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Oceans apart? Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and Pacific Oceans determined from pop-off satellite archival tagging

J. M. Brunnschweiler*†, N. Queiroz‡§ and D. W. Sims§‖

**ETH Zurich, Raemistrasse 101, CH-8092 Zurich, Switzerland, ‡CIBIO – Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-668 Vairão, Portugal, §Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, U.K. and ‖School of Marine Sciences and Engineering, University of Plymouth, Drake Circus, Plymouth PL4 8AA, U.K.*

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Adult bull sharks *Carcharhinus leucas* were monitored with electronic tags to investigate horizontal and vertical movements in the Atlantic and Pacific Oceans. In both locations, *C. leucas* showed some fidelity to specific coastal areas with only limited horizontal movements away from the tagging sites after tag attachment. Fish tagged in the Bahamas were detected mostly in the upper 20 m of the water column in water 25–26° C, whereas *C. leucas* tagged in Fiji spent most of their time below 20 m in water usually >26° C. The results highlight the importance of coastal inshore habitats for this species.
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Key words: Fiji; habitat use; migration; satellite telemetry; Shark Reef Marine Reserve; site fidelity.

INTRODUCTION

The development of highly sophisticated satellite telemetry technology has produced novel insights into marine species ecology, physiology and behaviour (Gunn & Block, 2001; Hays *et al*., 2002; Sims *et al*., 2003, 2008; Block *et al*., 2005; Croxall *et al*., 2005; Teo *et al*., 2007; Sims, 2010). This information has improved basic knowledge of the oceans, species and key processes linking predators to their ocean environments that may become useful for mapping habitats including oceanic diversity hotspots, highlighting the need for marine reserves and international co-operation in marine species management (Block *et al*., 2003; Block, 2005; Sims *et al*., 2005; Blumenthal *et al*., 2006; Hays *et al*., 2006; Weng *et al*., 2009).

Despite many cartilaginous fish species being among the most abundant apex predators in the oceans, ecological baseline data on them are still lacking. Satellite telemetry offers an approach to fill this knowledge gap, in that it allows rapid mapping

†Author to whom correspondence should be addressed. Tel.: +41 43 305 7967; fax: +41 44 362 5085; email: juerg@glueckLich.net

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of their habitats and defining their ecological niches, habitat use and behaviour, an objective that is critical to their future protection. To date, the majority of studies using pop-off satellite-linked archival tags (PSAT) to monitor shark behaviour and ecology have been published from pelagic taxa (Hulbert *et al.*, 2005; Weng *et al.*, 2007) and large shark species such as white shark *Carcharodon carcharias* (L.), whale shark *Rhincodon typus* Smith and basking shark *Cetorhinus maximus* (Gunnerus) (Bonfil *et al.*, 2005; Sims *et al.*, 2006; Brunnschweiler *et al.*, 2009), but attempts are increasingly being made to deploy PSATs on smaller, for example, coral-reef or coastal shark species (Chapman *et al.*, 2007; Conrath & Musick, 2008; Jorgensen *et al.*, 2009).

Bull sharks *Carcharhinus leucas* (Müller & Henle) are widespread along the continental coasts of all tropical and subtropical seas and also occur around small and remote island states and archipelagos far away from continental waters (Brunnschweiler & Earle, 2006; Gadig *et al.*, 2006; Brunnschweiler & Compagno, 2008). A predominantly neritic species, *C. leucas* is described as a coastal, estuarine and riverine shark usually found close inshore in marine habitats in water <30 m deep and large individuals are frequently sighted in shallow coastal waters (Compagno, 1984). The general biology and life history of *C. leucas* has been studied in a number of populations around the world and is best known from neonate, young-of-the-year and juvenile individuals in estuarine and river habitats (Snelson *et al.*, 1984; Neer *et al.*, 2005; Pillans *et al.*, 2005; Simpfendorfer *et al.*, 2005; Curtis, 2008; Heupel & Simpfendorfer, 2008; Heithaus *et al.*, 2009; Ortega *et al.*, 2009). Few studies, however, have examined movement patterns and habitat use of adult *C. leucas*. The availability of this information is important, not least because the latest assessment indicates *C. leucas* is 'near threatened' (Camhi *et al.*, 2009). In order to prioritize areas for protection to aid in the conservation of *C. leucas*, more information, especially on behaviour away from shallow water areas that is currently lacking, is needed to help characterize the species' critical and essential habitat.

To address directly the lack of information on the movements and behaviour of adult *C. leucas*, the objectives of this study were to: (1) monitor *C. leucas* with PSATs at Walker's Cay, Bahamas, and off the southern coast of Viti Levu, Fiji; (2) to gain preliminary insight into horizontal *C. leucas* movements, including the species' potential for long-distance migrations and (3) to evaluate vertical behaviour in terms of time spent at different depths and water temperatures.

MATERIALS AND METHODS

STUDY SITES AND TAG ATTACHMENT

Between 2003 and 2009, a total of 20 *C. leucas* were taggged with PSATs manufactured by Microwave Telemetry, Inc. (Block *et al.*, 1999; Brunnschweiler *et al.*, 2009; www.microwavetelemetry.com) (Table I). In April 2003, six *C. leucas* (two males, four females) were tagged in shallow water close inshore at a former fish cleaning site at Walker's Cay, northern Abaco Islands, Bahamas. *Carcharhinus leucas* were attracted with food to a platform built partly over the water on the north-east side of the island and tags were driven into the dorsal musculature below the first dorsal fin using a fibreglass pole spear. In Fiji, *C. leucas* were tagged in the Shark Reef Marine Reserve off the southern coast of Viti Levu, where a local dive operator attracts large *C. leucas* with food for the purpose of marine

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TABLE I. *Carcharhinus leucas* tagged in the Atlantic (B1–B6) and South Pacific (F1–F14) Oceans

Tag number	Sex	Attachment method	Deployment date (programmed pop-off date)	Pop-off date (first Argos position)	Duration of deployment (days)
Walker's Cay, Bahamas			2003		
B1	M	1	8 April (8 May)	27 April (2 May)	19
B2	F	1	8 April (8 May)	16 April (21 April)	8
B3	M	1	8 April (7 June)	15 April (20 April)	7
B4	F	1	8 April (7 June)	27 April (1 May)	19
B5[a]	F	1	9 April (8 July)	NA (13 April)	<4
B6[a]	F	1	8 April (8 July)	8 April (12 April)	<1
Viti Levu, Fiji			2004		
F1[a]	F	1	18 April (30 November)	18 April[d]	<1
F2[a,b]	F	1	18 April (5 December)	NA[d]	>17<40
F3[a,c]	M	1	23 April (20 December)	NA[d]	NA
F4	F	1	30 September (5 December)	NA[d]	>22<26
F5[b]	F	2	1 October (30 November)	9 October[d]	8
F6	M	2	1 October (10 December)	20 October[d]	19
F7[b]	F	2	3 October (1 December)	14 October[d]	11
F8[b]	F	2	4 October (15 December)	10 October[d]	6
F9	F	2	4 October (20 December)	28 October[d]	24
F10[b]	F	2	6 October (25 December)	NA[d]	>5<9
F11	F	2	6 October (30 December)	28 November[d]	53
			2008		
F12	F	2	5 March (4 April)	30 March (4 April)	25
			2009		
F13[a,c]	F	2	5 February (25 February)	NA	NA
F14[b]	F	2	7 February (30 April)	16 February (18 April)	9

Attachment method: 1, pole spear; 2, spear gun. NA, not available; B, Bahamas; F, Fiji.
[a]Excluded from analysis; [b]tag reported data but failed to report position estimates; [c]tag failed to report position estimates and data; [d]because the constant-pressure release feature was disabled in tags attached in Fiji in 2004 (see also Table II), tags only uplinked to the Argos satellites on their programmed pop-off date.

tourism (Brunnschweiler, 2010). *Carcharhinus leucas* were attracted with food to an area *c*. 30 m deep, and a scuba diver drove the tag into the dorsal musculature below the first dorsal fin using a custom-made metal tagging pole (F1–F4) or a spear gun (F5–F14). At both tagging sites, the sizes of the fish were visually estimated and all tagged *C. leucas* were >1·8 m. During the weeks following attachment, both tagging sites were regularly checked for tagged animals remaining in the area.

TAG MODELS AND SET-UP

Two tag models were used in this study: 17 *C. leucas* were equipped with PTT-100 tags and three animals (F12–F14) were tagged with X-tags (see Table II for tag model specifications). The full tag set-up consisted of the PSAT unit, a monofilament line (B1–B6, F1 and F2) or braided stainless steel wire (F3–F14) marked with an individually coloured plastic (B1–B6, F1–F11) or heat shrink tube (F12–F14) and a double-barbed stainless steel anchor (modified

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TABLE II. Summary of pop-off satellite archival tag (PSAT) model specifications

Tag number	B1–B6 & F1–F3	F4–F11	F12–F13	F14
Model	Standard PTT-100 (v2.0)	Standard PTT-100 (v3.0)	High rate* X-tag	Standard X-tag
Dimensions (length† × diameter, cm)	34.0 × 4·1	34.0 × 4·1	27.0 × 3·2	27.0 × 3·2
Mass (g)	65–68	65–68	40	40
Sampling interval (min)	60	15	*c*. 5	15
Resolution (± error)				
Depth (m)	5·38 (5·38)	5·38 (5·38)	1·34 (1·34)	1·34 (1·34)
Temperature (° C)	0·18 (0·18)	0·18 (0·18)	0·18 (0·18)	0·18 (0·18)
Constant pressure‡ enabled§	Yes (B), No (F)	No	Yes	Yes
Constant-pressure band (m)	±10.0 (B), NA (F)	NA	1·5	1·5
Time at constant depth before initiation (days)	4 (B), NA (F)	NA	5 (F12), 1 (F13)	3

*High rate pop-off tags record sensor readings at a higher sampling interval compared to standard PSATs for up to a maximum of 30 days. Additionally, depth is recorded at a higher resolution. The trade-off with the higher depth and temperature sampling interval and depth resolution is a shorter maximum deployment time and light-level geolocation is not a feature of Microwave Telemetry's high rate PSATs. †length includes antenna; ‡PSATs manufactured by Microwave Telemetry have an optional automatic release feature, whereby a tag pops off and begins to transmit when it has been at a constant depth for a pre-set time period; §based on depth data obtained from sharks tagged in 2003 in the Bahamas, the constant-pressure release feature was disabled in tags F1–F11 attached in Fiji in 2004. B, Bahamas; F, Fiji; NA, not available.

Floy FH-69 dart; Floy Tag & Mfg Inc.; www.floytag.com). PSATs were programmed to pop off after deployment intervals of between 20 days and 8 months (Table I).

POP-OFF POSITIONS AND DEPTH AND TEMPERATURE DATA ANALYSIS

The pop-off date was determined by constant 0 m depth readings. After pop-off, all tags did float at the surface for several days before uplinking to the Argos satellites (Table I), and therefore true pop-off positions are unknown. The number of available light-based latitude and longitude position estimates for individual *C. leucas* for the time between tag attachment and release ranged between three and 18 for PSATs attached in the Bahamas (Table III). Only four tags attached to *C. leucas* in Fiji reported back position estimates for the time period between tag attachment and premature pop-off (Table III). Therefore, and because the distances moved between tag deployment and pop-off positions were smaller than geolocation error, geolocation using satellite relayed data was not performed. Light-level longitude estimates, which are typically accurate and robust (Teo *et al*., 2004), were used to obtain information on longitudinal movements over time. Vertical movements and diel patterns in behaviour were analysed for individual *C. leucas* using the archival records relayed *via* Argos. Due to the non-Gaussian distribution of the data, mean and median were used to summarize the results, and the non-parametric Mann–Whitney U-test for comparisons. To characterize and compare the depth and temperature data for *C. leucas* tagged in the Bahamas and in Fiji, the mean and S.D. were

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TABLE III. Pop-off satellite archival tag (PSAT) performance and number of resightings of tagged *Carcharhinus leucas* from the Bahamas (B1–B6) and Fiji (F1–F14)

Tag number	Pressure data available (%)	Temperature data available (%)	Latitude and longitude positions available (days)	Number of resightings
B1	89·7	100	17/17	1
B2	100	100	3/3	1
B3	100	100	5/5	0
B4	100	100	18/18	1
B5	100	100	NA	7
B6	100	100	NA	0
F1	100	0	NA	0
F2	5·9	17·7	NA	0
F3	NA	NA	NA	0
F4	28·4	25.0	5/5	2
F5	55·2	71·1	NA	0
F6	89·7	85.0	1/5	0
F7	55·1	66·2	NA	0
F8	80.0	79·4	NA	0
F9	79·5	76·4	1/13	0
F10	25·2	20·2	NA	0
F11	28·5	33·2	36/36	7
F12	93·9	93·9	NA	1
F13	NA	NA	NA	1
F14	77·7	76·4	NA	3

NA, not available.

calculated for each site, such that error bars represent variation between individuals. All times given here are local times (GMT −4 hours for the Bahamas; GMT +12 hours for Fiji).

RESULTS

RESIGHTINGS AND TAG PERFORMANCE

All tags deployed in the Bahamas and Fiji detached prematurely after being attached for <1 to a maximum of 53 days (Table I). Tags detached prematurely for unknown reasons with the exception of tag F12, which popped off due to a full memory (Microwave Telemetry Inc., pers. comm.), and one PSAT attached in the Bahamas (B5). Tag B5 was attached for little less than 4 days indicated by non-0 m depth readings (maximum depth recorded was 10·8 m). After 4 days, the constant-pressure release mechanism was triggered and the tag popped off and started to uplink to the satellites (Table I).

Four of the six *C. leucas* tagged in the Bahamas were resighted at the tagging site (Table III). Fish B1, B2 and B4 were resighted once with PSATs attached: B1 and B2 were seen on the day following tagging and B4 was resighted 16 days after tagging. B5 was seen at the tagging site with the tag attached 1 and 4 days after tagging, respectively. On day 5, this fish was resighted without the PSAT but with

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the coloured monofilament line still anchored in the dorsal musculature. This colour marked female *C. leucas* was seen at the tagging site a further four times starting 1 month after the tag detached. At the tagging site in Fiji, five *C. leucas* were resighted with tags attached (Table III). F4 was observed twice, 1 and 5 days after tagging. F11 that was tagged on the last day of September 2004 was resighted a total of seven times during the last 2 weeks of October into beginning of November. All *C. leucas* tagged with X-tags were resighted with PSATs attached: F12 and F13 were resighted once, 14 and 5 days after tagging, respectively. F14 was resighted three times, after 2, 3 and 9 days.

Except for the two tags F3 and F13 (10%), which never uplinked to Argos satellites, PSATs reported back between 5·9 and 100% (mean ± S.D. = 72·7 ± 31·5%) of the archived depth and 0 and 100% (mean ± S.D. = 69·1 ± 34·2%) of the archived temperature data (Table III). Tag F13 was attached on 5 February 2009 to the right side of a female *C. leucas* that was resighted with the PSAT attached after 5 days. On the following day, a female *C. leucas* of similar size was seen at the tagging site with a white marking on the right side where the tag was attached, indicating that this tag had been shed. The constant-pressure release mechanism was set to release the PSAT after 1 day at constant depth (Table II), but this tag did not uplink to Argos.

HORIZONTAL MOVEMENTS

Available pop-off positions, light-level longitude estimates and resightings data from the Bahamas and Fiji indicate that tagged *C. leucas* did not perform large-scale movements away from the reef-located tagging sites. Pop-off locations for *C. leucas* tagged in the Atlantic Ocean show that the fish remained in the Blake Plateau area during the short time period when they had tags attached with one notable exception: the first position estimate of tag B2 was received from north of Fort Pierce on the south-east coast of Florida 5 days after the tag detached from the animal [Fig. 1(a)]. A more accurate position estimate (LC 2) was received 3 days later placing the tag further south. Eventually, the tag was recovered in the Indian River Lagoon system, *c*. 210 km west of Walker's Cay, Bahamas.

Because the constant-pressure release mechanism was disabled in PSATs F1–F11 and all these tags popped off well before the programmed release date (Table I), only three tags attached in Fiji provided useful information on the horizontal movements of *C. leucas* in the South Pacific Ocean. *Carcharhinus leucas* F11 was tagged on 30 September 2004 and resighted at the Shark Reef Marine Reserve with the tag attached between 18 October and 3 November. The tag prematurely popped off on 28 November and started uplinking to the satellites on its programmed pop-off date on 30 December. Argos position estimates were received from the southern coast of Viti Levu [Fig. 1(b)]. The tagged *C. leucas* F12 was resighted at the tagging site 2 weeks after it was equipped with the PSAT. After 11 days, the tag popped off on the south-western coast of Viti Levu from where the tag floated on the surface away from the Viti Levu coast into open ocean water before it uplinked on the programmed pop-off date [Fig. 1(b)]. This female that could be reliably recognized using natural distinguishing markings (Castro & Rosa, 2004) was resighted back at the tagging site 4 weeks after it had lost the PSAT. No sign of the tether and where it was attached could be detected. Similarly, the fish carrying tag F14 was resighted several times

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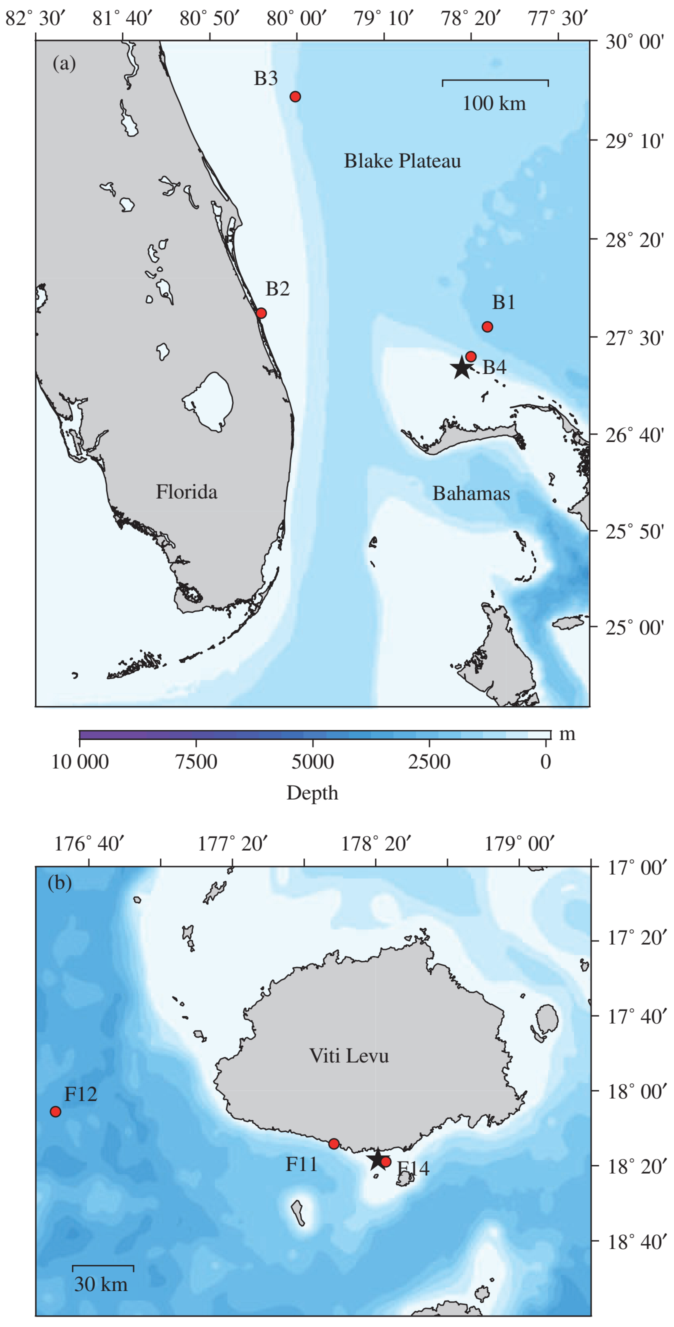

FIG. 1. First Argos position estimates for *Carcharhinus leucas* (a) B1–B4 [all location class (LC) 0 Argos position estimates; reported accuracy: service providers, >1000 m; field tests (mean ± S.D.), 5179 ± 3677 m (Hazel, 2009)] tagged with pop-off satellite archival tags (PSAT) in the Bahamas in 2003 and (b) F11 (LC 3; nominal accuracy 0–150 m), F12 (LC 2; nominal accuracy 150–350 m) and F14 (LC 3) tagged in Fiji in 2004, 2008 and 2009, respectively. The tagging locations are marked (★).

at the tagging site during tag attachment and after the PSAT prematurely popped off in the Beqa Passage (Brunnschweiler, 2009), *c*. 4 km away from the tagging site.

DEPTH, TEMPERATURE AND DIEL PATTERNS

Carcharhinus leucas tagged in the Bahamas stayed shallower (mean ± S.D. = 15·0 ± 6·1 m in the Bahamas *v*. 39·1 ± 13·6 m in Fiji; Mann–Whitney U-test, d.f. = 1, $P < 0{\cdot}001$) and in slightly cooler water (mean ± S.D. = 25·3 ± 0·6° C in the Bahamas *v*. 26·2 ± 0·7° C in Fiji) compared with fish tagged in Fiji (Fig. 2). On average, Walker's Cay *C. leucas* spent 77·5% of their time in the upper 20 m of the water column in water 25–26° C, whereas Viti Levu fish spent 87·8% of their time below 20 m in water usually >26° C (Fig. 3). Minimum and maximum depths and water temperatures recorded ranged from 0·0 to 139·9 m (B1) and 20·0 to 27·1° C (B2) in the Bahamas and 0·0 to 204·4 (F11) and 21·4 (F11 and F14) to 29·5° C (F12) in Fiji, respectively (Table IV and Fig. 2). Overall, the only *C. leucas* (B2) for which a mean temperature <25° C was recorded was also logged at the minimum temperature of 20° C [Fig. 2(b)]. The light-based longitude estimates available from the 3 days prior to pop-off (Table III), as well as the depth record of this

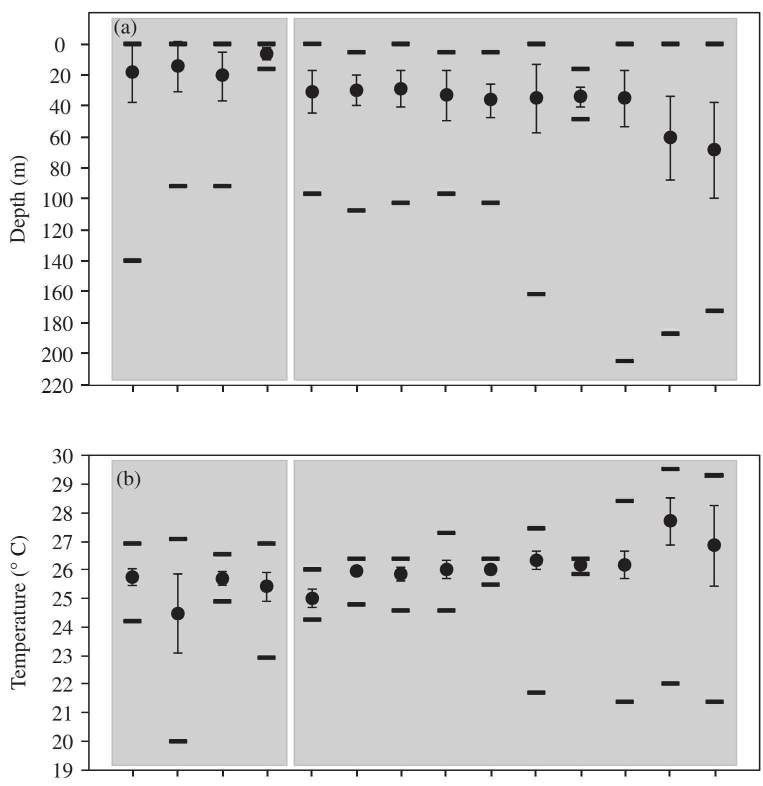

FIG. 2. Minimum, maximum and mean ± S.D. (a) depth and (b) temperature for *Carcharhinus leucas* tagged with pop-off satellite archival tags (PSAT) in the Bahamas (B1–4) and Fiji (F4–14).

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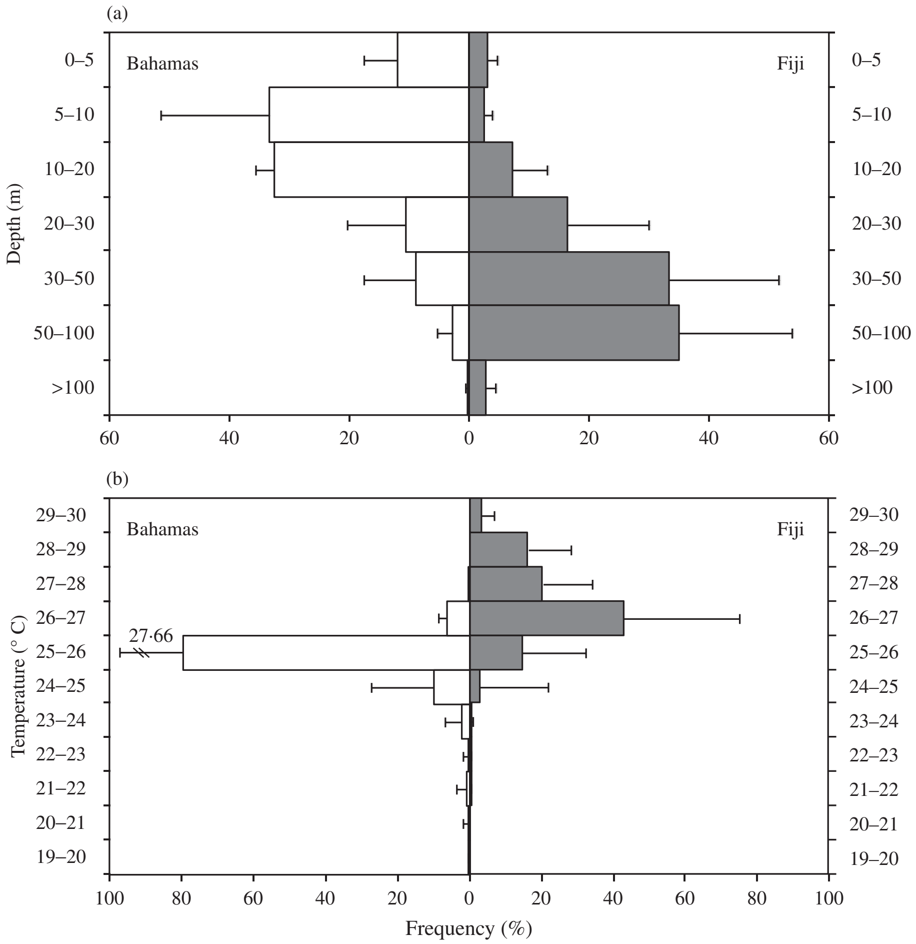

FIG. 3. Histograms of mean + S.D. per cent time spent at (a) depth and (b) temperature for Atlantic (□) and South Pacific (■) *Carcharhinus leucas* tagged with pop-off satellite archival tags (PSAT).

C. leucas, indicate that it spent the first 5 to 6 days in the shallow waters of the Bahama Banks at a mean depth of 7·9 m (Fig. 4). During the following 2 days, the female *C. leucas* was in deeper waters possibly between the Bahamas and the east coast of Florida [Fig. 1(a)] showing increased diving behaviour to a maximum depth of 91·5 m (recorded mean depth of 30 m). During this part of its movement, the mean ambient water temperature dropped from 24·7 to 23·9° C (Fig. 4).

The shallowest mean depth of 6·7 m (B4) was found in the Bahamas while the deepest mean depth of 68·0 m (F14) was recorded in a *C. leucas* tagged in Fiji [Fig. 2(a)]. The former *C. leucas* only used a narrow depth band at the water surface to a maximum depth of 16·1 m, whereas *C. leucas* tagged in Fiji used the water column more extensively. No thermocline could be detected in either location, indicating *C. leucas* dived in well-mixed layers. All four *C. leucas* tagged in the Bahamas spent part of their time at the water surface, whereas three fish tagged in Fiji were never detected at 0 m, but at a minimum depth of 5·4 m [Table IV and Fig. 2(a)].

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TABLE IV. Day and night depth summary statistics for pop-off satellite archival tags (PSAT) from the Bahamas (B) and Fiji (F)

	Day				Night				
Tag number	*n*	Mean ± S.D.	Median	Range	*n*	Mean ± S.D.	Median	Range	*P**
Walker's Cay, Bahamas									
B1	205	18·1 ± 16·6	16·1	0·0–96·8	211	19·0 ± 20·8	10·8	0·0–139·9	>0·05
B2	97	14·0 ± 14·0	10·8	0·0–69·9	98	14·4 ± 18·6	5·4	0·0–91·5	>0·05
B3	85	24·6 ± 15·7	21·5	0·0–91·5	88	16·8 ± 14·3	10·8	0·0–69·9	<0·001
B4	225	6·9 ± 3·8	5·4	0·0–16·1	228	6·6 ± 4·2	5·4	0·0–16·1	>0·05
Viti Levu, Fiji									
F4	299	35·7 ± 12·5	32·3	10·8–96·8	300	25·8 ± 13·1	26·9	0·0–91·5	<0·001
F5	222	29·5 ± 6·9	26·9	16·1–91·5	218	29·4 ± 11·8	26·9	5·4–107·6	>0·05
F6	840	31·2 ± 9·4	32·3	5·4–102·2	823	25·7 ± 12·7	26·9	0·0–96·8	<0·001
F7	306	38·8 ± 16·4	32·3	16·1–96·8	291	27·1 ± 14·2	26·9	5·4–75·3	<0·001
F8	223	37·4 ± 9·7	37·7	5·4–69·9	228	35·0 ± 12·3	32·3	5·4–102·2	<0·001
F9	936	34·0 ± 20·7	32·3	0·0–161·4	917	36·0 ± 23·6	32·3	0·0–156	>0·05
F11	732	37·0 ± 13·4	37·7	0·0–96·8	727	32·8 ± 21·7	32·3	0·0–204·4	<0·001
F12	3445	61·1 ± 25·5	61·9	0·0–186·9	3450	59·5 ± 27·7	63·2	0·0–137·2	>0·05
F14	354	75·7 ± 30·7	72·6	17·5–172·1	355	60·4 ± 29·8	56·5	0·0–161·4	<0·001

n, number of depth readings.
*Mann–Whitney *U*-test.

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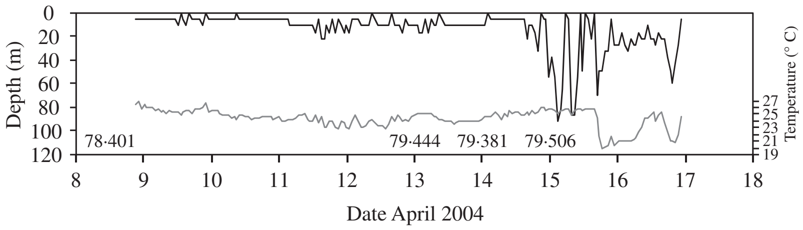

FIG. 4. Time depth (—) and the corresponding time-temperature (—) series for *Carcharhinus leucas* B2 tagged with Pop-off satellite archival tags (PSAT) on 8 April 2004 at Walker's Cay, Bahamas (longitude 78·401° W). Numbers above dates indicate light-based longitude (W) position estimates.

Carcharhinus leucas tagged in the Bahamas and Fiji showed inter-individual differences in diel diving patterns. Day and night depth differences were detected in one and six *C. leucas* in the Bahamas and Fiji, respectively. Mean depth for fish B3 was shallower at night than during the day, but no statistically detectable difference between day and night was found for the other three *C. leucas* tagged in the Bahamas (Table IV). Three Fijian *C. leucas* (F5, F9 and F12) showed no day and night depth differences while the mean depth of fish F4, F6, F7, F8, F11 and F14 was deeper during the day than during the night (Table IV).

DISCUSSION

Ninety per cent of the 20 deployed PSATs uplinked to the Argos satellite system resulting in a cumulative total of 235 days on *C. leucas* depth and ambient water temperature occupancy and some limited information on movements away from the tagging sites. These first such data available for large *C. leucas* expand the knowledge about the ecological niche of this species. In both the Atlantic and Pacific Oceans, *C. leucas* showed some fidelity to specific coastal areas and did not move away from these shallow habitats at large scale during the time of tag attachment. Fish in both locations used the water column from the surface down to *c*. 200 m, but in the Bahamas the species spent most of the time in shallow waters while in bathymetrically less constraining Fijian coastal habitats *C. leucas* were usually found deeper than 30 m. The results highlight the importance of coastal inshore habitats for this species.

Reliable satellite tag performance still faces many challenges (Hays *et al*., 2007), with premature pop-off being one of the prime reasons for obtaining shorter than planned tracks from marine vertebrates (Chapman *et al*., 2007; Arrizabalaga *et al*., 2008). In most cases, it is difficult to identify reliably the reasons for premature detachment (Hays *et al*., 2007). The tag attachment method chosen in this study to attach pop-off tags to *C. leucas* from a platform (Bahamas) or by scuba (Fiji) might have resulted in insufficient tag anchoring and consequently a higher rate of premature tag loss. For example, environmental factors such as currents or the fact that the fish to be tagged could move around freely in the water column pose difficulties to the diver when approaching the animal or might affect the accuracy of tag placement. Nevertheless, data sets obtained *via* satellite telemetry that span days rather than months or years can still provide meaningful insight into horizontal and

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vertical movement patterns and behaviour of sharks (Dewar *et al*., 2004; Chapman *et al*., 2007; Pade *et al*., 2009).

HORIZONTAL MOVEMENT AND SITE FIDELITY

Previous research has shown that large-scale movements tend to be comparatively limited in *C. leucas* with pronounced site fidelity in coastal and continental shelf waters (Kohler *et al*., 1998; Kohler & Turner, 2001; Tremain *et al*., 2004; Curtis, 2008). Resightings and the admittedly limited horizontal movement data obtained from this study support this proposition. It remains, however, largely unknown why *C. leucas* show fidelity to certain coastal inshore habitats. A plausible factor that might explain a certain degree of site fidelity in this study is that at both tagging sites, Walker's Cay and in the Shark Reef Marine Reserve, *C. leucas* have been attracted with food for the purpose of sightings by tourists. This might have affected the behaviour of the tagged *C. leucas* in that, for example, fish would not leave the tagging sites on large-scale movements, but remain in the area. The majority of the tagged *C. leucas* in this study were resighted at the tagging sites indicating indeed some level of site fidelity. None of the *C. leucas* tracked for >17 days (B1, B4, F4, F6, F9, F11 and F12) with the exception of F11, however, was resighted more than twice (mean $= 0{\cdot}8$) in the weeks following tagging, despite the fact that the means of attracting the *C. leucas* to the site continued. *Carcharhinus leucas* F11 was resighted most during tag attachment (Table III), but all seven appearances at the tagging site occurred in a relatively narrow time frame (18 October to 3 November 2004) of its entire 53 days track. This, together with results from other studies (Kohler *et al*., 1998; Kohler & Turner, 2001; Tremain *et al*., 2004; Curtis, 2008), indicates that tagged *C. leucas* in this study showed specific horizontal movements.

The finding of tag B2, which was attached to a female *C. leucas*, floating on the surface in the Stuart Inlet, Florida, at the entrance to the Indian and St Lucie Rivers is noteworthy. The Indian River Lagoon system is considered a nursery area for different shark species including *C. leucas* (Snelson & Williams, 1981; Snelson *et al*., 1984; Curtis, 2008). The light-based longitude estimates indicate that fish B2 moved away from the tagging site in the Bahamas in a westward direction and the tag popped off in waters off the east coast of southern Florida (Fig. 4). Given the lack of accurate geolocation and the fact that this tag was floating on the surface for several days before starting to transmit its position, it is unknown how close to the coast this tag detached from the animal. Despite this finding, it therefore remains unknown whether or not female *C. leucas* from the Bahamas move to nursery grounds in Florida. The possibility of such a migratory link to reproductive areas in Florida could be tested conclusively in the future using, for example, acoustic telemetry methods.

VERTICAL DISTRIBUTION

Clear diel vertical migration patterns known from other shark species (Weng & Block, 2004; Sims *et al*., 2005; Weng *et al*., 2007; Andrews *et al*., 2009) were not identified in *C. leucas* in this study. Although diel patterns were found in some *C. leucas* from the Bahamas and Fiji, the relatively small differences between day and night mean depths are unlikely to be of biological significance. The general notion that *C. leucas* spend the majority of their time in water <30 m deep (Compagno, 1984) was confirmed for individuals tagged in the shallow waters of the Bahamas,

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but not for *C. leucas* tagged in Fiji, where they were recorded below 30 m for most of the time. Most depth data collected to date come from studies looking at the behaviour of immature *C. leucas* in estuarine habitats (Simpfendorfer *et al.*, 2005; Curtis, 2008); data on depth preferences of adult *C. leucas* away from shallow habitats are limited. The data from this study provide the first evidence that adult *C. leucas* preferably stay between 30 and 100 m in bathymetrically non-constraining habitats with frequent visits to the surface and only occasionally dive to below 100 m. Dives below 200 m would have been possible in both locations. Defining the northern edge of the Little Bahama Bank, Walker's Cay is part of the Abacos and the northernmost island of the Bahamas. The shallow waters of the Bahama Banks surrounding the island descend into deep Atlantic Ocean waters a few km north-east of Walker's Cay. This is contrary to the situation on the southern coast of Viti Levu where the ocean-facing sides of the fringing reefs immediately drop to well below *c*. 250 m deep waters. Depth and location records obtained from PSATs and direct observation indicate that *C. leucas* tagged in the Bahamas stayed in shallow waters close to the tagging site, but showed increased diving activity in deeper waters off the Bahama Banks. Such behaviour is similar to what was found for *C. leucas* tagged on Shark Reef in Fiji where fish spend the majority of their time in the deeper waters just off the fringing reefs on the southern coast of Viti Levu.

MANAGEMENT AND CONSERVATION

The fact that adult *C. leucas* show a certain degree of site fidelity punctuated by limited migratory movements up and down coastlines makes this apex predator an important species of coastal ecosystems and underpins the need for local and possibly national or even international co-operation. Estuarine habitats have been determined to be habitats of great concern for coastal sharks, in that these areas continue to suffer from dramatic anthropogenic environmental interactions and destruction. Identifying the movement corridors between or along coasts will therefore help when devising conservation strategies for *C. leucas*.

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