CSIRO PUBLISHING

Marine and Freshwater Research, 2010, **61**, 1446–1456 www.publish.csiro.au/journals/mfr

Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters

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Abstract. Documenting free-swimming fish in their natural environment using acoustic transmitters equipped with acceleration and pressure sensors may contribute to knowledge of locomotory behaviour for a variety of aquatic species. Previously, collection of acceleration data has been limited to archival loggers, necessitating retrieval of the devices; however, recent advances in biotelemetry have allowed for acceleration data to be transmitted to a remote receiver. To illustrate the application of this technology, relative locomotory activity and depth utilisation of adult great barracuda (*Sphyraena barracuda*) were monitored across habitat types and diel periods using acoustic transmitters equipped with tri-axial acceleration and pressure sensors within an acoustic telemetry array ($n = 53$ receivers) deployed in The Bahamas. Although there were no differences in acceleration or depth use across habitats or diel periods, there was evidence of movement into shelf habitat during mid-day where they occupied depths >10 m. Given both the method of calculating the accelerometer output, and that the transmitters were unable to store and transmit large quantities of data, we suggest choosing transmitter settings with a short average delay and high transmission frequency to optimise data quality and resolution. This paper represents one of the first reports of the use of telemetered acceleration values from free-swimming fish.

Additional keywords: accelerometer, acoustic biotelemetry, Bahamas, pressure sensor.

Introduction

Documenting the distribution of free-ranging marine animals in space and time is fundamental to understanding their basic natural history, intra- and inter-specific interactions, and habitat requirements (Cooke *et al.* 2004*a*; Ropert-Coudert and Wilson 2005; Cooke 2008). To that end, there have been hundreds of studies that have used different biotelemetry, biologging, and mark–recapture techniques to document the spatial ecology of marine animals in habitats ranging from inshore coastal flats to the high seas (Kohler and Turner 2001; Cooke *et al.* 2004*a*; Ropert-Coudert and Wilson 2005). This information has improved our knowledge of the spatial ecology of marine animals, enabling managers and conservation practitioners to identify and protect critical habitats (Cooke 2008; Hofmann and Gaines 2008; Wilson *et al.* 2008).

Far fewer studies have evaluated the spatial ecology and mobility of marine animals at smaller temporal and spatial scales. Although some animals undertake large-scale migrations, sometimes transiting oceanic basins (Block *et al.* 2005; Holdsworth *et al.* 2009), many animals also make localised small-scale movements as they engage in activities such as locating food and avoiding predators (Cooke and Philipp 2004; Meyer and Holland 2005; Wearmouth and Sims 2009). Locomotory activity, on the scale of seconds to hours, influences the activity costs that are primary drivers in fish energy expenditure (Boisclair and Leggett 1989; Webber *et al.* 1998; Cooke *et al.*

 10.1071/MF10046 1323-1650/10/121446

2004*b*). Another aspect of spatial ecology that is rarely considered in marine animals is the third dimension of space – depth. Information on the depth distribution of marine fish is relevant to ecological processes such as foraging activity, refuge, and habitat preferences (Brill *et al.* 1999; González-Sansón *et al.* 2009; Wearmouth and Sims 2009), and has implications for various management strategies (e.g. regulations concerning deployment position of fishing gear: Cartamil and Lowe 2004; Hoolihan and Luo 2007). In addition, daily movement patterns are also an important component of fish ecology, as many marine species exhibit diel changes in activity or diel vertical migrations (Cartamil and Lowe 2004; Meyer and Holland 2005; Wearmouth and Sims 2009).

With recent advances in biotelemetry and biologging technology, researchers have been provided with new tools for studying the fine-scale activity and depth distribution of animals in the ocean (Cooke *et al.* 2004*a*; Wilson *et al.* 2008). Depth has been measured for more than 20 years using inexpensive and robust pressure transducer sensors on a range of taxa including diving birds, turtles, marine mammals and fish (e.g. *Makaira nigricans*: Block *et al.* 1992; *Caretta caretta*: Houghton *et al.* 2002; *Halichoerus grypus*: Austin *et al.* 2006; *Aptenodytes forsteri*: Zimmer *et al.* 2008). Depth information can easily be transmitted or logged; however, acceleration sensors for estimating field activity level are a more recent development and the use of this type of technology is in its infancy. Early deployment of accelerometers has relied on archival loggers (e.g. *Triaenodon obesus*: Whitney *et al.* 2007; *Negaprion brevirostris*, *Rhincodon typus*: Gleiss *et al.* 2009*a*, 2009*b*; Accipitridae: Halsey *et al.* 2009). However, given that acceleration data can be collected on the order of milliseconds in multiple axes, it has not been until recently that such data can be transmitted in real time. Transmitters of this kind are a new advancement in acoustic biotelemetry technology enabling acceleration data to be recorded in three dimensions and averaged, calculating a vector (*g*) such that it can be transmitted to a receiving device.

Great barracuda (*Sphyraena barracuda*) are predatory fish found in tropical and subtropical nearshore systems worldwide (de Sylva 1963); although it is a relatively common species, little is known about its behavioural ecology. Adult great barracuda have generally been regarded as diurnally active (de Sylva 1963; Randall 1967; Blaber 1982) and observed in a broad range of water depths from shallow, coastal waters to those at depths of over 50 m (de Sylva 1963). However, these observations are largely anecdotal, primarily from visual observations by divers, commercial fishers, and anglers. Differences in activity have been observed relative to water depth and position in the water column, and attributed to foraging activity, predator avoidance, and pre-spawning activity (de Sylva 1963; Blaber 1982; Paterson 1998). To date, barracuda movement has only been studied using mark–recapture methods (Springer and McErlean 1961; Villareal *et al.* 2007) and body markings to identify individuals in a localised area (Wilson *et al.* 2006*b*). With an increasing awareness of the ecological importance of apex marine predatory fish (Myers and Worm 2003; Heithaus *et al.* 2008), as well as the economic and cultural significance of reef fish in tropical and subtropical regions (Sadovy 2005), there is great value in understanding the behavioural ecology of top predators to facilitate management and conservation.

The objective of our study was to describe, for the first time, a method using commercially available acoustic transmitters that are capable of transmitting both acceleration and depth and can be used on free-swimming fish in the ocean. Previous attempts to use accelerometers have relied on biologging techniques and, although small tags are commercially available (Tsuda *et al.* 2006), studies typically have focussed on larger animals that are capable of supporting large electronic tags (Wilson *et al.* 2008). Beyond discussing technological constraints and opportunities, we also present an example of the technique for studying the localised behavioural activity and depth utilisation of wild great barracuda across habitat types and diel periods.

Materials and methods

Study site

The study site was off the coast of Cape Eleuthera, The Bahamas (24°54′N, 76°20′W; Fig. 1). This marine environment includes a unique variety of habitat types ranging from shallow tidal flats, nearshore reefs, and seagrass beds of the Grand Bahama Bank to deep, continental shelf environments along the Exuma Sound. An array consisting of 53 autonomous acoustic receivers (VR2 and VR2W; Vemco/Amirix Systems, Shad Bay, Nova Scotia) was deployed along the ocean floor, each receiver attached to a short length of rebar cemented into a cinder block. The receiver stations were positioned in three curtains projecting from Powell Point on Cape Eleuthera, with additional receiver units placed in a net formation between the curtains and along the edge of the continental shelf (receiver detection ranges generally did not overlap). Range tests were performed, revealing that receivers deployed in coastal habitats (less than 1 m deep) had an average coverage radius of 250 m and receivers deployed in mosaic and shelf habitats had an average coverage radius of 500–600 m. The entire receiver array spanned an area of ~44 km^2.

Habitat type was divided into three categories: coastal, mosaic, and shelf. Coastal habitat was generally <5 m deep, within ~1 km from shore, typically included tidal flats, some seagrass, small patch reefs, and often exposed to some wave and tidal action. Anthropogenic structures such as marinas or blasted rock cuts (regardless of deeper water) were also included in the coastal habitat as these locations were near other available coastal habitat. Mosaic habitat was generally <10 m deep, usually within 2 km from shore and characterised as having a mosaic of patch reefs, seagrass beds, and areas of sandy bottom. Shelf habitats were located along the continental shelf, at depths >10 m deep (the greatest depth of a receiver station was over the edge of the shelf at 42 m), characterised by some patch reefs and exposure to currents. Some of the locations were somewhat closer to shore (<1 km) than other shelf habitat locations. All barracuda were monitored until the transmitter batteries expired or until the individual fish left the detection range of the array.

Capture and tagging methods

All barracuda were captured and surgically implanted with acoustic transmitters during December 12–15, 2008 ($n = 13$). The fish ranged in total length from 62 to 120 cm. Individual

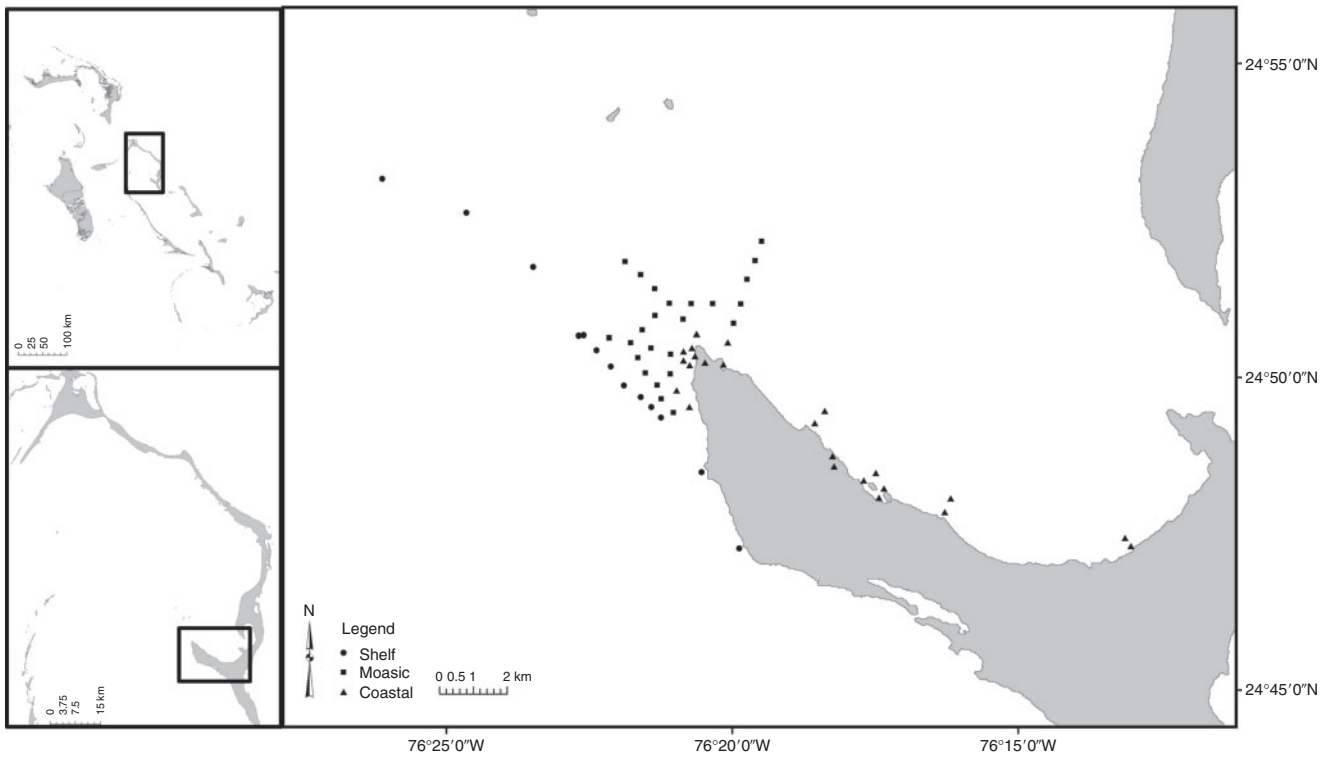

Fig. 1. Map of study site off the coast of Cape Eleuthera, The Bahamas. VR2 receiver stations are depicted according to habitat type location.

barracuda were captured within the geographical confines of the array by trolling with heavy-action recreational angling gear (14 kg (30 lb) test fishing line: O'Toole *et al.* 2010) and artificial lures. Each fish was landed in a mesh cradle, lifted onboard the boat and placed into a 100-L cooler of seawater infused with 3-aminobenzoic acid ethyl ester (MS222) at a dosage that would render each barracuda unable to maintain equilibrium ($\sim$100 mg L^{-1}). Once the fish were anaesthetised, they were held in a supine position with the head and gills completely submerged to ensure adequate irrigation of the gills throughout the surgical procedure. An incision $\sim$1.5 cm long was made with a scalpel along the ventral midline of the fish midway between the pelvic and anal fin and the disinfected transmitter was placed into the abdominal cavity. The incision was closed with two to three simple interrupted PDS II 3/0 absorbable sutures (Ethicon Ltd, NJ: Cooke *et al.* 2003). Fresh seawater was added to the cooler partway through the surgery to dilute the anaesthetic concentration and begin reviving the fish. After the completion of the surgery, all fish were given ample time ($\sim$45 min, depending on the size of the fish) to recover with frequent additions of fresh seawater to the recovery bath, and released at a fixed point within the array. All surgeries were completed by the same trained surgeon.

We implanted the fish with individually coded acoustic transmitters (V9AP; Vemco/Amirix Systems, Shad Bay, Nova Scotia) equipped with acceleration and pressure sensors. The transmitter was orientated corresponding to the anterior–posterior axis (i.e. *y*-axis) of each fish. Ensuring relative axial positioning is important because, although the tags measure average acceleration over three axes and the majority of the data is derived from the surge axis in free-swimming fish, placing the transmitter along the same relative axial position reduces error and improves the signal-to-noise ratio of the accelerometer output (Watanuki *et al.* 2003; Gleiss *et al.* in press). The tag dimensions were 46 mm $\times$ 9 mm and weighed 3.3 g in water (6.3 g in air). The V9AP accelerometer contains a microprocessor that uses a high-pass filter to remove static acceleration (i.e. tilt or inclination of the accelerometer to the Earth's gravitational field) from the overall acceleration, leaving only the dynamic acceleration values (i.e. fast-changing acceleration caused by body movement). The transmitter squares and sums the differences in acceleration measured on each of the three axes (x, y, z) and then calculates the root mean square (RMS) or a vector (g) resulting from overall acceleration on all three axes. The value is then converted into a digital value ranging from 0 to 255, which is transmitted during each sensor transmission cycle. The transmitter is capable of measuring approximate raw acceleration changes of $\pm 3\,g$ before the filter and RMS method reduces the transmitted data to 0–0.35 g or 0–3.47 m s^{-2} (D. Webber, pers. comm.).

We used three groups of transmitters with different settings, all of which measured five samples per second over a specified sampling period. The first group of transmitters ($n = 5$) had an average delay of 45 s with an acceleration sampling period of 19 s, so that the accelerometers were sampling for 21% of the time. The second group of transmitters ($n = 5$) also had an average delay of 45 s, but with a sampling period of 37 s so that the transmitter sampled acceleration 41% of the time. These two groups of transmitters had an estimated battery life of 95 or 65 days respectively. The third group of transmitters ($n = 3$) had

an average delay of 90 s with an acceleration sampling period of 25 s, and the accelerometer was sampling 14% of the time. The third group of transmitters had an estimated battery life of 160 days.

Each transmitter had two coded tag IDs, one for each sensor (pressure and acceleration). Once a unique ID and pressure value were recorded and transmitted, the transmitter immediately began to record acceleration values over a specified sampling period (for example, in our study we deployed transmitters with 19-, 25- and 37-s sampling periods). After the acceleration measurement during the sampling period has been completed, the vectoral product is calculated and stored in memory until the tag transmits an acceleration value (g) and a unique ID over a specified average delay to an acoustic receiving device. Thus, the tags used in our study ran on 45- or 90-s cycles with acceleration and pressure measured intermittently. Raw acceleration data was later converted from g into m s^{-2} by multiplying the acceleration value (g) by 9.8 m s^{-2} (acceleration defined as change in velocity over time). The maximum capability of the acceleration sensor was 3.47 m s^{-2} (0.35 g) and the maximum depth capability of the pressure sensors were 50 m (Fish #149–153) or 100 m (Fish #203–253).

Accelerometer calibration

As the V9AP transmitters are relatively new technology and have not been tested in great barracuda, we performed accelerometer calibration trials on six barracuda ranging from 69 to 94 cm in total length from January 15 to 25, 2009. All fish were captured (via trolling, as described above), transported back to a seawater facility in large coolers, and implanted with transmitters using the same surgical methods outlined previously. Fish were placed in a large 13 180-L circular tank, where they were held overnight to recover from any potential capture, transport, or surgical stress. Twelve hours later, the undisturbed activity (i.e. 'Low' activity) of the barracuda in the holding tank was monitored using a manual tracking receiver (VR100; Vemco/Amirix Systems, Shad Bay, Nova Scotia) for 30 min. Each fish was exposed to two bursting trials in two consecutive cycles of sensor logging, where the fish were forced to burst by chasing around a large tank for 30 s to quantify high acceleration activity (i.e. 'High' activity), followed by a 120-s rest period, and then another 30-s burst trial. Once both burst acceleration trials were run, the fish was left undisturbed and monitored for a further two cycles (i.e. 'Low' activity). To quantify 'Still' or minimal movement (to represent readings of a dead fish in the wild), transmitters were placed undisturbed on a table top and monitored with the manual tracking receiver for 60 min before implantation into barracuda for calibration trials. In addition, we placed a dead fish (implanted with a transmitter) at the bottom of a tank and monitored acceleration readings for 25 min. Values from both trials (undisturbed on table top and in the dead fish) were pooled to calibrate for a non-moving, dead fish.

Data analysis

Only fish with more than 50 detections, and those that were detected for more than one day, were used in the analysis. Detections collected within 24 h of tagging were excluded to account for potential behavioural changes associated with the surgery. A residency index (I_R) was calculated to determine the proportion of days each barracuda was detected within the array across the period of the expected battery life for each transmitter. To account for repeated measurements on each individual fish (random effect), a mixed-model one-way repeated-measures ANOVA was used to assess differences in acceleration across the three habitat types (coastal, mosaic, shelf) and between diel periods (according to local sunrise and sunset times). Diel depth utilisation was assessed for each habitat type separately using a mixed-model one-way repeated-measures ANOVA. A $\log_{10}$ transformation was used to satisfy the assumption of residual normality and homogeneity of variances for both acceleration and depth data. All statistical analyses were performed using JMP v. 8.0 (SAS Institute, Raleigh, NC) software program.

Results

Of the 13 fish tagged, only six fish were detected on more than 50 occasions (ranging 73–1230 hits (acceleration) and 56–1184 hits (depth); Table 1), thus only these six individuals were included in the analysis. Of these six fish, two individuals were present within the array region for less than 10 days, whereas the other four were present for 21–115 days; however, within these time frames individual barracuda were only actually detected on 5–77 days during the study period (Table 1). Individual barracuda exhibited residency indices (I_R, proportion of time spent within the array during the expected transmitter battery life) ranging from <0.01 to 0.70. Over the study period, barracuda were detected by 32 of the 53 receivers within the array and one fish (#253) was detected by up to 19 of the receivers (Table 1).

Acceleration

Laboratory calibration trials revealed that undisturbed or 'Still' transmitters had mean acceleration readings of 0.06 m s^{-2}, a modal value of 0.05 m s^{-2} and ranged from 0.05 to 0.08 m s^{-2}. Mean 'Low' locomotory activity was 0.22 m s^{-2} but most frequently 0.12 m s^{-2} (ranging 0.010–0.74 m s^{-2}), which typically corresponded to a fish swimming in place or swimming slowly around the tank. 'High' locomotory activity was measured during constant barracuda burst activity over 30 s, and these values were consistently 3.47 m s^{-2} (the maximum capability of the V9AP transmitter).

Acceleration values for wild great barracuda ranged across nearly the entire capacity of the acceleration sensors (0.05–3.47 m s^{-2}) for the three habitat types (Fig. 2; Table A1, available as an Accessory Publication to this paper) and we found that mean acceleration values across all three habitats were similar ($F_{2,48} = 0.18$, $P = 0.83$; Accessory Publication, Table A2). The modal acceleration values recorded for each habitat type were: coastal habitat, 0.54 m s^{-2}; mosaic habitat, 0.422 m s^{-2}; shelf habitat, 0.52 m s^{-2}, and when all observations were pooled the modal value was 0.52 m s^{-2} (Accessory Publication, Table A1). Although there was not a difference in locomotory activity across habitat types, there were differences among individual barracuda ($F_{10,3462} = 21.32$, $P < 0.0001$; Table A2, Accessory Publication). Overall, wild fish primarily exhibited Low locomotory activity, spending ~58% of the time swimming slowly or swimming in place, but they also showed a

Table 1. Summary table of wild *Sphyraena barracuda* tagged with V9AP transmitters Dec 12–15, 2008 near Cape Eleuthera, The Bahamas ($n = 13$)
Individuals with >50 hits were included in the analysis ($n = 6$) and are highlighted in bold. TL, total length; I_R, residency index

Tag ID	Date tagged	TL (cm)	No. hits (acceleration)	No. hits (depth)	No. days in array	No. days detected	I_R	No. receivers	Est. tag life (days)	Sampling time (%)
149	13 Dec 2008	81	15	15	116	7	0.04	1	160	14
151	13 Dec 2008	79	46	43	3	3	0.02	6	160	14
153	**12 Dec 2008**	**83**	**403**	**404**	**115**	**77**	**0.48**	**10**	**160**	**14**
203	14 Dec 2008	60	0	0	1	1	0.01	0	95	21
205	**13 Dec 2008**	**62**	**73**	**56**	**104**	**19**	**0.20**	**5**	**95**	**21**
207	13 Dec 2008	79	0	1	1	1	0.01	1	95	21
209	15 Dec 2008	85.5	35	36	3	3	0.03	10	95	21
221	**13 Dec 2008**	**92**	**1131**	**1166**	**74**	**46**	**0.71**	**12**	**65**	**41**
223	**12 Dec 2008**	**120**	**431**	**431**	**9**	**9**	**0.13**	**5**	**65**	**41**
225	14 Dec 2008	79	77	74	3	1	0.01	3	65	41
227	14 Dec 2008	99	0	0	1	0	0.00	0	65	41
229	**12 Dec 2008**	**94**	**207**	**189**	**5**	**5**	**0.08**	**7**	**65**	**41**
253	**15 Dec 2008**	**81**	**1230**	**1184**	**21**	**18**	**0.19**	**19**	**95**	**21**

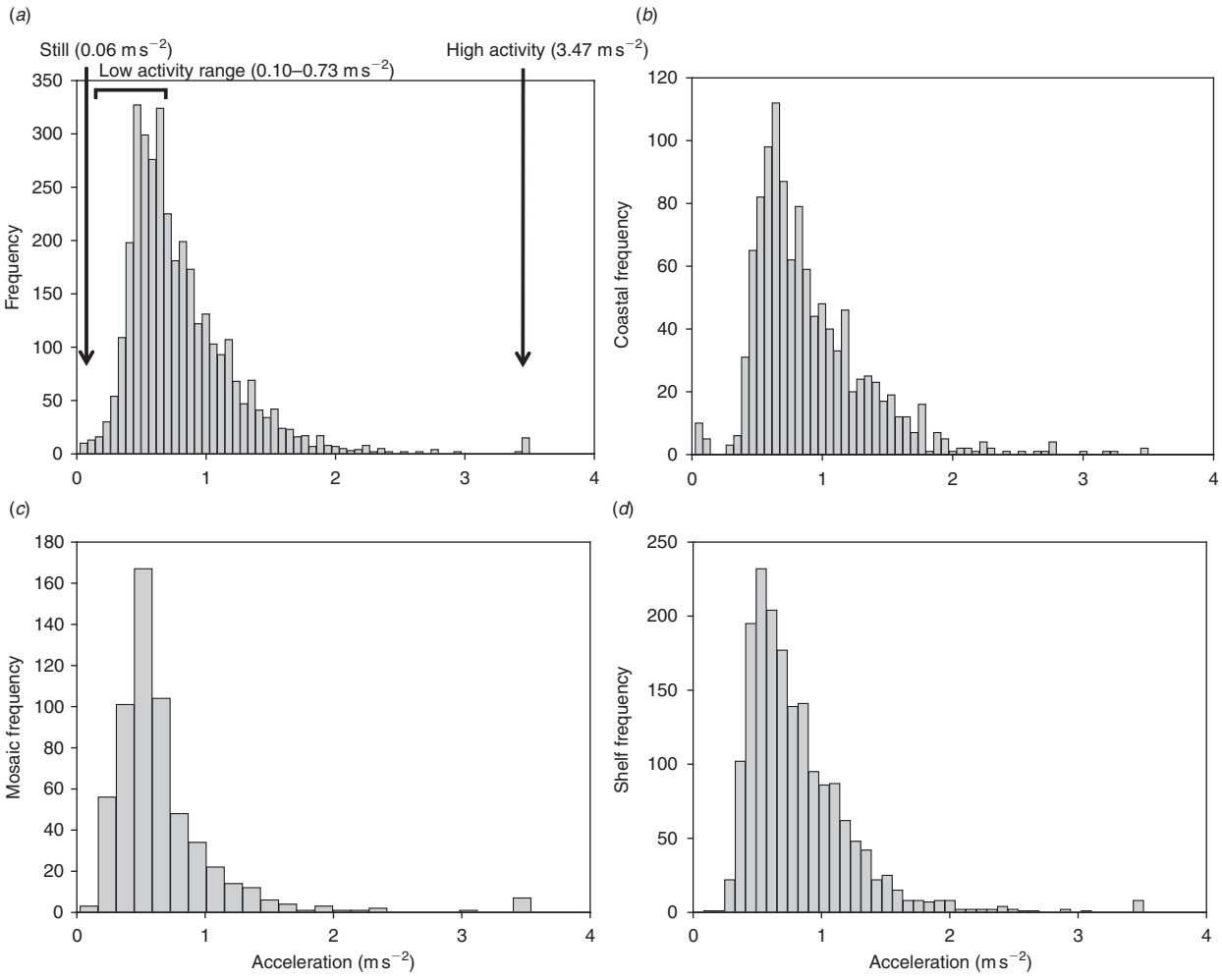

Fig. 2. Frequency histograms of wild *Sphyraena barracuda* acceleration ($m\,s^{-2}$) in (*a*) all habitats combined, (*b*) coastal habitat, (*c*) mosaic habitat and (*d*) shelf habitat. Laboratory accelerometer calibration values are included in (*a*) for relative comparison with acceleration values collected from fish in the wild.

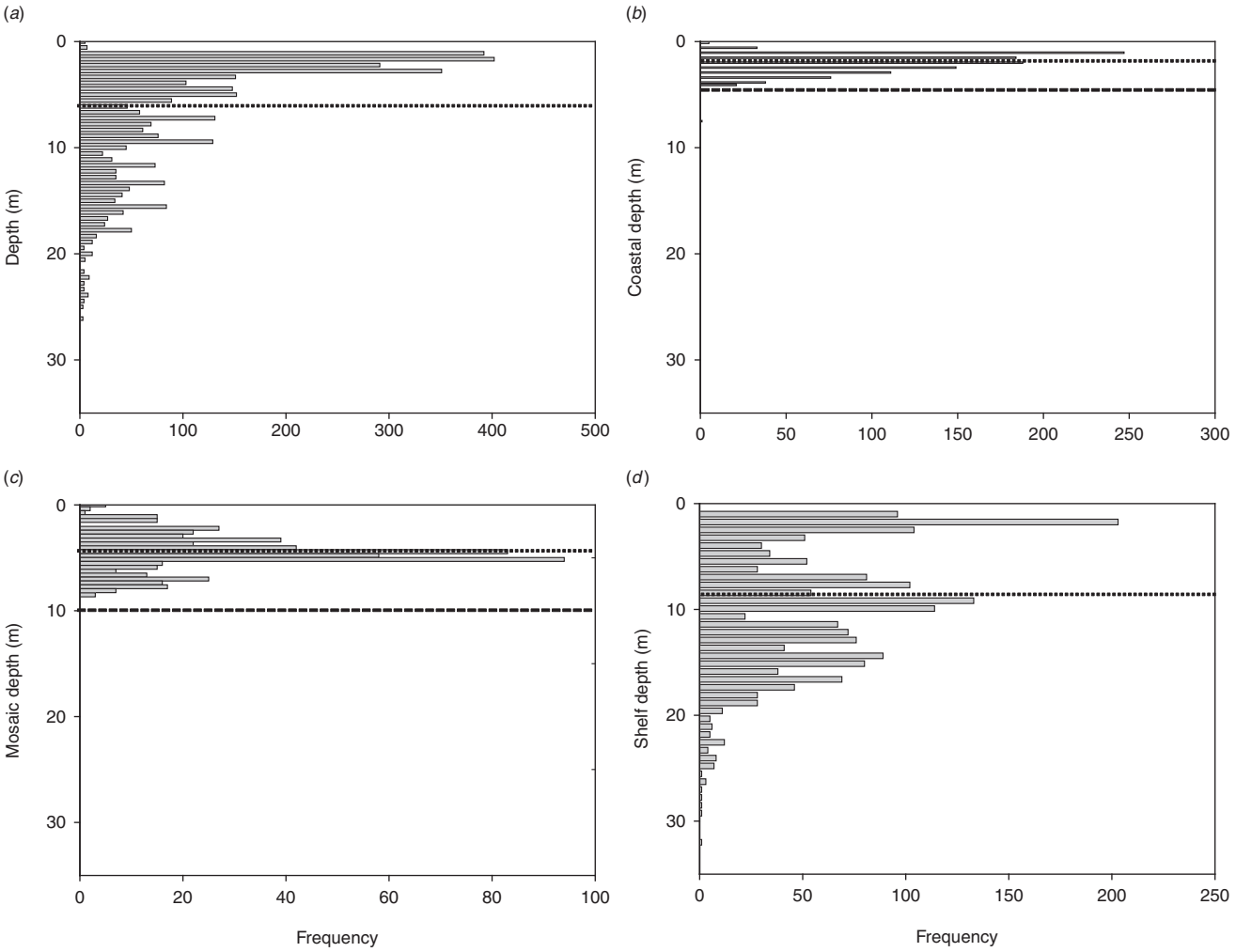

Fig. 3. Frequency histogram of wild *Sphyraena barracuda* depth (m) utilisation in (*a*) all habitats combined, (*b*) coastal habitat, (*c*) mosaic habitat and (*d*) shelf habitat. Fine dashed lines indicate mean fish depth (m) within each habitat type. Heavy dashed lines signify the maximum available depth for coastal (5 m) and mosaic (10 m) habitats; shelf habitat had >10 m of available depth.

range of values from very minimal movement to High activity (Fig. 2*a*). Low activity was generally consistent across the three habitat types, whereas High activity was also evident but not frequently detected (Fig. 2). We also did not detect a diel effect ($F_{1,12} = 0.04$, $P = 0.85$; Table A2, Accessory Publication), although we did observe variation among individual fish across diel periods ($F_{10,3463} = 50.37$, $P < 0.0001$; Table A2, Fig. A1, Accessory Publication).

Depth

Barracuda depth-use values across the three habitat types ranged from 0 to 32.22 m (coastal, 0.12–7.6 m; mosaic, 0–8.5 m; shelf, 1–32.2 m, Fig. 3; Table A3, Accessory Publication). The fish were detected most frequently near the surface at depths < 5 m (modal values across habitats: coastal, 1.00 m; mosaic, 4.62 m; shelf, 1.44 m; Table A3, Accessory Publication). There was also a lack of diel effect on depth of barracuda within each of the three habitat types, but we noted individual variation in depth use within the three habitat types (Table A4, Accessory Publication). To some extent, barracuda appear to use the entire available water column within each habitat type, with the deepest detection at 32 m below the surface (Fig. 3), but not all individuals used each habitat type (Table A3, Accessory Publication).

Despite efforts to quantify how much of the available depth was actually utilised by the tagged barracuda, we were limited in our abilities to decipher where the fish was located in relation to a specific receiver. This was of particular concern in deeper shelf habitats where the receiver was placed near the edge of the deep drop-off of the Exuma Sound and the detection range of the transmitters may have reached depths greater than the depth of the nearest receiver. The V9AP transmitters are equipped to measure up to a maximum depth of 50 or 100 m and, according to our results, barracuda were only using up to ~20–30% of the capacity of the pressure sensor.

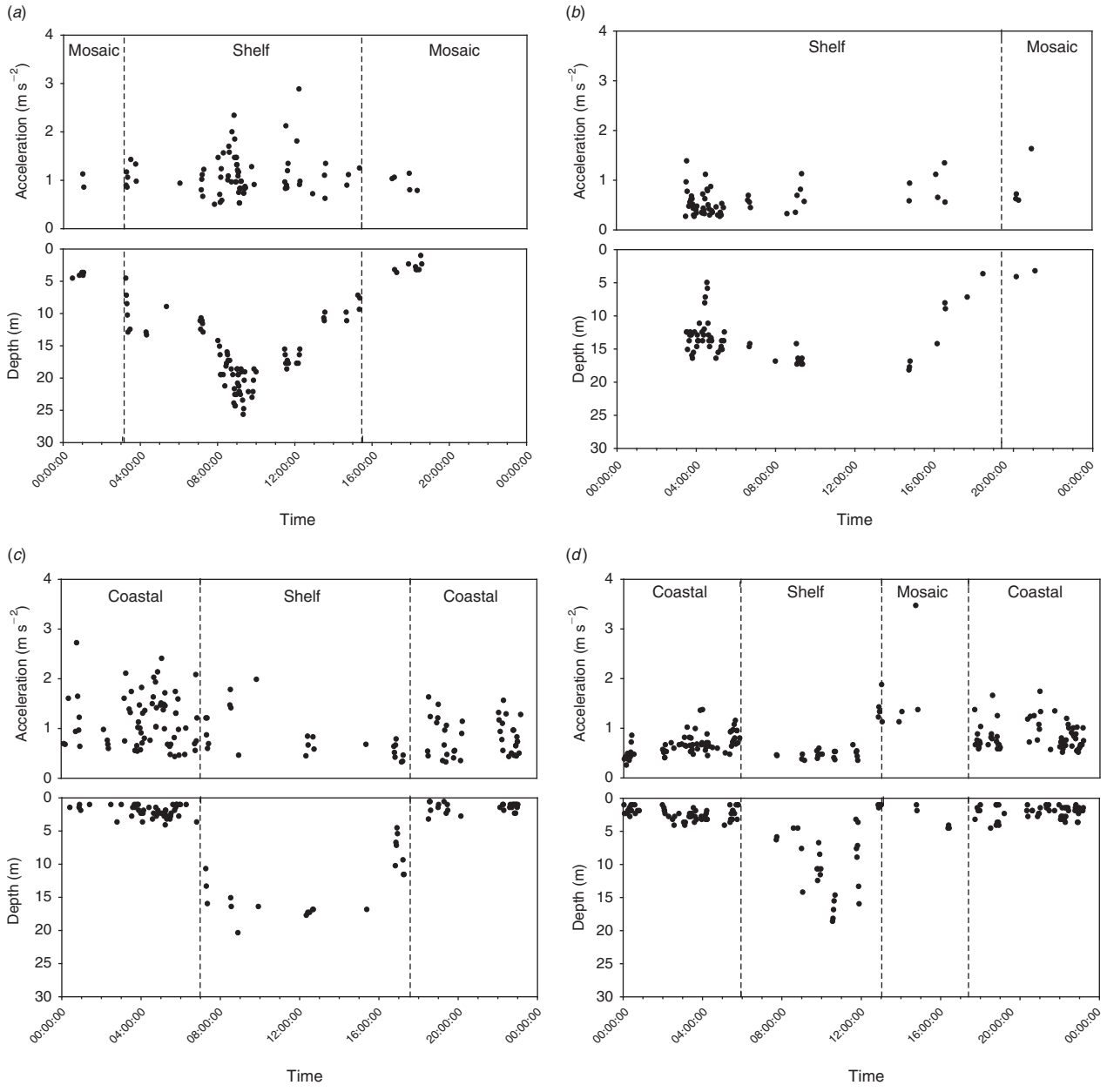

Fig. 4. Examples of behavioural patterns across habitat types of two wild *Sphyraena barracuda* over two 24-h periods for each fish. Acceleration (m s^{-2}) and depth (m) of fish #223 on (*a*) December 16, 2008 and (*b*) December 19, 2008 and acceleration (m s^{-2}) and depth (m) of fish #253 on (*c*) December 19, 2008 and (*d*) December 23, 2008. Dashed lines represent movement into a different habitat type.

Although there were no apparent trends in acceleration across 24-h time periods, fishes #223 and #253 appeared to move from coastal and mosaic areas into shelf habitat, where they spent time deeper in the water column (>10 m deep) during the middle of the day (~08:00–16:00 hours), before returning to shallower, coastal or mosaic habitats in the late afternoon (Fig. 4). This trend was not apparent with other individuals in the study as there were minimal or inconsistent detections over the 24-h period to draw conclusive results. Fishes #223 and #253 were also only detected for nine and 18 days respectively, with few full days of complete data.

Discussion

Acceleration transmitters

This is the first study to deploy acoustic telemetry transmitters equipped with acceleration and pressure sensors in wild fish. The ability to quantify the behaviour of fish in their natural environment over long time periods without needing to recapture the fish make the transmitting capabilities of the V9AP device highly desirable. However, the transmitting function limits the capacity of the tag to produce high-resolution data, such as that available from data loggers (e.g. Tsuda *et al.* 2006;

Whitney *et al.* 2007; Gleiss *et al.* 2010). This is mainly a result of the inability of the tag to store large quantities of data in the tag memory before transmission. Data resolution from the transmitters is also affected by the method of measuring and calculating the acceleration value, where even the slightest change in acceleration on a single axis may affect the overall calculation of the vectoral product. Thus, our ability to decipher individual, fine-scale behavioural occurrences was often impeded, as we were unable to determine acceleration readings from specific axes. Given the problems with transmitting large quantities of data, efforts to obtain more detailed information may need to rely on logging technology such as 'daily diaries' (Wilson *et al.* 2008). Nonetheless, transmitters equipped with acceleration sensors provide one of the few tools available for obtaining fine-scale activity on free-swimming fish that are difficult to recapture, and we anticipate much technological innovation in the use of acceleration sensors on transmitters in the near future.

The maximum acceleration sensor capability was 3.47 m s^{-2} (0.35 *g*, as per the manufacturer's specifications) and continuous bursting behaviour ('High locomotory activity'), evident from laboratory calibration trials, consistently resulted in maximum values. Consequently, the full range of barracuda acceleration may not have been captured as it is apparent that this species is capable of achieving accelerations greater than 3.47 m s^{-2}. Our laboratory calibration trials did not show direct cause and effect of locomotory activity because of the inability for the barracuda to display all possible behaviours that occur in the wild. The trials did, however, allow us to better understand the relative activity values associated with High and Low activity in the wild for this species. The tags were programmed to measure acceleration over a specified period of time (with the lowest setting at 14% sampling time), which may not have captured as many short-term events (i.e. bursting) as the tags set with longer sampling times. In addition, the transmission intervals were infrequent (90 or 120 s) and the fish were not always within the detection range of the receivers in the array, further limiting our ability to consistently detect barracuda over time. Initially we had intended to make direct comparisons among the three different settings chosen for the transmitters in the study; however, owing to resultant low sample sizes (non-detections as a result of tagged fish moving outside of the detection range of the array within days of release is a common occurrence in open array telemetry studies: Heupel *et al.* 2006; Meyer *et al.* 2007), this was not possible, although the data still provide important insights into the biology of these animals. Users can select and modify a variety of transmitter settings (e.g. sampling frequency, number of axes monitored – either simultaneously or sequentially, averaging period, calculation of vector) in the devices we used for our study. Given that the implications (in terms of performance) of different settings are not fully understood, a detailed laboratory study comparing different settings would be useful. However, even if such studies existed, having some knowledge of the biology of the animal that is the focal point for study is also needed to help to inform the selection of transmitter settings.

Great barracuda behaviour

The present study is the first to use acoustic telemetry techniques to monitor behaviour of great barracuda by focusing on relative acceleration and depth utilisation across habitat types and diel periods. Overall, barracuda locomotory activity ranged from stationary holding to High activity, although most observations were on the lower end of the activity spectrum (low cruising speeds followed by quick bursts have also been documented in other species, i.e. *Makaira nigricans*: Block *et al.* 1992). This finding was consistent with anecdotal observations that barracuda spend significant time swimming slowly or hovering in place (de Sylva 1963; Paterson 1998). Barracuda are ambush predators that lie in wait and burst at high speeds (burst velocities have been measured at 12.2 m s^{-1}; Gero 1952) to capture a prey item (Grubich *et al.* 2008). Although not the most frequently observed behaviour in the present study, occasional High activity was apparent (Fig. 2), which may have been attributed to foraging events or predator avoidance (by sharks or larger conspecifics: Paterson 1998). Fast-start performance in northern pike (*Esox lucius*), a freshwater fish, has been shown to be energetically expensive (Frith and Blake 1995). Like northern pike, barracuda are morphologically suited for high performance acceleration (fusiform body shape with high percentage of white muscle), so it may be advantageous for barracuda to spend the majority of time being less active (i.e. slow swimming and cruising or hovering) as a means to reserve energy for feeding or predator avoidance.

Energy expenditure in fish is largely driven by locomotion (Boisclair and Leggett 1989; Webber *et al.* 1998; Cooke *et al.* 2004*b*). Unfortunately, there have been limitations to studying bioenergetics in wild marine fish owing to the lag in development of acoustic activity-driven activity sensor technology, compared with available radio-telemetry technology that is more suited for freshwater applications (Ebner 2009; Gollock *et al.* 2009; Jellyman 2009). Rate of oxygen consumption has been shown to be positively correlated with acceleration logger output in avian species (*Phalacrocorax carbo*: Wilson *et al.* 2006*a*; *Gallus gallus domesticus*: Green *et al.* 2009; Halsey *et al.* 2009), mammals (*Eumetopias jubatus*: Fahlman *et al.* 2008), amphibians (*Bufo marinus*: Halsey and White 2010), and sharks (*Sphyrna lewini*: Gleiss *et al.* 2010). Using triaxial accelerometers affixed to bantam chickens, Halsey *et al.* (2009) showed that although individual measures of dynamic acceleration in each of the three dimensions were the best predictor of oxygen consumption rate, overall dynamic body acceleration (using a similar technique as in this study) was also highly correlated with energy expenditure. However, detailed laboratory respirometry experiments must be performed to calibrate energy consumption and behaviour on a species-specific basis (Lucas *et al.* 1993; Butler *et al.* 2004), something that we did not do in the current study. Furthermore, although locomotion makes up a considerable component of the overall energy budget in animals, energy is still being expending during times of inactivity (such as resting, digestion) and thus other techniques (e.g. heart rate monitoring) may need to be employed in tandem with accelerometry to more accurately predict energy consumption (Green *et al.* 2009). Other factors such as the medium in which the animal is moving (i.e. water, air, or soil), depth, temperature, and ecological or morphological characteristics of a species may also affect the relationship between activity and energy use (Gleiss *et al.* in press). Although triaxial accelerometry has not been widely used in teleosts, the V9AP transmitter may prove to

be a suitable tool for estimation of energy expenditure in barracuda and other marine species.

Many animals show variation in diel activity levels, often associated with foraging (Meyer and Holland 2005; Whitney *et al.* 2007). Based upon stomach content analyses, great barracuda have generally been regarded as diurnal foragers (dependent on sight to capture prey items), feeding in shallower habitats during the early morning and early evening, and spending time in surface waters over deeper habitats when not feeding (de Sylva 1963; Blaber 1982). In contrast to those previous anecdotal observations, we did not detect significant diel differences in activity, and would require more complete monitoring of full diel cycles across multiple days to draw sound conclusions about daily barracuda activity. Incomplete temporal sequence data is often a shortcoming of open, non-overlapping acoustic array designs (Heupel *et al.* 2006). Moreover, our array boundaries did not cover all potential areas where the tagged barracuda could potentially swim (i.e. vast sections of the ocean). Our findings actually indicate that barracuda may be quite transient, and that techniques for monitoring movement on broader spatial scales will be necessary to fully document the spatial ecology and migrations of barracuda. Our results did show significant individual differences in activity levels, which may have explained more of the variation than any potential differences in mean activity across diel periods and habitat types. Although we expected to see a relationship between total length and activity levels, our data did not reveal such a trend, potentially as owing to a small sample size. Similarities in locomotory activity for great barracuda across habitat types (Fig. 2) may also reflect consistencies in prey availability and foraging opportunities throughout the study region.

Blaber (1982) and Paterson (1998) documented that barracuda were typically found higher in the water column over deeper, shelf environments, often at depths of 5 m below the surface, similar to the results found in the present study, where most fish were generally observed in the top 5–10 m of the available water column (Fig. 3). Although two individuals appeared to consistently move into shelf habitat, spending time in deeper water during the middle of the day, it was difficult to draw conclusive results owing to temporal inconsistencies in the data. It is uncertain whether some of the tagged individuals were resident to the area or were migrating through the array during the study period. As a result of the open boundary nature of our receiver array, potential fluctuations in the detection range of individual receivers within different regions of the array (as a function of environmental factors), and non-overlapping detection ranges, the detection efficiency of the array may have, at times, been reduced. A possible way to address this is through the use of other telemetry techniques, such as archival pop-up satellite tags that first store data on animal position and depth use before transmitting the data to satellites, and are jettisoned from animals after a period of time (Block *et al.* 2002).

Tools used in the present study, as well as forthcoming acoustic technology, have far-reaching applications for studying behavioural ecology (e.g. spawning patterns or post-release behaviour) in other free-ranging marine species. Furthermore, potential exists to gain a greater overall understanding of barracuda biology and natural history by recording additional parameters (such as light, temperature, and speed) combined on a single electronic tag. Although these transmitters were effective in helping understand relative activity, a greater maximum sensor capability, as well as potential disengagement of one or two of the axes on the accelerometer, may present a clearer picture of locomotory activity for barracuda and other marine species. Ideally, the V9AP transmitter would be useful for studies of highly resident fish within an array with overlapping receiver detection ranges. In future studies, we encourage researchers to select transmitters that average over as short of a period as possible, sample acceleration over longer periods, and transmit data as frequently as possible, to maximise resolution and the capacity to detect short-duration, but high intensity activity.

Acknowledgements

The authors would like to acknowledge the staff and volunteers at the Cape Eleuthera Institute and the Island School. Thank you to A. Shultz, C. Haak, E. Brooks and J. Cooke for field and laboratory assistance. Adrian Gleiss and two other anonymous reviewers provided comments on the manuscript. The Bahamas Department of Marine Resources provided scientific collection permits and animal care approval was obtained from the Canadian Council on Animal Care through Carleton University. The receiver array was partially supported by grants from Bonefish and Tarpon Trust, the Charles A. and Anne Morrow Lindbergh Foundation, and the Baldwin Foundation. Additional financial support was provided by Ontario Ministry of Research and Innovation (through an Early Researcher Award to S.J.C.), the Canada Foundation for Innovation, the Canada Research Chairs Program and Carleton University. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USA Fish and Wildlife Service.

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Manuscript received 21 February 2010, accepted 18 September 2010