

Generation 5 Data Storage Tags, GPS and Developed Methodology for Studying the Hydrostatic Pressure Environment of the Juvenile Lemon Shark (*Negaprion brevirostris*)

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BIOGRAPHY

Lauren Smith is in the second year of her PhD at Aberdeen University investigating hydrostatic pressure sensing in crustacea and sharks. Dr Samuel H. Gruber runs a long term project studying the behaviour and ecology of sharks around the Bimini islands in the Bahamas with the help of volunteers, research students and staff. Steve Kessel is a PhD student based in South Bimini whose research interests include; Lemon Shark population dynamics and community structure and long-line sampling potential and accuracy. Dr Julian Metcalfe is an expert in fish telemetry based at Cefas Laboratories, Lowestoft. Dr Peter J. Fraser is a Senior Lecturer in the Zoology Department at Aberdeen University, who has discovered that the angular acceleration receptors in crabs and sharks also function as sensors for very small changes in hydrostatic pressure.

ABSTRACT

Following pioneering laboratory work at Aberdeen University in Scotland, which identified a hydrostatic sensor in sharks, field work was conducted from August through to October 2006 in South Bimini, Bahamas, to investigate the normal hydrostatic pressure range and usage including determining whether *Negaprion* showed significant changes in depth over time, and how any depth changes related to barometric pressure, daily and tidal cycles. Juvenile lemon sharks <1 m previously fitted with internal acoustic transmitters were used for the study. Generation 5 Data Storage Tags manufactured by CEFAS Technology Limited UK were used and secured externally to the first dorsal of the shark, using an innovative method developed for this study. The DSTs logged both pressure and temperature every 5 seconds for 20 days. During this time observational data was gathered by manual tracking using hydrophone and receiver equipment allowing GPS points to be taken which complemented the DST data.

After the 20 days the DSTs were actively retrieved and the data downloaded. Depth profiles have been determined for 6 juvenile sharks and relationships between depth and environmental or meteorological variables, and behaviour patterns of the sharks have been identified.

INTRODUCTION

Hydrostatic pressure, which increases by approximately 1 bar for every 10 m in depth, is an influential factor for aquatic organisms requiring an accurate pressure sensing mechanism to allow depth reception. In some teleost fish, depth regulation is made possible by the utilization of a gas filled swim bladder. The inflation or deflation of the swim bladder is a means of responding to changing pressure, which allows them to maintain neutral buoyancy (Carwardine, and Watterson 2002). It is easy to imagine that volume changes in the swimbladder could be sensed via mechanoreceptors allowing this to serve as a pressure sensor. However for those organisms, which do not possess swim bladders, the method used to sense pressure remained elusive. It has only been in the last decade that a sensory mechanism has been proposed in crabs (Fraser and Macdonald, 1994). The piston / plunger mechanism for hydrostatic pressure reception in crabs involves the sensory hair receptors within the statocyst or balancing organ, which respond to hydrostatic pressure via mechanoreceptors. These are activated by the alteration of the interior volume of cuticular hairs by differential compression of the fluid contents. This in turn displaces their dendrites via the linked cuticular rod.

Using the comparative approach, this has led to recent work being conducted on other organisms which do not possess swimbladders. Elasmobranchs (sharks and rays) had previously served as subjects for pioneering studies concerned with components of the vestibular system (Arthur and Myberg 2001, Dijkgraaf 1963, Lowenstein and Sand 1940, Muller 1999, New 2001) and the responses of the semicircular canals to angular and linear acceleration (Lowenstein and Compton 1978,

Lowenstein and Sand 1940). In 2002, Fraser and Shelmerdine investigated the effect of hydrostatic pressure on the vestibular hair cells located in the labyrinth of the dogfish *Scyliorhinus canicula*. Extracellular recordings were made from vestibular type II hair cells within horizontal canal units in isolated elasmobranch labyrinths (which code for angular acceleration). Results showed these vestibular hair cells also responded to small step changes in hydrostatic pressure and to slow sinusoidal cycles of pressure. This study alongside a later publication where the results were discussed further (Fraser, Cruickshank and Shelmerdine 2003) is important as it provides the first evidence of hydrostatic pressure sensitivity in the shark hair cell system or indeed in any vertebrate.

Behavioural responses to changing hydrostatic pressure have been exhibited by aquatic organisms. The prawn (*Palaemonetes varians*) which when confined to a bottle will actively swim to the surface when a pressure of 40 LB/in. is applied and then allow itself to sink again when released (Digby 1961) and more recent studies on the vertical movements of Cod (*Gadus morhua*) provide evidence for depth adaptation behaviour in some fish undergoing a post-release period of adaptation (after being brought to the surface for tagging) to increasing depth as they re-adjust their buoyancy to that experienced pre-tagging (Heffernan, Righton and Michalsen 2004). Extensive records examining vertical movement behaviour exist for teleosts predominantly Cod (*Gadus morhua*) (as a result of projects such as CODYssey) due to the current need for effective fisheries management of this commercially important species.

In comparison relatively few studies exist concerning elasmobranchs and more specifically shark, behavioural responses to pressure, with no studies directly encompassing hydrostatic pressure sensing as a primary focus. Vertical movement patterns of sharks have been studied, however such investigations would appear to address topics such as sexual segregation and aggregation of the dogfish *Scyliorhinus canicula* (D'Onghia *et al.*, 1995, Sims *et al.*, 2006, Sims, Nash and Morritt 2001), or as part of general observations of the ecology of sharks in order to categorise them based upon the depth of ocean they occupy. Sixgill sharks *Hexanchus griseus* were observed to spend most of their time at depths of 600-1000 m parallel to bottom contours (Carey and Clark 1995) a distribution which classifies them as deep-sea sharks. A preference for staying close to the surface or the bottom whilst not exceeding a depth of 300 m is behaviour associated with the Tiger shark (*Galeocerdo cuvier*) (Holland *et al.* 1999).

It wasn't until a few years ago when a tagging study by Heupel *et al* (2003) investigating the home ranges of a population of juvenile (< 1 year old) Blacktip sharks (*Carcharhinus limbatus*) coincided with the arrival of Tropical Storm Gabrielle, that the importance of

hydrostatic pressure was realized. *C. limbatus* responded to the approach of the tropical storm by moving to deeper water. Meteorological variables were examined they suggested that the movements of the blacktip sharks were triggered by a drop in barometric pressure associated with the approach of the storm. Based on the changes in barometric pressure for a given depth, the relative hydrostatic pressure was shown to be different within the study site at the time Tropical Storm Gabrielle passed from that which the fish would have experienced had the storm not occurred. Thresholds for hydrostatic pressure sensitivity can be inferred from Fraser and Shelmerdine's recordings from horizontal canal afferents during changes in pressure (Fraser, Cruickshank and Shelmerdine 2003). A reasonable threshold level is 5-10 mb which allows responses to the storm related atmospheric changes.

The movement out of the area was consistent for all the fish being studied, with all sharks returning to the nursery ground after the passage of the storm. This is the first study to report behavioural changes associated with barometric pressure in elasmobranchs. In conclusion the paper hypothesises that the changes in barometric pressure, and thus hydrostatic pressure provided the environmental stimulus to leave the nursery. Also the synchronicity of departures coupled with similar behaviour and their young age (3-4 months) suggest that the behaviour observed was an innate response. Heupel *et al* (2003) propose that due to the shark nursery grounds providing protection from predators and an abundance of food, leaving the nursery in response to irregular changes of hydrostatic pressure may be a mechanism to prevent individuals from becoming trapped in a shallow area during an extreme storm event. An alternative suggestion is that it may be due to disorientation of the pressure sensing mechanism, which drives the animals to deeper water, this is much less likely given the relatively small changes in pressure involved.

Studies investigating hydrostatic pressure reception in sharks have been undertaken solely within the laboratory, with none in the field. Despite work done on vertical movement patterns these investigations were not underpinned by knowledge of the ability of sharks to sense hydrostatic pressure, and the study by Heupel *et al* (2003) merely coincided with a storm event and did not intend to examine sharks' responses to changing barometric pressure.

Here we explore the normal usage of the shark hydrostatic pressure sensor, by reporting initial findings from a pioneering study using data storage tags attached to juvenile lemon sharks (*Negaprion brevirostris*) undertaken in situ at the Bimini Biological Field Station (BBFS), South Bimini, Bahamas. Experiments assessed whether *N. brevirostris* showed significant changes in depth over time, and how any depth changes relate to environmental parameters including barometric pressure, day/night and tidal cycles.

MATERIALS AND METHODS

SPECIES AND LOCATION

The lemon shark, *Negaprion brevirostris*, is found mainly along the subtropical and tropical part of the Atlantic coast of North and South America and belongs to the family *Carcharhinidae*. A relatively stable population of lemon sharks inhabit the waters surrounding South Bimini, Bahamas (Fig 1a) which is located approximately 80 km due east of Miami Florida and is home to a main shark nursery area along its South coast. The juveniles of the species are particularly suitable as they are highly site attached inhabiting the same nursery grounds for the first 2 years of their life (Morrissey and Gruber 1993). Thus the life strategies of the juvenile sharks make them readily available for study in contrast to open ocean dwelling sharks.

South Bimini is also the location of a unique field station, the BBFS (N 25°41.87, W 79°17.787) which provides a study environment allowing a variety of experiments to be conducted on the lemon sharks inhabiting coastal waters.

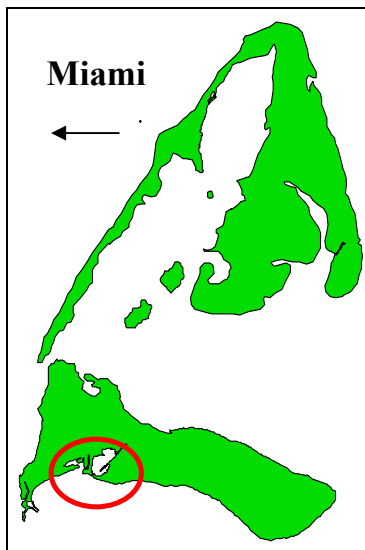


Figure 1a. The Bimini islands located 80 km due east of Miami Florida are approximately 23 sq km in total area; the area circled is shown in greater detail in Fig 1b.

COLLECTION AND MAINTENANCE

9 juvenile lemon sharks *Negaprion brevirostris* were captured along the South Bimini coastline which is a known shark nursery area. Subdivisions occur within this area with the sharks occupying localised home ranges. Seven of the juveniles used were Duck Pond sharks and two were from Nobels (Fig 1b). All had been previously implanted internally in the peritoneal cavity, with standard

coded tracking transmitters (Sonotronics, CT-series) and Passive Integrated Transponders (Destron Fearing PIT tags) inserted under the surface of the skin close to the first dorsal fin for identification purposes. Sharks were located by manual tracking using standard hydrophone and receiver equipment to recover the acoustic signal emitted by the shark's transmitter. Each signal consisted of a series of beeps at a set frequency and particular sequence allowing sharks to be individually recognised. When a reasonably accurate position of the shark could be ascertained a gill net was then used to capture it. All 9 sharks were captured between 06/09/06 and 08/09/06. Sharks were manually removed from the gill net and transported via boat to a pre-erected enclosure (Fig 1b) (30 ft diameter) (N 25°41.87, W 79°17.787) within the sharks known home ranges (which were determined by prior manual tracking studies), where they were kept within the enclosure for a total of 6 days. The longest time for any one shark to be in captivity was 6 days and the shortest 4 days, with variation due to the ease or difficulty encountered when locating and capturing the required animals. All captive sharks were fed every 2-3 days on Barracuda (*Sphyraena barracuda*) steaks at random time intervals and in areas of the enclosure also chosen at random, thus keeping behavioural conditioning to a minimum.

PREPARATORY WORK AND DST ATTACHMENT

Prior to release all juvenile *N. brevirostris* were prepared on board a Carolina Skiff with the aid of a 1 m measuring trough. Pit numbers, acoustic transmitter codes, site of capture, pre-caudal, fork and total length, dry weight and sex were recorded (Table 1). Tag attachment was also achieved on board the Carolina Skiff with the shark housed in a transport box. Prior to this, part of the attachment had been constructed (Fig 2) and the DST set to log both pressure and temperature every 5 seconds for 20 days. The DST was then threaded onto a 50 ILB breaking strain monofilament, a loop was made and a double crimp used to hold it in place. A single crimp was then fixed 2 inches further up the monofilament and a self fashioned plastic washer threaded on. For the attachment onto the shark two people were required; one supported the shark with a hand in front of the first and second dorsal, whilst the second person performed the surgery. A small incision was made using a scalpel on the left side of the first dorsal, approximately 1 inch in from the front of the fin (head end) and 0.5 inch from the base of the fin. A needle with part of the attachment previously constructed was threaded into it and then pushed through the fin at a 45 ° angle until the skin on the opposite side was broken. The monofilament was pushed through the needle to remove any flesh and then pulled out leaving the needle in place. The attachment was then re-threaded into the needle on the right side of the fin, the needle was then removed and a plastic washer followed by a single crimp, threaded onto the monofilament on the left side. The crimp was clamped into place and any excess cut off. The shark was immediately released (Fig 3a, 3b). The entire attachment

process totalled less than 10 minutes per shark, with the attachments taking place 2 days after completion of the preparatory work.

ACOUSTIC TRACKING

Additional data was obtained by means of manual tracking using shallow-draft Carolina Skiffs. Transmitter pulses from a shark's internal coded transmitter were monitored through stereo-headphones detected using a staff mounted, directional headphone connected to a manual ultrasonic receiver. The signal range of the transmitters reached 1 km and the position of a shark was calculated by taking estimated distance, bearing and global position using GPS (Global Positioning Satellite) technology. This horizontal movement data (Fig 4) comprised another dimension of the shark within its environment, when coupled with time, pressure and temperature information obtained from the DST (Fig 5a, 5b). The total track time for all sharks was 52 daylight hours, from the 18th-20th and the 22nd-27th of September 2006 with 348 positional fixes obtained.

ENVIRONMENTAL OBSERVATIONS

Tidal cycle was monitored over the same 20 day period as the sharks (from 18:00 11/09/2006 to 18:00 30/09/2006), a DST also set to log every 5 seconds was housed in a porous container and weighted down at a chosen point (within the duck pond Fig 1b). This served as a bottom monitor within the sharks' home range. All sharks with the exception of two, occupied this area.

However due to the sheltered nature of this site with only a relatively narrow channel allowing water in and out, a tidal lag was expected and in order to gauge this after completion of the study, two DSTs were placed outside this area and in the study site respectively (Fig1b). Both were set to log for 3 days enabling any tidal lag to be established.

Barometric Pressure was obtained from the nearest meteorological station; Fowey Rock FL. (N 25° 59, W 80° 10), courtesy of National Data Buoyancy Centre (NDBC) as part of their C-man program (The Coastal-Marine Automated Network). Sunrise, Sunset and Nautical Twilight times were obtained from the United States Naval Observatory. Temperature was also logged by the DSTs so shark temperature profiles were observed as well as the environmental temperature ranges logged by the bottom monitor.

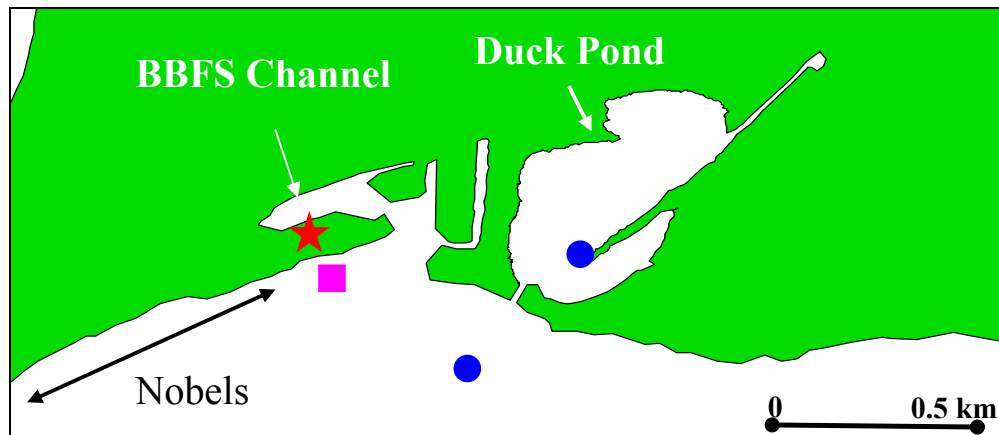


Figure 1b. Main study site of the South Bimini coastline, with approximate locations of central features; red star: BBFS, purple square: enclosure for holding captured juveniles and blue circle: DST serving as bottom monitor inside the duck pond for the main study, with this same site used together with another DST being placed outside the duck pond for the tidal study measuring potential tidal lag in the duck pond.

PIT Tag	Acoustic code	Capture site	PCL cm	FL cm	TL cm	WT kg	Sex
445C4D2851	555	South Bimini, Sect.2.	63	69.5	80	2.1	M
423B626A14	666	Off BBFS Dock	74	81.6	94.8	5.3	F
423B316F53	444(71)	South Bimini, Sect.2.	63.5	71	81.5	2.4	F
445E0B6F58	444(74)	Nobels	56.6	62.2	73	1.7	F
451C5B1B05	233	R.H.S. Duck Pond	60.7	67.5	77.2	1.7	F
454B044272	223	R.H.S. Duck Pond	59	66	76	1.9	M

Table 1. Preparatory data from the sharks successfully recaptured after the 20 day study period. PCL: Pre Caudal Length, FL: Fork Length, TL: Tail Length, WT: Weight.



Figure 2. Partial construction of the DST attachment, the DST is threaded onto the monofilament (50 ILB breaking strain) and held in place with a double crimp.



Figure 3a. Part of the surgical process of DST attachment, showing the needle and first stage of tag attachment being passed through the first dorsal.



Figure 3b. Completion of DST attachment to D1, prior to release.

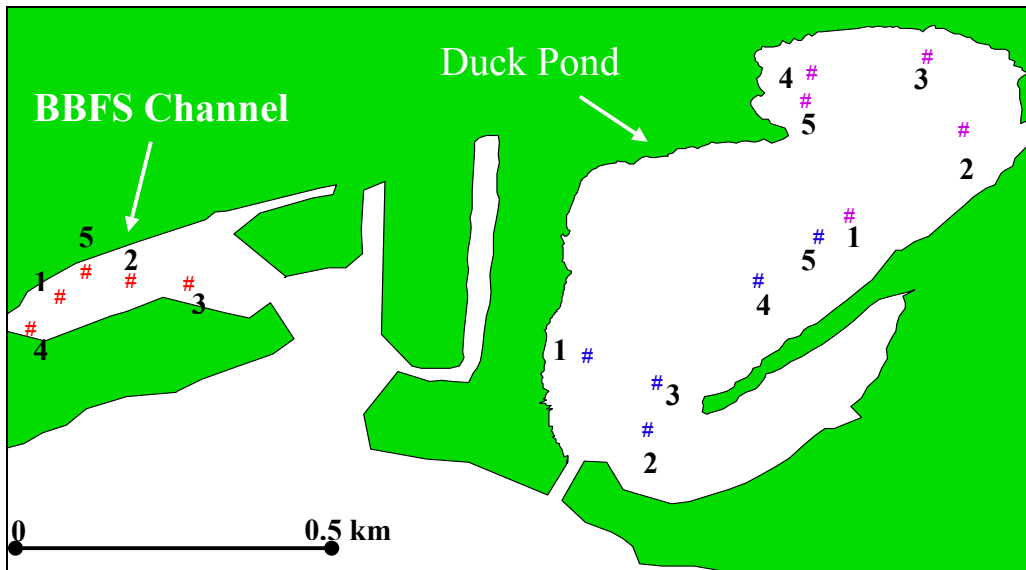


Figure 4. GIS image for the 18/09/06 produced from the bearing, distance and GPS data obtained from manual tracking. Red: 444(71), Blue: 666, Purple: 555. Numbers indicate 5 minute increments with 1 being the initial positional fix.

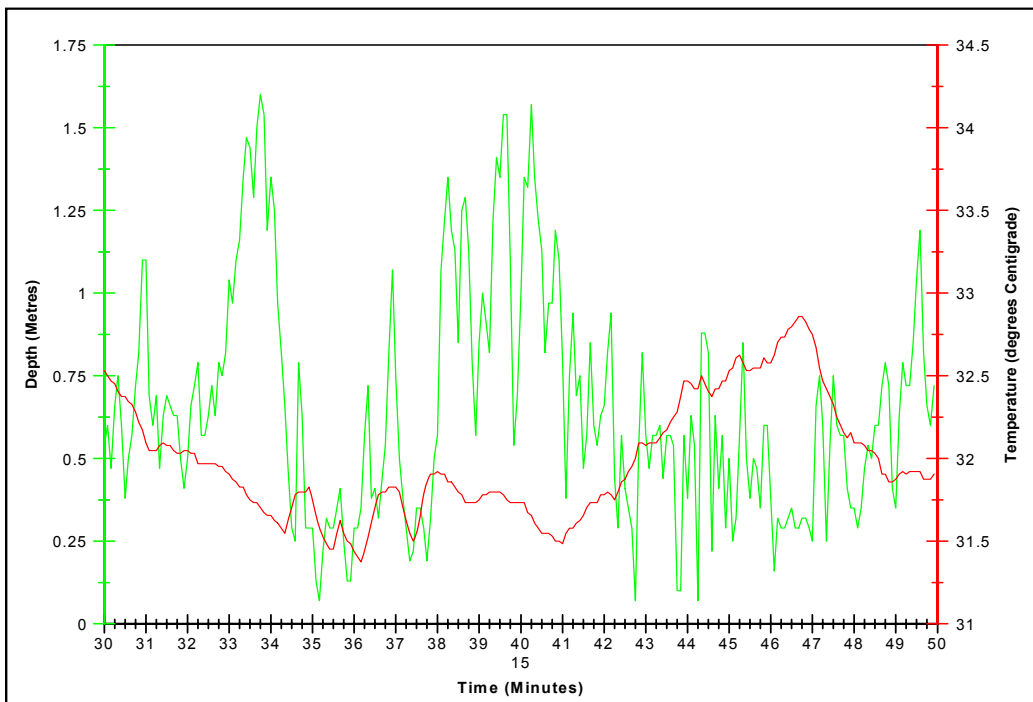


Figure 5a. The depth and temperature profile logged by the DST attached to shark 444(71) on the 18/09/06 from 15:30 to 15:50 when the shark was being manually tracked in the BBFS channel as shown in Fig 4. The dives over 1 m and the lower maximum temperature (when compared with figure 5b) correspond with the shark occupying the BBFS channel.

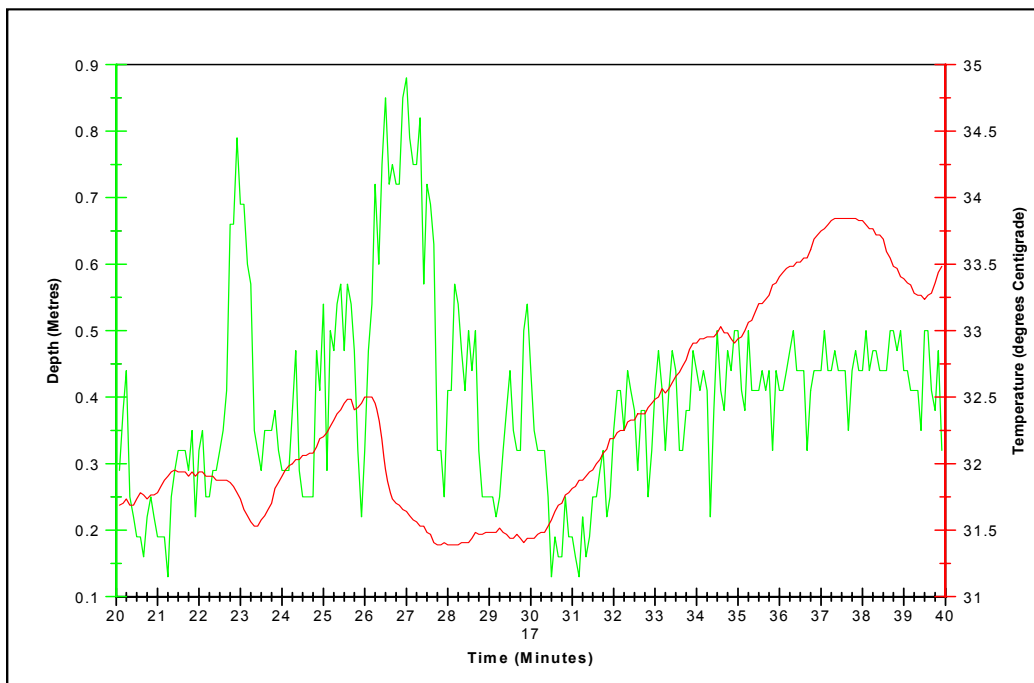


Figure 5b. The depth and temperature profile logged by the DST attached to shark 666 on the 18/09/06 from 17:20 to 17:40 when the shark was being manually tracked in the BBFS channel as shown in Fig 4. The activity less than 1 m and the higher maximum temperature (when compared with figure 5a) correspond with the shark occupying the duck pond.

RESULTS

DSTs were actively retrieved from sharks following manual tracking and the use of gill nets. Recapture success was 66 % from those DSTs deployed on sharks. Two juveniles died during the study and 1 DST became detached. The bottom timer was retrieved manually by free diving. For the purposes of this study 1 decibar equates to approximately 1 metre depth from the surface.

DEPTH UTILIZATION AND TRACKING STUDIES

During the 20 day study preliminary results indicate that sharks occupied a depth range of 0-5.6 m and spent on average 91.3 % of their time occupying 0-1 m, 7.3 % (av.) 1-2 m, 0.9 % (av.) 2-3 m, 0.02 % (av.) 3-4 m, 0.001 % (av.) 4-5 m and 0.0001 % (av.) 5-6 m. However these figures vary between individuals (Table 2) with the sharks spending a considerable proportion of time in very shallow water, this has been investigated further by dividing the 0-1 m results into ten 0.1 m depth brackets (Fig 6), again figures vary between individuals and it is evident that the sharks are utilizing some depths more than others even within very shallow water. Habitat depths determined by previous studies are known (Fig 7) and are being used to determine whether the shark is being

constrained to these depths by its habitat, i.e. sharks are moving parallel to bottom contours in very shallow water or alternatively sharks are actively seeking out shallow water despite deeper depths being available. Average depth (between 0–5.6 m) appears to be correlated with total shark length (from the tip of the snout to the end of the upper caudal fin) although this may be dependent on the individual sharks' home range.

Only one data set was successfully retrieved from a Nobels shark (444(74)). Despite being the smallest (length) shark in the study its average depth occupation was at a higher pressure than anticipated and it had the greatest depth range together with the deepest dive of all test sharks (5.6 m). Shark 666 spends more time utilizing a higher pressure (1-2 m) when compared to the other juveniles; home range appears to be an important contributing factor here too, prior tracking studies revealed 666 to be a duck pond shark however during this study 666 was predominantly found in deeper water outside the duck pond, 444(71) was also found frequently in this area (Fig 1b), this may indicate a move to deeper water triggered by shark size (length). Manual tracking provided evidence that all of the duck pond sharks do at times leave the safety of the area (perhaps due to the extreme shallow waters occurring at low tide).

SHARK ID	0 - 1 m	1 - 2 m	2 - 3 m	3 - 4 m	4 - 5 m	5 - 6 m
666	68.5	27.4	3.7	0.1	0.001	0
444(71)	92.4	7.3	0.1	0.0009	0	0
444(74)	93	6.4	0.4	0.05	0.006	0.0009
555	97.7	1.3	0.7	0.006	0	0
233	97.9	1.1	0.7	0.005	0.002	0
223	98.8	0.7	0.3	0.001	0	0

Table 2. Occupation of depth ranges (in m) by individual sharks, results expressed in percentages.

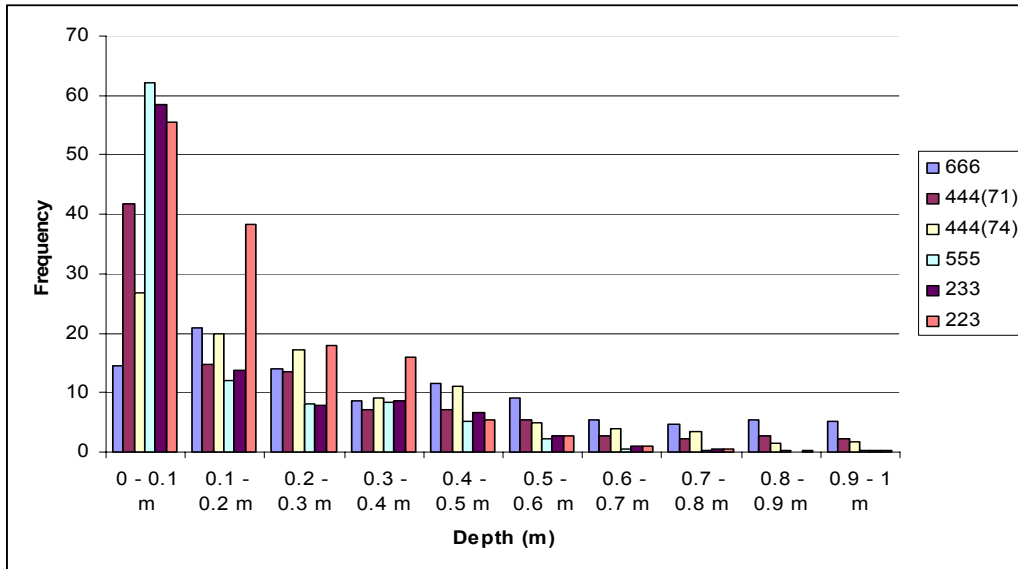


Figure 6. A histogram displaying the occupation of 0-1 m depths by sharks utilizing very shallow water.

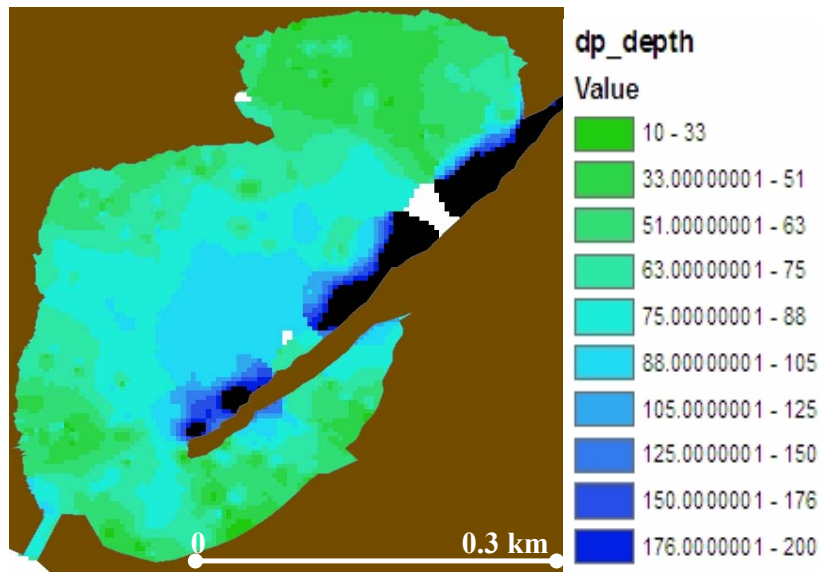


Figure 7. Known depths of the duck pond, measurements in Centimetres. (Image courtesy of Bryan Franks, Drexel University, Philadelphia.)

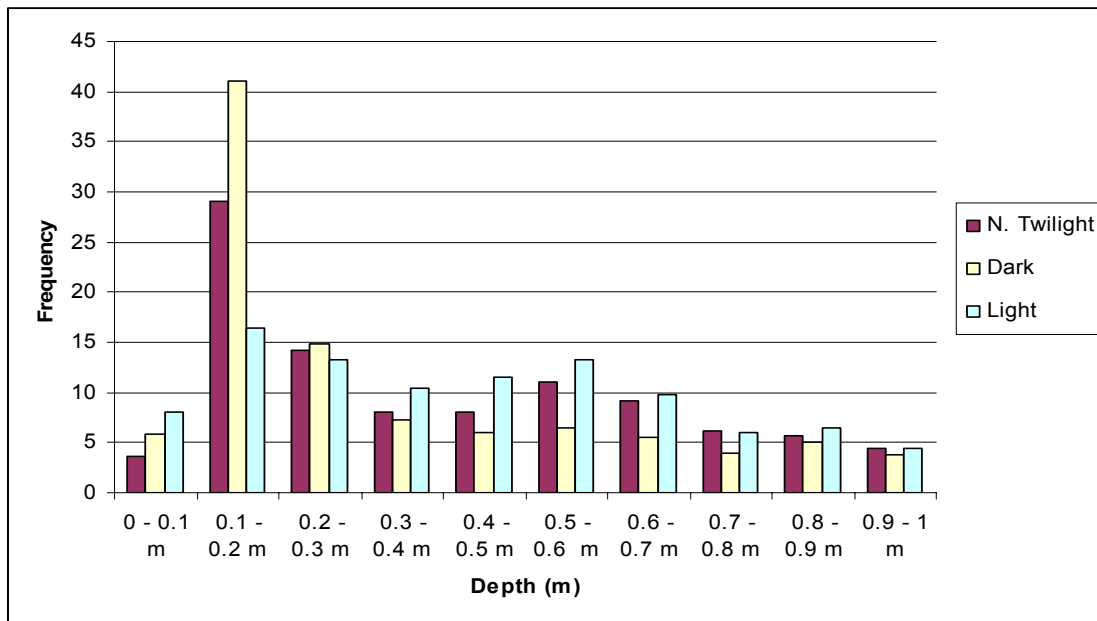


Figure 8. A histogram using data from shark 666, displaying the occupation of 0-1 m depths during Nautical Twilight, Darkness and Daylight hours.

TIDAL CYCLE

A clear tidal cycle was observed from pressures logged by the DST serving as a bottom monitor in the duck pond, a tidal shift was seen with high and low tide being reached approximately 40 minutes later with each consecutive day and a tidal range of around 0.72 m was found. A tidal lag of 40 minutes was present in the duck pond monitor when compared to pressures logged by the DST placed outside this area, pressures and times associated with the tidal cycle do show some variance in accordance with changing weather conditions, however these are extremely slight. The tidal cycle can be visually observed in all of the sharks' depth profiles but not continuously (obscured by the sharks own vertical migration), it is most apparent in sharks 555, 233 and 223 which appear to spend a high proportion of their time utilising depths between 0-1 m. At present results do not suggest any correlations between stages of the tidal cycle and depth utilization.

TEMPERATURE

A large temperature range of 18.57° was encountered by the sharks; falling between 19.05 and 37.62 °C, a much smaller range of 5.1° was experienced by the bottom monitor (27.73° - 32.83°C). A daily cycle was found with temperatures typically peaking late afternoon to early

evening (17:00 – 18:00) and reaching minimum temperatures in the early morning (07:00). Investigations as to whether a shark's behaviour as signalled by depth utilization, alters in relation to temperature, are underway.

PHOTOPERIOD

Shark vertical activity was assessed in relation to different amounts of light exposure. Data was obtained from the U.S. Naval Observatory from which 3 categories were devised; Nautical Twilight, Darkness and Daylight. Investigation suggests that for all of these times occupation of very shallow water (0-1 m) predominates, however migration between depths of 0-1 m varies in accordance with the aforementioned categories (Fig 8), with all sharks utilising shallower depths during darkness and nautical twilight, which may be associated with increased hunting success (of their primary food source Mojarras) due to their eyes experiencing peak sensitivity around crepuscular periods (Gruber and Cohen 1978).

BAROMETRIC PRESSURE

Data recorded by the NDBC suggests minimal changes in barometric pressure took place during the 20 day study period; analysis of this in respect to shark vertical movements' show no relationship or patterns exist.

DISCUSSION

VERTICAL MOVEMENT BEHAVIOUR

This study is the first of its kind to investigate the normal usage of the shark hydrostatic pressure sensor in situ, and presents results which provide a good measure of what the pressure sensor is exposed to as well as the sharks' behaviour at these depths whilst also assessing the influence of environmental / meteorological variables. Shark behaviour can be classified into two broad groups in respect to observed vertical movement. (i) Resting / Minimal movement and (ii) Active. The latter behaviour by a shark was deemed to be taking place when logged pressure data fluctuated over a larger range of depths, whereas a shark was considered to be resting when logged pressure data remained fairly constant with few rapid fluctuations, the tidal pressure cycle is also clearly apparent within the sharks' depth profile. A previous study on the rate of movement of juvenile lemon sharks also conducted at the BBFS suggested three types of activity, 'non-linear movement', 'parked' and 'milling' (Sundstrom *et al.* 2001) (no such classifications have existed for vertical movement until now) the observation of 'parked' activity lends credence to resting behaviour with the authors defining it as 'the signal direction and amplitude remaining the same over time, suggesting they were motionless on the bottom'. From the results, activity can be seen to occur over a range of depths and can be divided accordingly into 6 divisions of active vertical movement: (i) Very shallow water activity (0-1 m), (ii) Shallow water activity (1-2 m), (iii) Medium shallow water activity (2-3 m), (iv) Medium deep water activity (3-4 m) (v) Deep water activity (4-5 m) and (vi) Very deep water activity (5-6 m). Very Shallow Water Activity can then be divided into ten 0.1 m depth increments. Further analysis on consistency of behaviour patterns between individual sharks and on vertical movement behaviour and the environment is in progress.

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