Journal of Fish Biology (2003) **63,** 1357–1363
doi:10.1046/j.1095-8649.2003.00250.x, available online at http://www.blackwell-synergy.com

Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle

M. R. Heupel*, C. A. Simpfendorfer and R. E. Hueter

Center for Shark Research, Mote Marine Laboratory, Sarasota, FL 34236, U.S.A.

(Received 2 April 2003, Accepted 21 August 2003)

A small population of juvenile (<1 year old) blacktip sharks *Carcharhinus limbatus* responded to the approach of a tropical storm by moving to deeper water. Examination of meterological variables suggested that the movement of the blacktip sharks was triggered by a drop in barometric pressure associated with the approach of the storm. This response was consistent for all the fish being studied, and all blacktip sharks returned to the shallow nursery area after the storm's passage, suggesting that this was an innate behaviour.

Hurricanes and tropical storms produce major impacts on both land and sea. Much of the water column and benthos can be disturbed during these storms. Although many teleost species have been shown to alter their movement patterns in response to changes in weather patterns (Markham *et al.*, 1991; Guy *et al.*, 1992; Jones & Rogers, 1998; Watterson *et al.*, 1998; Jeffrey & Edds, 1999), little information is available concerning the specific responses of fishes to extreme weather events due to the inability to survey animals during severe conditions. Some studies suggest that hurricanes directly affect the movements and distribution patterns of fishes, but these results are usually based on *a priori* and *a posteriori* measurements, not observations during the storm itself (Watterson *et al.*, 1998).

Recent advances in acoustic telemetry technology have provided the means to continuously monitor the movements and distribution patterns of marine fishes within their natural environment. In this study this technology was employed to monitor the long-term use of a coastal nursery area (Terra Ceia Bay, Florida) by juvenile blacktip sharks *Carcharhinus limbatus* (Müller & Henle). During the summer of 2001, a series of 25 underwater acoustic receivers continuously monitored the positions of 41 young-of-the-year (YOY) blacktip sharks fitted with transmitters (Heupel & Hueter, 2001; Heupel & Simpfendorfer, 2002) for periods of 1–145 days. Data from the acoustic array were used to define the position of each individual at 15 min intervals (Simpfendorfer *et al.*, 2002).

*Author to whom correspondence should be addressed. Tel.: +1 941 388 4441; fax: +1 941 388 4312; email: mheupel@mote.org

This information was collected to define long-term movement patterns, home ranges and mortality of juvenile blacktip sharks in the nursery over multiple years.

During the course of the study, Tropical Storm Gabrielle formed in the Gulf of Mexico and made landfall on the central Gulf coast of Florida on 14 September 2001. When it struck the Florida coast Gabrielle was at near-hurricane strength with sustained winds of $>100\,km\,h^{-1}$ in some locations. At the time of the storm event 13 tagged blacktip sharks were being monitored within Terra Ceia Bay (27°33′ N; 82°35′ W). Monitoring data retrieved after the storm revealed that all 13 blacktip sharks left the nursery area just prior to the storm making landfall (0700 hours local time) 52 km south of Terra Ceia Bay. Sharks began to leave the bay at 0130 hours and all the animals had left by 0520 hours. Blacktip shark movements in the 12 h period during the storm's approach revealed a significantly increasing rate of movement (ANOVA, $P = 0{\cdot}0039$, LSD *post-hoc* test) culminating in all blacktip sharks leaving the area prior to the storm making landfall. The fish all remained outside the study site for 5 to 13 days before returning to the bay, at which time they all resumed movement patterns similar to those observed prior to the storm event. The blacktip sharks' highly directed movement out of the bay, synchronicity of departures, and narrow time frame of the phenomenon indicate this change in behaviour was a response to an environmental cue associated with the storm. Such concerted 'flight' behaviour of these YOY blacktip sharks has never been observed in 4 years of continuous monitoring in this nursery area. Although some fish periodically make short excursions outside the Terra Ceia nursery area, most remain within the nursery until late autumn as they prepare to migrate. Any excursions outside the nursery area are transitory and are undertaken individually (Fig. 1). Monitored blacktip sharks have never been observed to leave the nursery simultaneously. Therefore the exit of all monitored sharks over a short time period was considered an unusual behavioural pattern in response to an environmental cue (Fig. 1).

Examination of rainfall data during the period before and throughout the storm revealed that all blacktip sharks had left the area prior to heaviest rainfall events [Fig. 2(a)]. This suggests that increased noise from rainfall and the subsequent decline in salinity were unlikely to have been a factor in the blacktip sharks' behaviour. In the days following the storm, however, salinity in Terra Ceia Bay declined to <15 as a result of the rainfall and subsequent runoff into the bay. Juvenile blacktip sharks in Florida Gulf coast nurseries are normally found in salinities from 15·8–41·1 (R.E. Hueter unpubl. data) and thus the post-storm hyposaline condition of the bay could have prevented the sharks from returning to the nursery until salinities reached higher levels, which took *c*. 1 to 2 weeks.

Wind speed increased while the blacktip sharks were leaving the bay from an initial speed of $26\,km\,h^{-1}$ to a maximum of $66\,km\,h^{-1}$. As the storm made landfall, wind speed increased in the vicinity of the bay to a maximum of $82\,km\,h^{-1}$ at *c*. 0745 hours, several hours after the last blacktip shark had left the study site [Fig. 2(a)]. Ten of the 13 fish left prior to wind speeds reaching $40\,km\,h^{-1}$. Summer thunderstorms, in which wind speeds reach $45\,km\,h^{-1}$ are common in the area, but the monitored blacktip sharks have never displayed flight

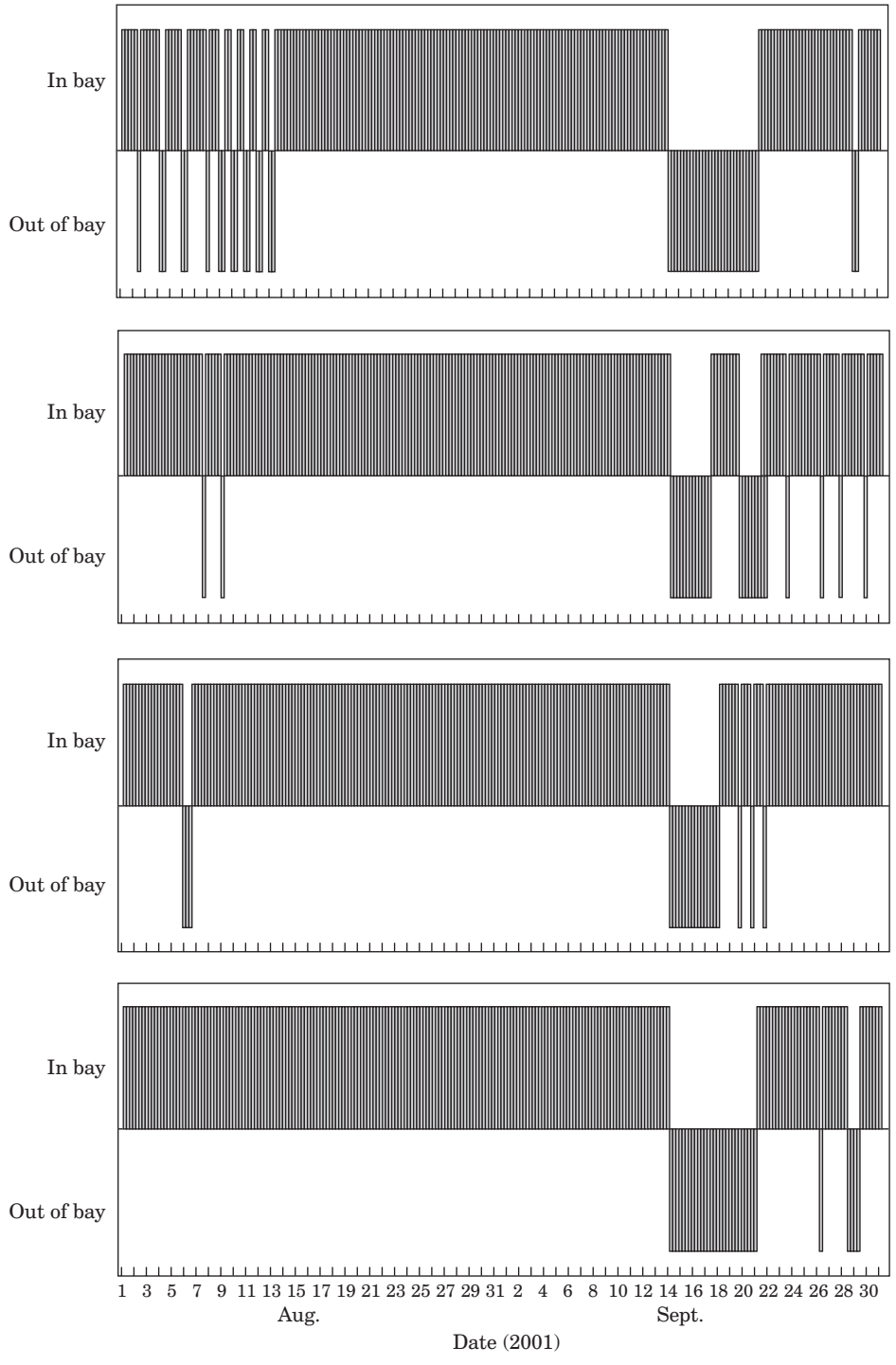

FIG. 1. Presence and absence data for four blacktip sharks monitored within Terra Ceia Bay in August–September 2001. Fourteen monitored fish (including the individual in the bottom panel) did not leave the study site during August. Note the synchronous flight behaviour shown by all individuals in mid-September.

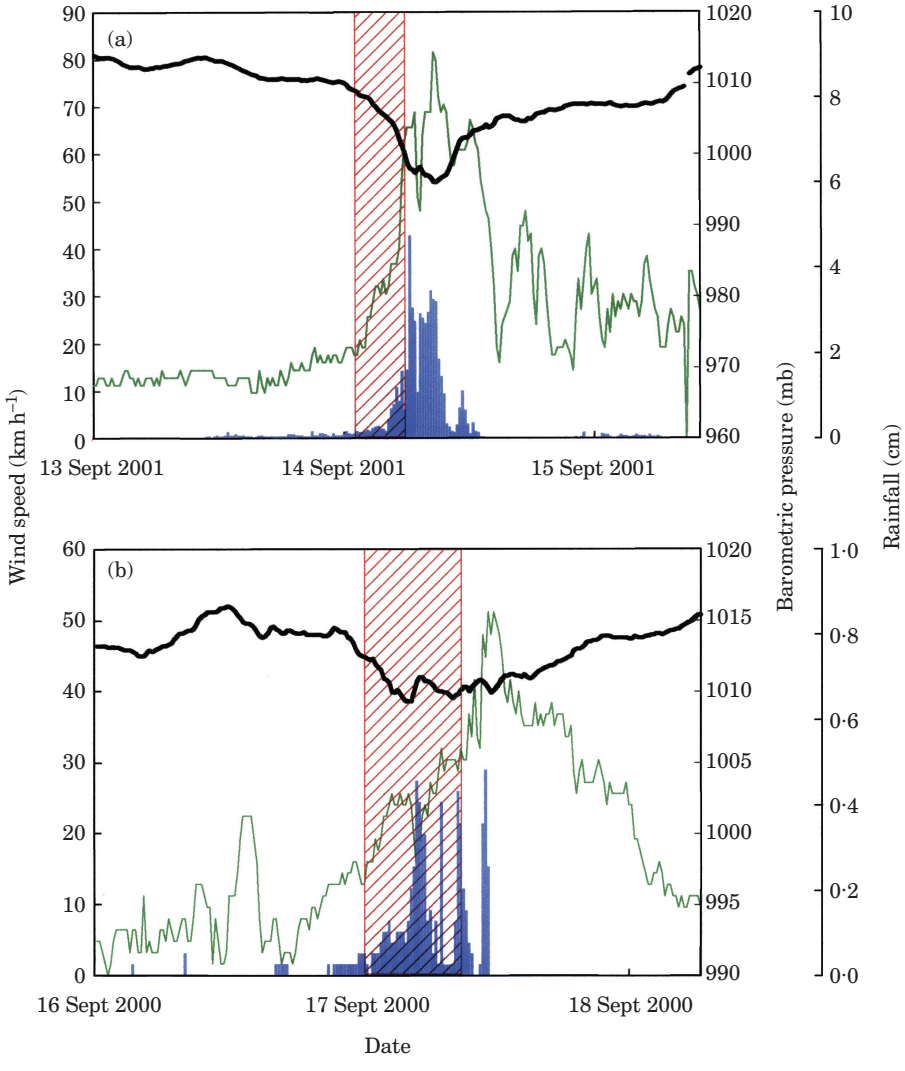

FIG. 2. Weather conditions (—, barometric pressure; —, wind speed; ■, rainfall; ▨, time period blacktip sharks left the nursery area; recorded every 15 min) prior to, during and after (a) Tropical Storm Gabrielle and (b) Hurricane Gordon.

behaviour in response to these milder storm events. This suggests that the wind associated with Tropical Storm Gabrielle was not the primary stimulus for the fish to leave the nursery.

Tidal level and tidal flow were also examined in relation to the blacktip sharks' movements. Based on tide gauge data, the tide was rising at the time of the first departures with the majority of fish departing at slack tide. The slack tide was due to strong winds preventing tidal influx. The normal tidal variation for 14 September 2001 should have been 0·7 m (based on tidal predictions), and prior to fish leaving the nursery the tide had only changed by 0·2 m. At the time

sharks left the area the tide was 0·1 m below predicted levels, but was well within the normal tidal range for the area.

The final environmental factor considered was barometric pressure. Barometric pressure normally does not fall <1009 mb in the Terra Ceia Bay region during summer months (Mote Marine Laboratory Weather Station, unpubl. data) and barometric pressure along the Gulf coast of Florida averaged 1016 mb during September 2001. On 13 September the barometer averaged 1012 mb, but began to decline in the final hours of the day. By 0130 hours on 14 September, as the first blacktip shark left the area, the barometer had dropped to 1008 mb and continued to decline at a steady rate over the next 6 h [Fig. 2(a)]. The final blacktip shark left the nursery as the barometer reached 999 mb. Barometric pressure reached a minimum of 996 mb 2 h later as the storm made landfall. The relative hydrostatic pressure (based on the changes in barometric pressure) during normal conditions and storm conditions is shown in Table I. These data show that the hydrostatic pressure within the study site at the time Tropical Storm Gabrielle passed was different from that which the fish would have experienced had the storm not occurred.

The environmental dynamics of the storm event and the period of time that the blacktip sharks left the study site are shown in Fig. 2(a). The two factors changing most dramatically during that period were barometric pressure and wind speed. Considering that fish began to depart from the bay during relatively low wind speeds ($<30\,km\,h^{-1}$), the falling barometric pressure probably 'triggered' them to leave the relative safety of the nursery for deeper waters nearby.

Although the drop in barometric and subsequently hydrostatic pressure was small in relation to changes during tidal fluctuations (Table I), the changes associated with the storm did deviate from the normal temporal pattern. Several previous studies have shown that fishes without swimbladders are entrained to tidal cycles (Gibson, 1970, 1971, 1982, 1984). Results of these studies suggested that hydrostatic pressure cycles are a Zeitgeber for these endogenous rhythms (Gibson, 1971, 1984). Gibson (1970) suggests that: 'The tidal rhythm of activity is therefore seen as a behavioural mechanism which allows the fish to anticipate changes in its environment.' This suggests that fishes are entrained to and can anticipate changes in tidal cycle based on variation in hydrostatic pressure. Additional pressure changes due to changes in barometric pressure would

TABLE I. Calculations of hydrostatic pressure (mb) within the water column based on varying levels of barometric pressure observed during normal and two storm conditions (Tropical Storm Gabrielle and Hurricane Gordon). Depth for pressure calculations was based on 3 m, the mean depth of Terra Ceia Bay

High Tide				Low tide			
Depth	Normal	Gabrielle	Gordon	Depth	Normal	Gabrielle	Gordon
Surface	1013·2	996·0	1008·0	Surface	1013·2	996·0	1008·0
Middle	1165·2	1148·0	1160·0	Middle	1114·5	1097·3	1109·3
Bottom	1317·2	1299·9	1311·9	Bottom	1215·8	1198·6	1210·6

alter the 'anticipated' tidal change and may have served as the cue for blacktip sharks to leave the nursery area.

Behaviours associated with barometric pressure change have been reported for teleosts in several studies, but this phenomenon has not previously been reported for an elasmobranch. Although it is not known if fishes, with or without swim bladders, have an absolute sense of pressure (Montgomery & Pankhurst, 1997), a recent study (Fraser & Shelmerdine, 2002) concluded that vestibular hair cells in the elasmobranch inner ear respond to changes in hydrostatic pressure. The study's results suggest that sharks could sense a change in barometric pressure as low as 5 mb (P. Fraser pers. comm.). Barometric pressure during the approach of Tropical Storm Gabrielle dropped at least 4 mb as the first blacktip sharks left and had declined by 13 mb as the last fish departed.

Additional analysis of previous years' monitoring data was conducted based on these results and it was determined that a similar, but less distinct response occurred for Hurricane Gordon in September 2000. Hurricane Gordon made landfall as a weakening tropical storm in the Big Bend region of Florida (545 km north of Terra Ceia Bay). The storm peaked on 17 September, 306 km south-west of Terra Ceia Bay. Once again blacktip sharks began to leave the nursery before the heaviest rainfall began and before wind speed peaked. The tide was high as fish began to leave the study site and began to drop during the period fish were leaving the nursery. As with Tropical Storm Gabrielle, the barometric pressure began to drop before and during the time the blacktip sharks left the study site [Fig. 2(b)]. The barometric pressure dropped *c.* 5 mb during the time the storm passed offshore of the study site. Blacktip sharks left the bay over a wider time range than with Gabrielle and were generally gone for shorter time periods. One individual was only gone for 3 h while most were gone for 7–11 h and one individual left for a period of 13 days. Of the 10 blacktip sharks being tracked at the time Hurricane Gordon was passing, eight left the study site.

It is clear that the response to Hurricane Gordon was not as distinct or synchronous as with Tropical Storm Gabrielle. Examination of barometric pressure data shows that the change in pressure was not as great with Hurricane Gordon (5 mb) as with Tropical Storm Gabrielle (13 mb) (Table I) and therefore would not have provided as strong a stimulus to leave the nursery. A drop in barometric pressure, however, is the only apparent similarity in these two events. The response of monitored blacktip sharks was similar in both instances, although less pronounced and comprehensive during Hurricane Gordon. These results suggest that the dramatic response of these blacktip sharks seen during Tropical Storm Gabrielle was not a unique occurrence and that this flight behaviour is in response to an environmental stimulus. Based on the available information, it is hypothesized that the changes in barometric, and thus hydrostatic, pressure provided the environmental stimulus to leave the nursery.

The synchronicity of departures, similar behaviour of monitored blacktip sharks, and their young age (3–4 months) suggest that the blacktip sharks' departure before these storms arrived was an innate response. Shark nursery grounds are typically thought to provide protection from predation and abundance of food (Branstetter, 1990). Leaving the nursery in response to

unusual or irregular changes in hydrostatic pressure may be a mechanism to prevent individuals from being trapped in a shallow area during an extreme storm event. Alternatively, it could be due to a disorientation of the pressure sensing mechanism, driving the animals to seek deeper water. Whatever the reason, the exact role this response plays in the behavioural ecology and life history of these animals is speculative at this time.

This research was funded by a grant from the National Science Foundation (Award No. OCE-9911295). We thank P. Fraser for his comments and advice and J. Morris and D. Rowles for assistance with field efforts.

References

Branstetter, S. (1990). Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. *NOAA Technical Reports, NMFS* **90,** 17–28.

Fraser, P. J. & Shelmerdine, R. L. (2002). Dogfish hair cells sense hydrostatic pressure. *Nature* **415,** 495–496.

Gibson, R. N. (1970). The tidal rhythm of activity of *Coryphoblennius galerita* (L.) (Teleostei, Blennidae). *Animal Behaviour* **18,** 539–543.

Gibson, R. N. (1971). Factors affecting the rhythmic activity of *Blennius pholis* L. (Teleostei). *Animal Behaviour* **19,** 336–343.

Gibson, R. N. (1982). The effect of hydrostatic pressure cycles on the activity of young plaice *Pleuronectes platessa*. *Journal of the Marine Biological Association of the United Kingdom* **62,** 621–635.

Gibson, R. N. (1984). Hydrostatic pressure and the rhythmic behaviour of intertidal marine fishes. *Transactions of the American Fisheries Society* **113,** 479–483.

Guy, C. S., Neumann, R. M. & Willis, D. W. (1992). Movement patterns of adult black crappie, *Poxomis nigromaculatus*, in Brant Lake, South Dakota. *Journal of Freshwater Ecology* **7,** 137–147.

Heupel, M. R. & Hueter, R. E. (2001). Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In *Electronic Tagging and Tracking in Marine Fisheries* (Sibert, J. R. & Nielsen, J. L., eds), pp. 217–236. Amsterdam: Kluwer Academic Publishers.

Heupel, M. R. & Simpfendorfer, C. A. (2002). Estimation of survival and mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 624–632.

Jeffrey, J. D. & Edds, D. R. (1999). Spring movements and spawning habitat of sauger (*Stizostedion canadense*) in a small midwestern USA reservoir. *Journal of Freshwater Ecology* **14,** 385.

Jones, M. S. & Rogers, K. B. (1998). Palmetto bass movements and habitat use in a fluctuating Colorado irrigation reservoir. *North American Journal of Fisheries Management* **18,** 640–648.

Markham, J. L., Johnson, D. L. & Petering, R. W. (1991). White crappie summer movements and habitat use in Delaware Reservoir, Ohio. *North American Journal of Fisheries Management* **11,** 504–512.

Montgomery, J. C. & Pankhurst, N. W. (1997). In *Deep Sea Fish* (Randall, D. J. & Farrell, A. P. eds), pp. 325–349. San Diego, CA: Academic Press.

Simpfendorfer, C. A., Heupel, M. R. & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones, and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 23–32.

Watterson, J. C., Patterson III, W. F. & Shipp, R. L. & Cowan J. H. Jr. (1998). Movement of red snapper, *Lutjanus campechanus*, in the North Central Gulf of Mexico: potential effects of hurricanes. *Gulf of Mexico Science* **16,** 92–104.