SE=1.45) than during the day (mean=10.9 $m \cdot min^{-1}$, SE=0.85). In contrast, individuals in tracks 4 through 7 moved faster during the day (mean=10.8 $m \cdot min^{-1}$, SE=0.86) than at night (mean=8.2 $m \cdot min^{-1}$, SE=0.88) (Fig. 4).

Significantly different swimming depth was observed among the six individuals (GLM, df=5, F=8.8128, $p<0.0001$). Mean depth of the river in tracking locations was 2.4 m and mean shark depth was 1 m from the surface. All six individuals displayed the same trend regarding depth and were therefore analyzed together. Each shark swam significantly closer to the surface during the night (mean=0.6 m, SE=0.005) and were deeper in the water column during the day (mean=1.5 m, SE=0.003) (GLM, df=6, F=29.2176, $p<0.0001$).

There was no significant difference in linearity either among tracks or between night and day within tracks for any individual (Table 2). No significant relationship existed between either linearity or shark depth with direction of travel (MANOVA, $p>0.05$). However, all sharks moved at a different rate relative to direction of travel (MANOVA, df=5, F=5.034, $p=0.007$). All sharks moved at an elevated speed as they traveled upriver (mean=17.5 $m \cdot min^{-1}$, SE=1.23) but there was no difference in ROM between travel downriver (mean=13.5 $m \cdot min^{-1}$, SE=0.94) or toward the shoreline (12.5 $m \cdot min^{-1}$, SE=1.75).

Table 2 Summary of movement variables separated by diel period for bull sharks tracked within the Caloosahatchee River

Track	Diel	Total dist (km)	ROM (m/min)	Shark depth (m)	Linearity
1	Day	8.13	11.5	2.2	0.2
	Night	12.45	18.5	0.8	0.3
	Total / Mean	20.60	15.1	1.4	0.2
2	Day	5.49	10.2	1.0	0.4
	Night	12.71	19.1	0.4	0.2
	Total / Mean	18.20	15.1	0.7	0.3
3	Day	7.20	21.4	1.2	0.4
	Night	N/A	N/A	N/A	N/A
	Total / Mean	7.20	21.4	1.2	0.4
4	Day	6.33	11.5	0.9	0.2
	Night	7.98	11.0	0.5	0.3
	Total / Mean	14.30	11.2	0.7	0.2
5	Day	6.21	9.2	1.7	0.4
	Night	4.74	7.1	0.5	0.2
	Total / Mean	10.90	8.1	1.1	0.3
6	Day	5.48	7.1	1.6	0.4
	Night	4.20	5.6	0.5	0.3
	Total / Mean	9.70	6.3	1.0	0.3
7	Day	8.56	14.9	1.7	0.4
	Night	6.87	9.2	0.6	0.3
	Total / Mean	15.40	12.1	1.1	0.3
8	Day	12.00	31.0	0.9	0.6
	Night	N/A	N/A	N/A	N/A
	Total / Mean	12.00	31.0	0.9	0.6

Spearman correlation analysis showed significant relationships between tidal stage and shark depth (p=0.004), linearity (p<0.001), and direction of travel (p=0.027), but no relationship was present with ROM (p=0.637). Sharks swam slightly deeper in the water column during a falling tide (mean=1.1 m, SE=0.07) versus a rising tide (mean=0.9 m, SE=0.06). Individuals displayed more random movements during a rising tide (mean=0.262, SE=0.02) than during a falling tide (mean=0.321, SE=0.01). All individuals followed the tide, traveling upriver during a rising tide and downriver during a falling tide. Relationships between shark depth and linearity (Spearman, p=0.005) and ROM and linearity (Spearman, p=0.011) were also significant. Each individual showed a higher degree of random movements at shallower depths and more linear travel in deeper depths. Animals also displayed a faster ROM when swimming a linear trajectory than when traveling a random pattern. No other movement variables showed significant correlations.

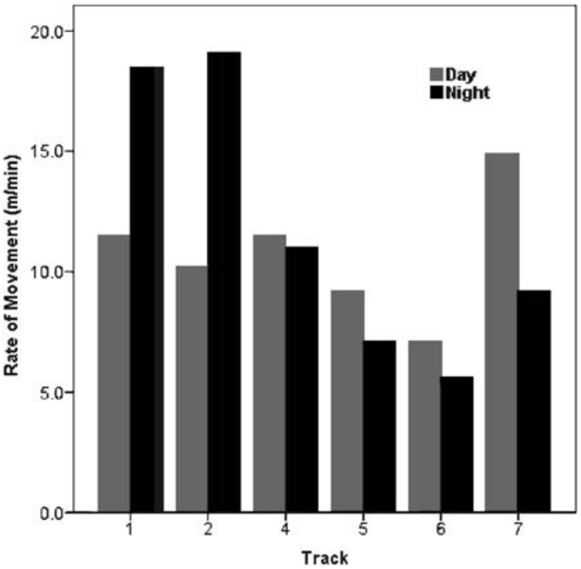

Fig. 4 Diel rate of movement for the six actively tracked bull sharks

Water quality

There were significant differences for all surface and bottom values of salinity, temperature, dissolved oxygen (DO), turbidity, and pH when compared across tracks. Water conditions therefore changed significantly over time (Table 3). All top and bottom water quality variables, except bottom pH, showed significant diel differences within each track (Table 3). However, when water quality from all tracks was analyzed together, it became evident that few variables exhibited clear diel trends (e.g. surface temperature was always higher during the daytime).

Linear regression showed a significant relationship between shark location and salinity ($p<0.0001$), temperature ($p<0.0001$), and dissolved oxygen ($p=0.012$) for tracks 1-2, and the model accounted for 0.609 of the sample variation. Tracks 4 through 7 were related to temperature ($p=0.017$), dissolved oxygen ($p<0.0001$), turbidity ($p<0.0001$) and pH ($p<0.0001$), and the model accounted for 0.560 of the sample variation (Tables 4, 5). No significant relationship was observed between shark swimming depth and water quality variables ($p>0.05$)

Discussion

Tagged juvenile bull sharks in the Caloosahatchee River often clustered in two groups with regards to their movement patterns. This grouping indicated movement patterns of individuals tracked in the northern part of the study site were different from those tracked approximately 10 km downriver in the southern region, suggesting that either individual differences or differences in location may influence movement patterns. Heupel and Simpfendorfer (2008) suggested that changes in environmental conditions within the Caloosahatchee River caused synchronous downriver movement of an entire monitored population (c. 18 sharks per year) of juvenile bull sharks. If this movement pattern is consistent, individuals captured in the southern portion of the site may have been displaced from upriver due to the large freshwater influx that occurred between tracks 3 and 4. Thus, differences in movement patterns between the two clusters may be related to location within the river (at a given point in time) and differences in habitat in those regions. The upriver portion of the estuary is slightly wider, shallower and more natural than downriver areas. This study documented a change in the distribution of young bull sharks which corresponded with a substantial shift in environmental parameters, suggesting that movement patterns may respond to environmental changes that affect movement and distribution within this estuarine system.

Examination of diel patterns revealed distinct differences in day and night movement patterns and locations for most individuals. The first two tracked animals displayed a larger nighttime space use accompanied by an increased ROM and distance traveled during the night. This result was not

Table 3 Results from univariate general linear models testing whether there was a significant difference in surface and bottom water quality variables between each track and for diel differences in surface and bottom water quality variables within each track

Water quality statistics				Difference in WQ between tracks			Diel difference in WQ within tracks		
Variable	Min	Max	Mean	df	F	*p*	df	F	*p*
T Salinity	2.4	12.8	7.5	5	45.30	0.001	6	7.13	0.001
B Saliinity	5.4	17.0	10.7	5	42.30	0.001	6	11.86	0.001
T Temp	27.0	37.3	30.4	5	68.90	0.001	6	18.70	0.001
B Temp	28.0	32.0	30.4	5	629.00	0.001	6	17.00	0.001
T DO	3.6	9.4	5.9	5	32.81	0.001	6	6.90	0.001
B DO	2.2	8.7	4.6	5	72.71	0.001	6	2.75	0.012
T Turbidity	1.4	5.9	3.0	5	117.92	0.001	6	15.83	0.001
B Turbidity	1.7	15.2	4.4	5	11.19	0.001	6	2.55	0.020
T pH	7.3	8.6	8.1	5	368.00	0.001	6	15.00	0.001
B pH	7.4	8.9	8.0	5	13.82	0.001	6	0.75	0.606

"T" denotes surface of the water column and "B" denotes the bottom of the water column

Table 4 Linear regression model summarizing water quality influence on actively tracked bull sharks 1-2

Variables	Coefficient	t Value	*p*	Model summary	
Salinity	−0.003	−8.207	0.001		
Temperature	−0.003	−4.198	0.001		
Diss. Oxygen	0.001	2.562	0.012		
Turbidity	0.001	1.548	0.124	N	125
pH	−0.004	−1.078	0.283	R^2	0.609
Diel	−0.008	−7.298	0.001	Standard error of est.	0.005
Constant	26.783	915.213	0.001	Significance (p-value)	0.001

unexpected since many shark species have been reported to increase activity space and swimming speed at night (Gruber et al. 1988; Holland et al. 1992; Ackerman et al. 2000; Vaudo and Lowe 2006). Tracks 5 through 7, however, showed larger daytime activity space with a faster ROM and larger distances traveled during the day. Those individuals were also shown to utilize more random movement patterns in shallow water at night. A substantial shift in environmental parameters could be the impetus for behavioral change between the two groups of juvenile bull sharks in this study. The magnitude of the freshwater influx that occurred prior to the tracking of sharks 4–7 moved the salt-wedge downriver and likely displaced many bony fish species upon which they prey (Snelson et al. 1984). Increased river discharge has been linked to behavioral changes in several bony fish species by altering their habitat selection (Albanese et al. 2004; Brenden et al. 2006). A positive relationship was found between freshwater inflow and fish abundance, however very high flows decreased abundance in a tidal Florida river (Flannery et al. 2002). This relationship may drive predators downstream during high freshwater influx events to maintain favorable foraging conditions.

A linearity index determines if sharks are traveling in long-ranging linear paths, or making small, random movements, which helps to understand how individuals use habitat. Morrissey and Gruber (1993b) calculated a linearity index value of 0.044 for juvenile lemon sharks and concluded they were highly site attached due to regular re-visitation of preferred areas. Rechisky and Wetherbee (2003) reported a linearity index of 0.2 (range=0.02–0.62) for neonate and juvenile sandbar sharks indicating a more linear pattern of movement. In the Caloosahatchee River, juvenile bull sharks had a linearity index of 0.29 (range=0.04–1.0) indicating more linear paths than both juvenile lemon sharks and sandbar sharks. This result is not unexpected as lemon sharks were tracked in an open lagoon, sandbar sharks in a large bay, and bull sharks in a narrow river which provided physical constraints to movement. Bull sharks in this study also exhibited more linear travel than that of bull sharks tracked in the Indian River Lagoon, Florida (mean=0.18; Curtis 2008). Individuals displayed a higher degree of circular or random movements at shallower depths and more linear travel in greater depths. Movement within a shallow nursery habitat by young sandbar sharks was attributed to predator avoidance, avoidance of currents, and distri-

Table 5 Linear regression model summarizing water quality influence on actively tracked bull sharks 4–7

Variables	Coefficient	t Value	*p*	Model summary	
Salinity	0.0000548	0.349	0.727		
Temperature	0.001	2.400	0.017		
Diss. Oxygen	0.001	4.085	0.001		
Turbidity	−0.001	−4.590	0.001	N	284
pH	−0.016	−5.797	0.001	R^2	0.560
Diel	−0.006	−11.956	0.001	Standard error of est.	0.004
Constant	26.644	951.004	0.001	Significance (p-value)	0.001

bution of prey (Rechisky and Wetherbee 2003). Since there are no natural predators of juvenile bull sharks in the Caloosahatchee River (Heupel unpublished data), and typically minimal current speed, it is likely that a large portion of juvenile bull shark movement patterns may be attributed to the distribution of and search for prey. Little is known about the movement patterns of their primary prey species, ariid catfishes and dasyatid stingrays, however, *D. sabina* was found to have small, restricted movements in a shallow tidal lagoon (Schmid 1988). Nursery areas provide abundant food sources and it is probable that the movement patterns of bull sharks are reflecting the distribution and movement patterns of their prey species.

The results demonstrated that tidal flow within the estuary had a significant effect on shark movement. Shark depth, linearity of movement, and direction of travel were all significantly correlated with tidal stage. Sharks have been reported to move in relation to environmental variables in previous studies and may use tidal transport as a means of conserving energy. For example, sandbar sharks and Atlantic stingrays have been reported to move with tidal flow (Teaf 1978; Medved and Marshall 1983; Rechisky and Wetherbee 2003). Leopard sharks also used currents for movement to and from muddy littoral zones that contained an abundance of food (Ackerman et al. 2000) potentially conserving 6% of their total energy expenditure. Bull sharks may also be utilizing passive transport to conserve or reallocate energy. An alternate explanation is that the bull sharks have preferences for specific environmental conditions as suggested previously (Simpfendorfer et al. 2005; Curtis 2008; Heupel and Simpfendorfer 2008), and this movement may be a means of remaining in a desired environmental regime. Movement downriver and swimming closer to the bottom on a falling tide would allow individuals to remain in potentially more saline or well-mixed water and avoid freshwater in the upper portion of the water column. Movement with tides may also be an indirect result from foraging for prey which are likely tidally influenced. Many bony fishes exhibit movement patterns that are influenced by tide (Krumme 2004; Kanou et al 2005; Dresser and Kneib 2007). Therefore bull shark movement is likely a means of optimizing energy allocation either via passive transport and/or maintenance of favorable environmental and foraging conditions.

Movements of juvenile *C. leucas* may also be directly related to changes in water quality, specifically salinity, to decrease energy expended for osmoregulation. The process of osmoregulation in seawater was determined to require 6% to 10% of the total energy budget of the euryhaline killifish, *Fundulus heteroclitus* (Kidder et al. 2006). This expenditure was suggested to be enough for behavioral osmoregulation, a process of seeking a medium isotonic with body fluids, to be a significant driving force in killifish movement (Kidder et al. 2006). While bull sharks are capable of osmoregulating in a wide salinity range (Pillans and Franklin 2004; Pillans et al. 2005; Pillans et al. 2006), Heupel and Simpfendorfer (2008) reported that young bull sharks remained within a salinity range of 7 to 20‰, and avoided areas of less than 7‰. Curtis (2008) reported that despite a range of available habitats, bull sharks selected locations with salinities above 11‰. In previous studies, salinity and temperature were found to be the most important factors determining the distribution and abundance of four elasmobranch species (Hopkins and Cech 2003; Heupel and Simpfendorfer 2008). Thus, changes in these variables may be key to juvenile bull shark movement and distribution. Water quality parameters may also play an indirect role in bull shark movement due to the influence of fluctuating conditions on the distribution of prey species. Temperature and salinity were found to be primary factors influencing movement (Harrison and Whitfield 2006) and community assemblages (Vega-Cendejas and Hernández de Santillana 2004) of fishes in estuaries. These water quality variables were specifically determined to be important in structuring estuarine assemblages on Florida's east coast (Kupschus and Tremain 2001; Paperno and Brodie 2004). *Arius felis* and *B. marinus*, two primary food items for bull sharks, are known to prefer salinity above 10 ‰ (Muncy and Wingo 1983). Therefore, during high freshwater influx events, these species may be displaced downriver to remain within a certain salinity range. The downriver movement of the sharks may have been to follow the prey populations, the distribution of which changed to fulfill physiochemical requirements.

Although significant differences in water quality variables over time and diel differences within tracks were reported, aside from the large freshwater influx event, changes were generally subtle. Locations of the first two sharks were related to salinity, temperature, and dissolved oxygen, while locations for sharks 4 through 7 were related to temperature, dissolved oxygen, turbidity and pH. These differences are likely due to the different locations in the river. Although dissolved oxygen, pH and turbidity influenced shark distribution it is unclear what role these factors play in influencing movement patterns. It is difficult to define the role that small variations in water quality have on movement over a short period of time, especially for a species that is known to have considerable environmental tolerances. Future research incorporating long-term trends with these short-term results would help form a more complete understanding of the degree to which environmental parameters influence movement. For example, temperature is more likely to have a role in shark presence over a longer period, showing seasonal variation (e.g. Simpfendorfer et al. 2005; Grubbs et al. 2007; Heupel 2007). Although there is evidence that salinity plays a role in long-term distribution of bull sharks in this estuary (Heupel and Simpfendorfer 2008), small variability in water quality made it impossible to determine movement drivers in the short-term. Therefore, mechanisms driving short-term movement patterns of bull sharks within the Caloosahatchee River may be dependent on a number of confounding variables and conditions. It did appear, however, that a large influx of freshwater changed the location of individuals within this habitat supporting the conclusion of Heupel and Simpfendorfer (2008) and suggesting water management practices causing large environmental fluctuations should be carefully examined.

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