Journal of Fish Biology (2004) **65,** 973–986
doi:10.1111/j.1095-8649.2004.00501.x, available online at http://www.blackwell-synergy.com

Short-term survival and movements of Atlantic sharpnose sharks captured by hook-and-line in the north-east Gulf of Mexico

C. W. D. Gurshin* and S. T. Szedlmayer†

Marine Fish Laboratory, Department of Fisheries, Auburn University, 8300 State Highway 104, Fairhope, AL 36532, U.S.A.

(Received 5 November 2003, Accepted 16 June 2004)

Ultrasonic telemetry was used to compare post-release survival and movements of Atlantic sharpnose sharks *Rhizoprionodon terraenovae* in a coastal area of the north-east Gulf of Mexico. Ten fish were caught with standardized hook-and-line gear during June to October 1999. Atlantic sharpnose sharks were continuously tracked after release for periods of 0·75 to 5·90 h and their positions recorded at a median interval of 9 min. Individual rate of movement was the mean of all distance and time measurements for each fish. Mean ± s.e. individual rate of movement was 0·45 ± 0·06 total lengths per second (L_T s^{-1}) and ranged from 0·28 to 0·92 L_T s^{-1} over all fish. Movement patterns did not differ between jaw and internally hooked Atlantic sharpnose sharks. Individual rate of movement was inversely correlated with bottom water temperature at capture ($r^2 = 0·52$, $P \leq 0·05$). No consistent direction in movement was detected for Atlantic sharpnose sharks after release, except that they avoided movement towards shallower areas. Capture-release survival was high (90%), with only one fish not surviving, *i.e.* this particular fish stopped movement for a period of 10 min. Total rate of movement was total distance over total time (m min^{-1}) for each Atlantic sharpnose shark. Mean total rate of movement was significantly higher immediately after release at 21·5 m min^{-1} over the first 1·5 h of tracking, then decreased to 11·2 m min^{-1} over 1·5–6 h, and 7·7 m min^{-1} over 3–6 h ($P \leq 0·002$), which suggested initial post-release stress but quick recovery from capture. Thus, high survival (90%) and quick recovery indicate that the practice of catch-and-release would be a viable method to reduce capture mortality for *R. terraenovae*.

Key words: hook-and-line; juveniles; rate of movement; *Rhizoprionodon terraenovae*; telemetry.

INTRODUCTION

Sustaining shark fisheries may be difficult because sharks are relatively long lived, slow growing and late maturing predators that produce few offspring over long reproductive cycles (Holden, 1988; Wourms & Demski, 1993; Castro, 1996; Musick, 1997). To help reduce shark mortality, present management plans recommend catch-and-release by both sport and commercial fisheries (NMFS, 1999). Present bag limits for the sport fishery are limited to one shark per vessel

†Author to whom correspondence should be addressed. Tel. and fax: +1 251 990 4858, email: sszedlma@acesag.auburn.edu

*Present address: Normandeau Associates, Inc., 25 Nashua Road, Bedford, NH 03110-5500, U.S.A.

per trip and one Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson) per person per trip. All additional sharks caught are released (NMFS, 1999). For this management strategy to be successful, a high rate of survival of released sharks is needed. Catch-and-release mortality in sharks has received little attention, but hooking mortality for marine teleosts has ranged from 1 to 90%. For example, post-release survival was 58–97% for striped bass *Morone saxatilis* (Walbaum) (Harrell, 1988; Diodati & Richards, 1996; Bettoli & Osborne, 1998), 42–92% for red drum *Sciaenops ocellatus* (L.), (Matlock *et al.*, 1993), 56–99% for red snapper *Lutjanus campechanus* (Poey) (Gitchlag & Renaud, 1994), 33–100% for red grouper *Epinephelus morio* (Valenciennes) (Wilson & Burns, 1996) and 1–90% for Atlantic salmon *Salmo salar* L., (Warner, 1979). Thus, if comparable to marine teleosts, a wide range in hooking mortality may be expected in sharks.

Factors that may affect hook mortality include the severity of hook injury, location of hooking, bait type, depth, salinity, temperature, fish size, angler experience and gear type (Taylor & White, 1992; Muoneke & Childress, 1994; Diodati & Richards, 1996). For example, studies of striped bass showed that hooking mortality increased with decreasing salinity and increasing temperature (Harrell, 1988; Diodati & Richards, 1996; Tomasso *et al.*, 1996), and higher mortality was shown for fishes hooked in vital organs such as the gills, stomach and eye (Warner, 1979; Diodati & Richards, 1996; Nelson, 1998). Also, hooking mortality increased with longer retrieval time due to oxygen debt, cardiac dysfunction and increased blood lactate levels associated with high exercise and injury (Wells *et al.*, 1986; Tomasso *et al.*, 1996). Longer retrieval times in hook-and-line capture of blue sharks *Prionace glauca* (L.) and shortfin mako sharks *Isurus oxyrinchus* Rafinesque were shown to elevate lactate, haematocrit, methaemoglobin and plasma electrolytes (Wells *et al.*, 1986).

Tanks, holding pens, ponds, impoundments or cages are most often used to study hooking mortality, but very few studies have been applied *in situ*. The major disadvantages of studying marine fishes in captivity are increased mortality from increased stress, or underestimations of mortality from the elimination of predators (Branstetter, 1987; Diodati & Richards, 1996). Ultrasonic telemetry is one approach to study post-release survival of fishes *in situ* (Bendock & Alexandersdottir, 1993; Bettoli & Osborne, 1998). This method has proved effective in other studies of shark movement, home range and habitat selection (Gruber *et al.*, 1988; Morrissey & Gruber, 1993*a*; Economakis & Lobel, 1998; Sundström *et al.*, 2001).

In this study, ultrasonic telemetry was used to estimate short-term survival and movements of the small coastal shark *R. terraenovae*, after hook-and-line capture. This species was used because of its abundance, commercial importance and occurrence in recreational hook-and-line catch. The coastal waters in the north-east Gulf of Mexico also serve as nursery grounds for this shark species (Carlson & Brusher, 1999).

MATERIALS AND METHODS

The study area was in coastal waters off Alabama in the north-east Gulf of Mexico (Fig. 1). Atlantic sharpnose sharks were caught, released, and tracked at three sites: (1) a

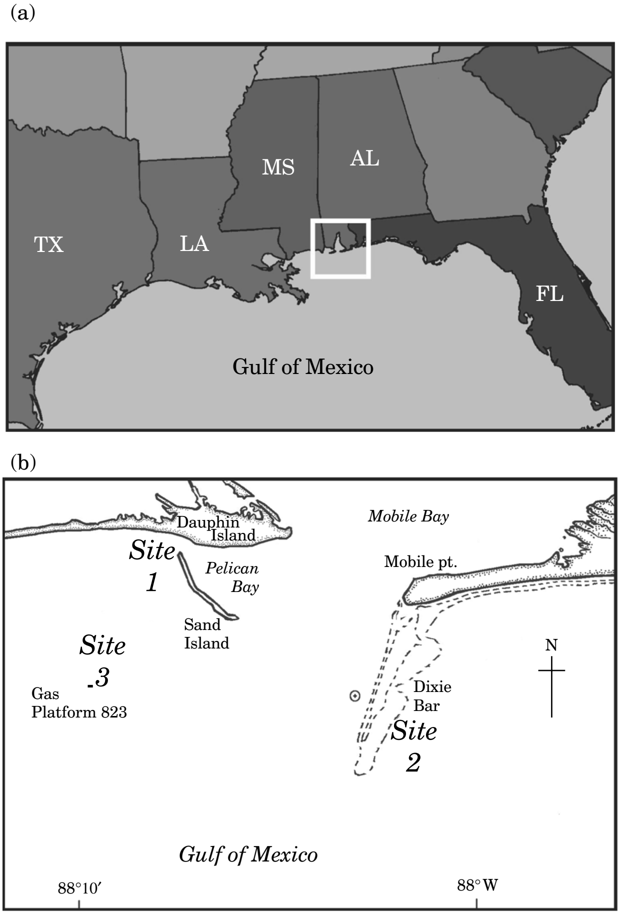

FIG. 1. (a) The study area in the northern Gulf of Mexico. (b) An enlarged map of the study area showing the catch-and-release sites.

barrier island, Sand Island, (2) a sandbar, Dixie Bar and (3) a gas platform, Exxon-MO-823-A. Sand Island was *c.* 2 km long and located 1 km south of Dauphin Island, Alabama. All fish caught at this site were at least 100 m off the west side of the island in 4–8 m depths. Dixie Bar ran parallel to the east side of the Mobile Bay ship channel south of the Bay mouth for *c.* 7·7 km with depths of 1–6 m. The gas platform was located *c.* 6 km south of Dauphin Island in depths of 12–14 m.

Ultrasonic telemetry was used to estimate movements and post-release survival of 10 juvenile and small adult *R. terraenovae*. Fishing conditions and gear were similar to local recreational fisheries. All fish were caught between 1000 and 1600 hours, from June to October 1999, with hook-and-line (13·6 kg test monofilament line, 68 kg barrel swivel, 1 m 39 kg steel leader and 9/0 bronze hook). Ground Gulf menhaden *Brevoortia patronus* Goode was used to attract the fish to the fishing area with the assumption it did not alter fish behaviour during telemetry under normal recreational fishing conditions (Sciarrotta & Nelson, 1977; Holts & Bedford, 1993). Fishing activities were conducted within state and federal regulations. Sand seatrout *Cynoscion arenarius* Ginsburg and mackerel scad *Decapterus macarellus* (Cuvier) were used as bait. The condition of each *R. terraenovae* at release was ranked from 3 (poor) to 5 (good). One point was given for each of the following observations: no bleeding, swimming away, not sinking, no external injury and not hooked in stomach or gills. The times of capture and condition of each fish were recorded (Table I). Hook location, total length (L_T), retrieval and handling time, sex, location and condition were recorded for each released Atlantic sharpnose shark. Temperature, salinity and dissolved oxygen were measured at each tracking site with a YSI-85 meter.

Tonic immobility was used throughout the study to sedate fish for measurements and tag attachment. Tonic immobility is a state of reduced animal movement when some elasmobranchs are inverted in a horizontal position (Gruber & Zlotkin, 1982; Henningsen, 1994). Individually coded ultrasonic transmitters (18×70 mm, model CT-82-3, Sonotronics, Tucson, Arizona, U.S.A.) were attached to a plastic sheep tag (Allflex, Dallas, Texas, U.S.A.) with a thin strip of magnesium that corroded and released the transmitter (0·75–5·90 h). Transmitters were individually attached to a styrofoam float so that transmitters floated to the surface for retrieval after tracking (Fig. 2). Sheep tags were used because they minimize tissue damage and allow growth of the dorsal fin (Heupel *et al*., 1998). All fish were tagged through the posterior edge of the first dorsal fin. After tagging, the steel leader from the hook-and-line was cut near the mouth of the fish to avoid injury and the fish was released with the hook in place.

A portable directional hydrophone and receiver (model USR-4D, Sonotronics) were used to continuously track each Atlantic sharpnose shark from a 10 m vessel for 0·75 to 5·90 h (mean $\pm$ S.E. $= 2{\cdot}65 \pm 0{\cdot}67$ h). While following fish, scans for tagged fish were made at least every 2 min. Their positions were determined when the strongest transmitter signal was detected below the vessel with the hydrophone pointed straight down. Latitude-longitude co-ordinates of fish positions were recorded at a median interval of 9 min. Depth was also recorded at each position. Mortality was assumed if no movement was detected for a period of at least 10 min, because *R. terraenovae* are obligate ram ventilators (Roberts & Rowell, 1988; Parsons & Carlson, 1998).

Distances and bearings between each recorded location were estimated with ArcView GIS 3.2a software. Net distance was the distance between the release position and the last position recorded. The total distance moved was the sum of the distances between each recorded location. Individual rates of movement were estimated as the mean of all two successive locations divided by the corresponding time interval for each individual and calculated in total lengths per second ($L_T\,s^{-1}$). A linear regression was used to estimate acceleration for individual fish (significant slope, *t*-test, $\alpha \leq 0{\cdot}05$; Sokal & Rohlf, 1995) by comparing the point to point estimates of rate of movement over the total track time of each fish (Bowerman & O'Connell, 1990). Net direction was the bearing from the release position to the last recorded position. Mean total rates of movement (m min^{-1}) were

TABLE I. Summary of catch-and-release data for 10 *Rhizoprionodon terraenovae* caught by hook-and-line during June to October 1999 in the north-east Gulf of Mexico

Fish	Date	L_T (cm)	Sex	Site	Stress time (min) Retrieval	Handling	Total	Hook location	Condition
1	22 Jun	80	M	Gas rig	3·0	2·8	5·8	Gills	4
2	3 Jul	90	M	Gas rig	5·5	3·5	9·0	Jaw	3
3	28 Jul	71	F	Dixie bar	4·5	7·0	11·5	Jaw	4
4	29 Jul	68	M	Sand Island	3·0	1·5	4·5	Jaw	3
5	1 Aug	86	M	Sand Island	4·0	7·0	11·0	Jaw	5
6	2 Aug	74	F	Sand Island	2·0	2·0	4·0	Jaw	5
7	2 Aug	67	M	Sand Island	2·0	2·0	4·0	Jaw	5
8	3 Aug	72	F	Sand Island	2·5	2·5	5·0	Gills	4
9	4 Aug	97	M	Sand Island	2·0	3·0	5·0	Gills	3
10	12 Oct	100	F	Gas rig	6·0	1·5	7·5	Gills	3

L_T, total length; F, female; M, male; condition, rank of fish condition.

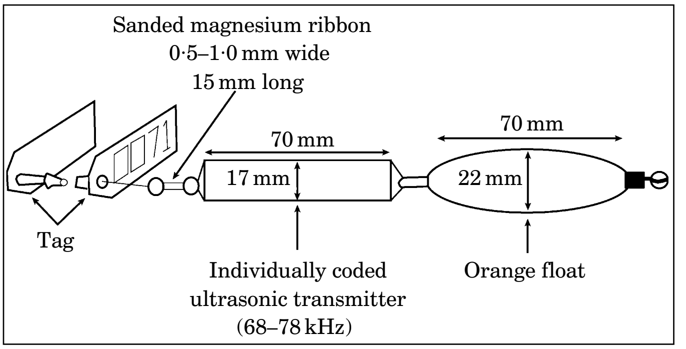

FIG. 2. Ultrasonic transmitter attached by a corrosive magnesium ribbon to a tag. All Atlantic sharpnose sharks were tagged in the first dorsal fin.

calculated as the mean over all *R. terraenovae*, for total distance over total time per individual, over three time intervals (0·7–1·5, 1·5–3·0 and 3·0–6·0 h). Differences in mean total rate of movement over three time intervals, and differences in individual rates of movement were tested by a one-way ANOVA ($\alpha \leq 0{\cdot}05$; Sokal & Rohlf, 1995). Differences were separated with Tukey's studentized range test ($\alpha \leq 0{\cdot}05$; Sokal & Rohlf, 1995). Difference in individual rate of movement between jaw and internally hooked fish was tested by a *t*-test ($\alpha \leq 0{\cdot}05$; Sokal & Rohlf, 1995). Environmental and capture-related variables that may explain variation in individual rate of movement, acceleration and net direction were examined by stepwise multiple regression (Zar, 1984).

RESULTS

Ten *R. terraenovae* were tracked after hook-and-line capture (Table I). Fish size ranged from 67 to 100 cm L_T. For all fish mean ± S.E. retrieval time = 3·5 ± 0·5 min (range of 2–6 min), handling time = 3·3 ± 0·6 min (range of 1·5–11·5 min) and stress time (retrieval and handling) = 6·7 ± 0·9 min (range of 4–11·5 min). At the surface, dissolved oxygen ranged from 4·3 to 7·2 mg l^{-1}, temperature ranged from 28·6 to 31·4° C and salinity ranged from 23·5 to 30·9. Near the bottom, dissolved oxygen ranged from 0.3 to 4.5 mg l^{-1}, temperature ranged from 24·5 to 28·9° C, and salinity ranged from 31·4 to 36·3 (Table II).

Most (90%) fish continually moved for the time periods tracked, which suggested high catch-and-release survival. Only shark 10 stopped moving for the last 10 min of the tracking session, which suggested it had died. The assessment of this individual was consistent with the condition at release and post-release behaviour. This gill-hooked Atlantic sharpnose shark was bleeding from the gills at release after the longest retrieval time of 6 min.

Net and total distance on a per minute basis was standardized for comparisons of fish with different track times. Net distance ranged from 1·5 to 17·9 m min^{-1} with a mean ± S.E. of 6·8 ± 1·6 m min^{-1}. Total distance ranged from 8·2 to 30·6 m min^{-1} with a mean of 17·1 ± 2·3 m min^{-1} (Table II). The net direction was the bearing from release position to last position and ranged from 2 to 314° with a mean ± S.E. of 202 ± 36°. No consistent direction was detected for these fish after catch-and-release, except that they avoided movement toward shallower shoreline areas (Figs 3 and 4). Differences in net direction were not

TABLE II. Movements for 10 *Rhizoprionodon terraenovae* after hook-and-line capture in the north-east Gulf of Mexico during June to October 1999. Rate of movement with different superscript letters were significantly different (Tukey's *post hoc* test, $P \leq 0{\cdot}05$) and acceleration rates with * were significantly different from zero (linear regression, $P \leq 0{\cdot}05$)

Shark number	Tracking time (min)	Change in depth (m)	Net distance ($m\ min^{-1}$)	Total distance ($m\ min^{-1}$)	Net direction (°)	Rate of movement ($L_T\ s^{-1}$) Mean ± S.E.	Acceleration ($L_T\ s^{-1}\ h^{-1}$)	Temperature (°C)	Salinity	Dissolved oxygen ($mg\ l^{-1}$)
1	267	−1·5	2·3	8·2	26	$0{\cdot}28^{a} \pm 0{\cdot}08$	0·06	28·0	32·5	4·5
2	87	−0·3	8·5	30·6	283	$0{\cdot}92^{b} \pm 0{\cdot}44$	−0·14	24·5	36·1	0·7
3	164	1·2	3·0	13·2	146	$0{\cdot}58^{ab} \pm 0{\cdot}07$	−0·18	28·9	30·7	4·3
4	193	1·0	6·9	11·6	158	$0{\cdot}47^{ab} \pm 0{\cdot}11$	−0·24*	28·9	31·4	2·6
5	309	0·6	5·6	15·0	277	$0{\cdot}31^{a} \pm 0{\cdot}04$	−0·03	27·6	36·2	0·5
6	68	−0·9	7·8	21·3	314	$0{\cdot}59^{ab} \pm 0{\cdot}13$	−0·38	28·6	35·0	2·1
7	52	−3·1	11·0	17·9	2	$0{\cdot}44^{ab} \pm 0{\cdot}08$	0·17	28·6	35·0	2·1
8	354	0·0	1·5	9·6	278	$0{\cdot}37^{ab} \pm 0{\cdot}07$	−0·13*	28·1	35·9	0·9
9	51	0·9	17·9	27·4	224	$0{\cdot}46^{ab} \pm 0{\cdot}11$	−0·80*	27·5	36·3	0·3
10	45	0·0	3·2	16·4	309	$0{\cdot}31^{a} \pm 0{\cdot}05$	0·49*			

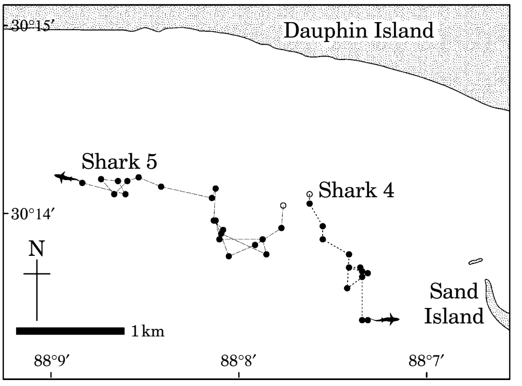

FIG. 3. Examples of movements for Atlantic sharpnose sharks (sharks 4 and 5) off Sand Island near Dauphin Island, Alabama. ○, The start of each track.

detected between jaw ($n=6$) and internally hooked ($n=4$) fish (t-test d.f. $=8$, $P=0{\cdot}88$). Seventy per cent of the fish remained in water of the same depth (± 1 m), 12% moved to shallower water and 10% moved to deeper water (mean $\pm$ S.E. depth change $=-0{\cdot}2\pm0{\cdot}4$ m). Individual rates of movement were inversely correlated with the bottom water temperature at capture (linear regression, $r^2=0{\cdot}42$, $P=0{\cdot}04$, Fig. 5).

Mean $\pm$ S.E. individual rate of movement for all fish was $0{\cdot}47\pm0{\cdot}06$ $L_T\,s^{-1}$ and ranged from 0·28 to 0·92 $L_T\,s^{-1}$ (Table II). No significant differences were detected for rate of movement between jaw ($0{\cdot}55\pm0{\cdot}09$ $L_T\,s^{-1}$) and internally hooked fish ($0{\cdot}36\pm0{\cdot}04$ $L_T\,s^{-1}$; t-test, d.f. $=8$, $P=0{\cdot}12$). Individual rate of movement for shark 2 was significantly higher compared to sharks 1, 5 and 10 (ANOVA, d.f. $=9$ and 104, $P=0{\cdot}04$; Table II). Six Atlantic sharpnose sharks showed constant rate of movement, *i.e.* no significant acceleration (linear regression, $r^2=0{\cdot}01$–$0{\cdot}19$, $P\geq0{\cdot}05$). Sharks 4, 8 and 9, however, significantly

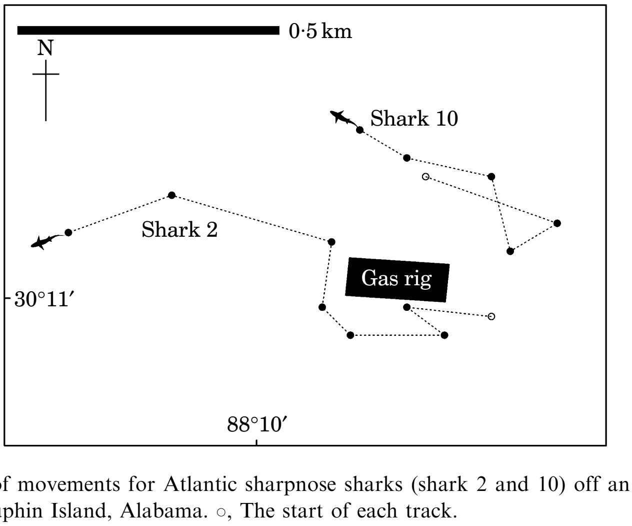

FIG. 4. Examples of movements for Atlantic sharpnose sharks (shark 2 and 10) off an offshore gas rig south of Dauphin Island, Alabama. ○, The start of each track.

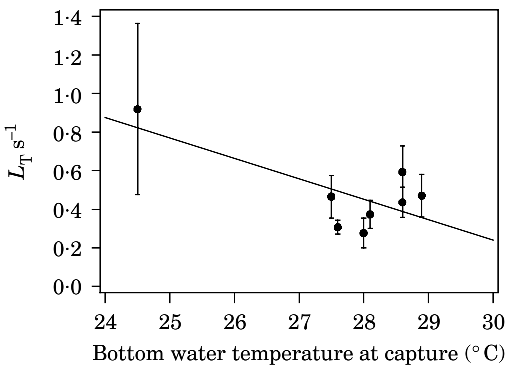

FIG. 5. Relation between mean ± S.E. rate of movement and bottom water temperature, after hook-and-line capture of Atlantic sharpnose sharks during June to October 1999 in the north-east Gulf of Mexico. The curve was fitted from: $y = -0{\cdot}11x + 3{\cdot}41$ ($n = 8$, $r^2 = 0{\cdot}52$, $P \leq 0{\cdot}05$).

deceased rate of movement over time after release (linear regression, $r^2 = 0{\cdot}36$–$0{\cdot}80$, $P \leq 0{\cdot}05$) and shark 10 significantly increased its rate of movement over its short track time before stopping (linear regression, $r^2 = 0{\cdot}81$, $P \leq 0{\cdot}05$, Fig. 6). Mean total rate of movement showed a significant decrease as time increased after release. After release fish initially moved at faster rates mean = 21 m min^{-1} at 0·7–1·5 h, then slowed their pace to 11·2 m min^{-1} at 1·5–3·0 h, and reached their lowest pace 7·7 m min^{-1} at 3·0–6·0 h (Fig. 7).

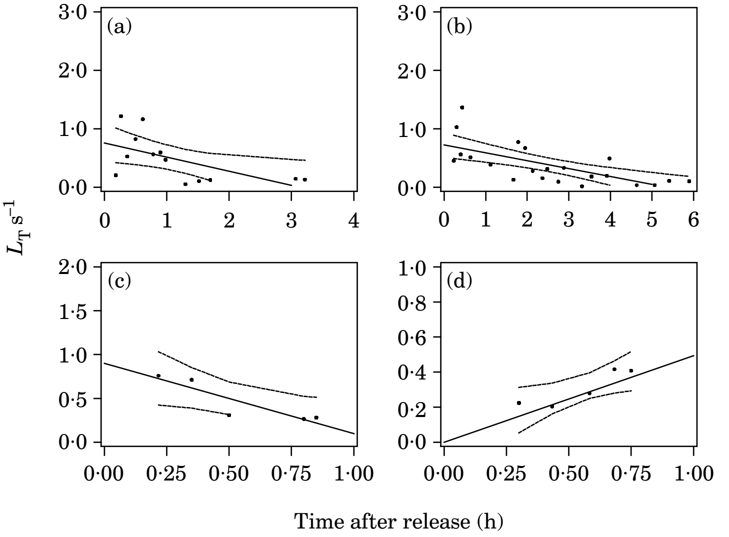

FIG. 6. Changes in rate of movement with time after release for individual Atlantic sharpnose sharks during June to October 1999 in the north-east Gulf of Mexico. Rate of movement significantly decreased after release for (a) shark 4 ($y = -0{\cdot}24x + 0{\cdot}76$; $n = 13$, $r^2 = 0{\cdot}36$, $P \leq 0{\cdot}05$), (b) shark 8 ($y = -0{\cdot}13x + 0{\cdot}72$; $n = 22$; $r^2 = 0{\cdot}45$, $P \leq 0{\cdot}05$) and (c) shark 9 ($y = -0{\cdot}80x + 0{\cdot}90$; $n = 5$, $r^2 = 0{\cdot}80$, $P \leq 0{\cdot}05$), but significantly increased for (d) shark 10 ($y = 0{\cdot}49x$; $n = 5$, $r^2 = 0{\cdot}81$, $P \leq 0{\cdot}05$). -----, the upper and lower 95% CL of the regression lines.

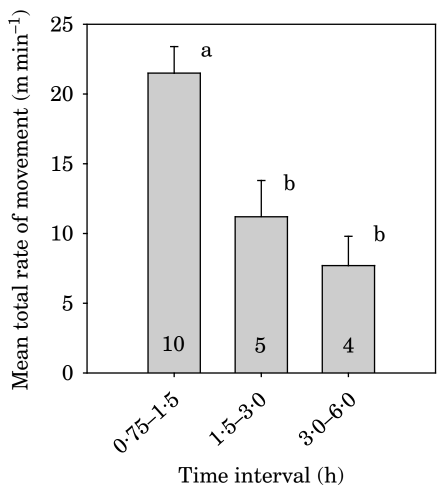

FIG. 7. Comparison of mean + S.E. total rate of movement over specific time intervals after release for all Atlantic sharpnose sharks during June to October 1999 in the north-east Gulf of Mexico. Significant differences are shown with different letters (ANOVA, $n = 19$, d.f. = 2 and 16, $P \leq 0{\cdot}05$). The rate of movement significantly decreased after the initial time period (0·7–1·5 h).

DISCUSSION

The present study suggested high (90%) post-release survival for small *R. terraenovae*. Other telemetry studies also showed high survival from released sharks caught on hook-and-line (Holts & Bedford, 1993; Holland *et al.*, 1999). Holts & Bedford (1993) showed post-release trauma may only last 30–90 min, as indicated by vertical dive profiles of shortfin mako shark. Increased and decreased swimming speeds of scalloped hammerhead shark *Sphyrna lewini* (Griffith & Smith), during the first 2 h of tracking also suggested post-release trauma (Holland *et al.*, 1993). In the tiger shark *Galeocerdo cuvieri* (Péron & Lesueur), Holland *et al.* (1999) observed no patterns of changes in swimming rates after release; however, bleeding or injured fish were not used. In the present study, higher mean total rates of movement over the first 1·5 h were similar to other studies and suggested initial post-release trauma. Individually, three *R. terraenovae* also significantly decreased rate of movement over the tracking period, and again suggested some post-release trauma but quick recovery (Fig. 6). This response differed from elevated speeds of juvenile lemon sharks *Negaprion brevirostris* (Poey) which were detected for 18 h after capture (Sundström & Gruber, 2002), *i.e. R. terraenovae* significantly decreased rate of movement within a much shorter time period after release (<2 h). Hoffmayer & Parsons (2001) reported lactate to increase and pH to decrease in *R. terraenovae* within 1 h after capture and handling stress. Carlson & Parsons (2001) showed that obligate ram ventilator species increased their speed in response to low dissolved oxygen. The increase in rate of movement for shark 10, which accounted for one mortality in the present study, might be a response to an oxygen debt and elevated lactate concentrations after a 6 min-retrieval time (longest in study) and bleeding gills. Significant correlations between movement and most environmental factors were not detected. The exception was between individual rate of movement and bottom water temperature at capture, which suggested that rate of movement was lower when Atlantic sharpnose sharks were captured in warmer water. This relation, however, appeared to be based on one individual and needs further study (Fig. 5).

Mean ± S.E. rate of movement estimated from each point to point track interval for all *R. terraenovae* was 0·47 ± 0·06 $L_T\,s^{-1}$. This mean was comparable to 0·34–0·48 $L_T\,s^{-1}$ for sandbar shark *Carcharhinus plumbeus* (Nardo) (Medved & Marshall, 1983), 0·35–0·53 $L_T\,s^{-1}$ for grey reef shark *Carcharhinus amblyrhynchos* (Bleeker) (McKibben & Nelson, 1986), and 0·31–0·57 $L_T\,s^{-1}$ for *N. brevirostris* (Gruber *et al.*, 1988; Sundström & Gruber, 1998). Similar movement rates of 0·36 ± 0·10 $L_T\,s^{-1}$, were also found for three finetooth sharks *Carcharhinus isodon* (Müller & Henle) and for two spinner sharks *Carcharhinus brevipinna* (Müller & Henle) after hook-and-line capture in the same area (unpubl. data). Although Gruber *et al.* (1988) showed actual speed determined by speed sensor telemetry may be twice that calculated by the point-to-point method, this study was based on short time periods between positions, suggesting that the present estimates approached actual rates.

Directional compass heading patterns were not detected for these Atlantic sharpnose sharks after release, as most individual tracks showed small movements in all directions (Figs 3 and 4). There was a general trend toward deeper water away from nearshore shallower waters, and these fish may have been seeking refuge in deeper offshore water in reaction to capture. These short movements in various directions, however, also suggested quick recovery from capture and 'normal' swimming behaviour (Medved & Marshall, 1983; McKibben & Nelson, 1986; Morrissey & Gruber, 1993*b*; Holland *et al.*, 1999).

High survival (90%) may be overestimated as a result of short tracking times and low sample size compared to hooking mortality studies of other fishes with telemetry (Bendock & Alexandersdottir, 1993; Bettoli & Osborne, 1998). Delayed mortalities due to infection and catch-and-release related injuries may not be detected in shorter tracking periods (Borucinska *et al.*, 2001, 2002). Ram ventilating fishes, however, probably die faster compared to branchial pumping fishes if movement is stopped (Roberts & Rowell, 1988). In addition, Bettoli & Osborne (1998) showed that most striped bass mortalities occurred within 2 h after release, suggesting short tracking periods are appropriate to assess most catch-and-release related mortalities. Also, Spargo (2001) showed that short track periods may be justified in hook-and-line mortality studies, as most juvenile *C. plumbeus*, showed complete physiological recovery within 6–10 h. Moreover, five *C. plumbeus* were recaptured between a day and a year after the exhaustive exercise associated with hook-and-line capture.

The timed self-release ultrasonic transmitters proved to be a successful method to study short-term movements and catch-and-release mortality in Atlantic sharpnose sharks. A major advantage was the quick retrieval of costly transmitters for reuse. Also, the present study showed the effectiveness of tonic immobility as a method to handle and tag this shark species. Tonic immobility is an unlearned defensive behaviour characterized by a temporary state of reversible motor inhibition induced by some form of physical restraint (Monassi *et al.*, 1999). Tonic immobility has been observed in all classes of vertebrates except Agnatha, but this study was the first documentation of successful induction of tonic immobility in this species (Gruber & Zlotkin, 1982; Whitman *et al.*, 1984; Henningsen, 1994).

Several Atlantic sharpnose sharks ($n = 4$) in the present study were hooked in the gills. Past studies of hook location have shown significant increases in mortality for internally hooked fishes (Bendock & Alexandersdottir, 1993; Nelson, 1998; Taylor *et al.*, 2001). In addition, sublethal effects associated with retained internal hooks may cause mortalities at a later date (Borucinska *et al.*, 2001, 2002). Thus, mortalities may take longer than tracking periods of the present study, especially for internally hooked fish. Diggles & Ernst (1997), however, showed that spanish flag snapper *Lutjanus carponotatus* (Richardson) and longfin grouper *Epinephelus quoyanus* (Valenciennes), both deeply hooked in the gut or oesophagus subsequently regurgitated the hooks over a 48 h observation period. In addition, Borucinska *et al.* (2002) reported six *P. glauca* with normal body mass did not suffer from pathological effects often associated with retained hooks from previous capture. Whether or not longer term mortalities will in fact affect *R. terraenovae* needs further study.

The present study was limited by low sample size ($n = 10$) which reduced the power of statistical testing. As with most telemetry studies on shark movements, small sample sizes ($n = 2$ to 39) were used, probably because of the difficulty in tagging and releasing these large predators. Yet, despite small sample sizes in shark studies compared to teleost studies, many studies were able to make valid conclusions concerning shark movements, rate of movements, swimming speeds and home range (Sundström *et al.*, 2001). If it is assumed that most capture mortality for *R. terraenovae* occurs in the first hour after release, the high (90%) short-term post-release survival observed in this study is probably accurate. Thus, the practice of catch-and-release will probably reduce mortalities of these frequently caught sharks, particularly juveniles, in coastal habitats of the north-east Gulf of Mexico.

We thank S. Kinsey, M. Topolski, P. Bielema, D. Moss and A. Ouzts for field assistance. We thank K. Kao and M. Ryan for supplying bait. Study sites were based on information from G. Parsons, D. Hornsby and M. Ryan. This is a contribution of the Alabama Agricultural Experimentation Station.

References

Bendock, T. & Alexandersdottir, M. (1993). Hooking mortality of chinook salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management* **13,** 540–549.

Bettoli, P. W. & Osborne, R. S. (1998). Hooking mortality and behavior of striped bass following catch and release angling. *North American Journal of Fisheries Management* **18,** 609–615.

Borucinska, J., Martin, J. & Skomal, G. (2001). Peritonitis and pericarditis associated with gastric perforation by a retained fishing hook in a blue shark. *Journal of Aquatic Animal Health* **13,** 347–354.

Borucinska, J., Kohler, N., Natanson, L. & Skomal, G. (2002). Pathology associated with retained fishing hooks in blue sharks, *Prionace glauca* (L.), with implications for their conservation. *Journal of Fish Diseases* **25,** 515–521.

Bowerman, B. L. & O'Connell, R. T. (1990). *Linear Statistical Models*. Belmont, CA: Duxbury Press.

Branstetter, S. (1987). Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Copeia* **1987,** 291–300.

Carlson, J. K. & Brusher, J. H. (1999). Index of abundance for coastal species of juvenile sharks from the northeast Gulf of Mexico. *Marine Fisheries Review* **61,** 37–45.

Carlson, J. K. & Parsons, G. R. (2001). The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. *Environmental Biology of Fishes* **61,** 427–433.

Castro, J. I. (1996). Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bulletin of Marine Science* **59,** 508–522.

Diggles, B. K. & Ernst, I. (1997). Hooking mortality of two species of shallow-water reef fish caught by recreational angling methods. *Marine and Freshwater Research* **48,** 479–483.

Diodati, P. J. & Richards, R. A. (1996). Mortality of striped bass hooked and released in salt water. *Transactions of the American Fisheries Society* **125,** 300–307.

Economakis, A. E. & Lobel, P. S. (1998). Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, central Pacific Ocean. *Environmental Biology of Fishes* **51,** 129–139.

Gitchlag, G. R. & Renaud, M. L. (1994). Field experiments on survival rates of caged and released red snapper. *North American Journal of Fisheries Management* **14,** 131–136.

Gruber, S. H. & Zlotkin, E. (1982). Bioassay of surfactants as shark repellents. *Naval Research Review* **2,** 18–27.

Gruber, S. H., Nelson, D. R. & Morrissey, J. F. (1988). Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bulletin of Marine Science* **43,** 61–76.

Harrell, R. M. (1988). Catch and release mortality of striped bass with artificial lures and baits. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* **41,** 70–75.

Henningsen, A. D. (1994). Tonic immobility in 12 elasmobranchs: use as an aid in captive husbandry. *Zoo Biology* **13,** 325–332.

Heupel, M., Simpfendorfer, C. & Bennett, M. (1998). Analysis of tissue response to fin tagging in Australian carcharhinids. *Journal of Fish Biology* **52,** 610–620.

Hoffmayer, E. R. & Parsons, G. R. (2001). The physiological response to capture and handling stress in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Fish Physiology and Biochemistry* **25,** 277–285.

Holden, M. (1988). Elasmobranchs. In *Fish Population Dynamics: the Implication for Management*, 2nd edn (Gulland, J., ed.), pp. 187–215. New York: Wiley.

Holland, K. N., Wetherbee, B. M., Peterson, J. D. & Lowe, C. G. (1993). Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia* **1993,** 495–502.

Holland, K. N., Wetherbee, B. M., Lowe, C. G. & Meyer, C. (1999). Movements of tiger sharks (*Galeocerdo cuvieri*) in coastal Hawaiian waters. *Marine Biology* **134,** 665–673.

Holts, D. B. & Bedford, D. W. (1993). Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the Southern California Bight. *Australian Journal of Marine and Freshwater Research* **44,** 901–909.

Matlock, G. C., McEachron, L. W., Dailey, J. A. & Unger, P. A. (1993). Short-term hooking mortalities of red drums and spotted seatrout caught on single-barb and treble hooks. *North American Journal of Fisheries Management* **13,** 186–189.

McKibben, J. & Nelson, D. (1986). Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science* **38,** 89–110.

Medved, R. J. & Marshall, J. A. (1983). Short-term movements of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae). *Bulletin of Marine Science* **33,** 87–93.

Monassi, C. R., Leite-Panissi, C. R. A. & Menescal-De-Oliveira, L. (1999). Ventrolateral periaqueductal gray matter and the control of tonic immobility. *Brain Research Bulletin* **50,** 201–208.
Morrissey, J. F. & Gruber, S. H. (1993*a*). Habitat selection by juvenile lemon sharks. *Environmental Biology of Fishes* **45,** 311–319.
Morrissey, J. F. & Gruber, S. H. (1993*b*). Home range of juvenile lemon sharks. *Copeia* **1993,** 425–434.
Muoneke, M. I. & Childress, W. M. (1994). Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* **2,** 123–156.
Musick, J. A. (1997). Restoring stocks at risk. *Fisheries* **22,** 31–32.
Nelson, K. L. (1998). Catch-and-release mortality of striped bass. *North American Journal of Fisheries Management* **18,** 25–30.
NMFS (1999). *Fishery Management Plan for Atlantic Tunas, Swordfish and Sharks*. Silver Spring, MD: National Marine Fishery Service, National Ocean and Atmospheric Administration.
Parsons, G. R. & Carlson, J. K. (1998). Physiological and behavioral responses to hypoxia in the bonnethead shark, *Sphyrna tiburo*: routine swimming and respiratory regulation. *Fish Physiology and Biochemistry* **19,** 189–196.
Roberts, J. L. & Rowell, D. M. (1988). Periodic respiration of gill-breathing fishes. *Canadian Journal of Zoology* **66,** 182–190.
Sciarrotta, T. C. & Nelson, D. R. (1977). Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. *Fishery Bulletin, U.S.* **75,** 519–528.
Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. New York: W. H. Freeman and Company.
Spargo, A. L. (2001). The physiological effects of catch and release angling on the post-release survivorship of juvenile sandbar sharks (*Carcharhinus plumbeus*). Master's thesis, University of Rhode Island.
Sundström, L. F. & Gruber, S. H. (1998). Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. *Hydrobiologia* **371-372,** 241–247.
Sundström, L. F. & Gruber, S. H. (2002). Effects of capture and transmitter attachments on the swimming speed of large juvenile lemon sharks in the wild. *Journal of Fish Biology* **61,** 834–838. doi: 10.1006/jfbi.2002.2058
Sundström, L. F., Gruber, S. H., Clermont, S. M., Correia, J. P. S., de Marignac, J. R. C., Morrissey, J. F., Lowrance, C. R., Thomassen, L. & Oliveira, M. T. (2001). Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes* **60,** 225–250.
Taylor, M. J. & White, K. R. (1992). A meta-analysis of hooking mortality of nonanadromous trout. *North American Journal of Fisheries Management* **12,** 760–767.
Taylor, R. G., Whittington, J. A. & Haymans, D. E. (2001). Catch-and-release mortality rates of common snook in Florida. *North American Journal of Fisheries Management* **21,** 70–75.
Tomasso, A. O., Isely, J. J. & Tomasso, J. R. (1996). Physiological responses and mortality of striped bass angled in freshwater. *Transactions of the American Fisheries Society* **125,** 321–325.
Warner, K. (1979). Mortality of landlocked Atlantic salmon hooked on four types of fishing gear at the hatchery. *Progressive Fish-Culturist* **41,** 99–102.
Wells, R., McIntyre, R., Morgan, A. & Davie, P. (1986). Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comparative Biochemistry and Physiology* **84A,** 565–571.
Whitman, P. A., Marshall, J. A. & Keller, E. C. Jr. (1984). Tonic immobility in the smooth dogfish shark, *Mustelus canis* (Pisces, Carcharhinidae). *Copeia* **1984,** 829–832.
Wilson, R. R. Jr. & Burns, K. M. (1996). Potential survival of released groupers caught deeper than 40 m based on shipboard and in-situ observations, and tag-recapture data. *Bulletin of Marine Science* **58,** 234–247.

Wourms, J. P. & Demski, L. S. (1993). The reproduction and development of sharks, skates, rays and ratfishes. *Environmental Biology of Fishes* **38,** 7–21.

Zar, J. H. (1984). *Biostatistical Analysis*, 2nd edn. Englewood Cliffs, NJ: Prentice-Hall, Inc.