

Effect of weight and frontal area of external telemetry packages on the kinematics, activity levels and swimming performance of small-bodied sharks

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(Received 14 June 2016, Accepted 3 February 2017)

This study sought to observe the effects of submerged weight and frontal cross-sectional area of external telemetry packages on the kinematics, activity levels and swimming performance of small-bodied juvenile sharks, using lemon sharks *Negaprion brevirostris* (60–80 cm total length, L_T) as a model species. Juveniles were observed free-swimming in a mesocosm untagged and with small and large external accelerometer packages that increased frontal cross-sectional area of the animals and their submerged weight. Despite adhering to widely used standards for tag mass, the presence of an external telemetry package altered swimming kinematics, activity levels and swimming performance of juvenile *N. brevirostris* relative to untagged individuals, suggesting that tag mass is not a suitable standalone metric of device suitability. Changes in swimming performance could not be detected from tail-beat frequency, which suggests that tail-beat frequency is an unsuitable standalone metric of swimming performance for small *N. brevirostris*. Lastly, sharks experienced treatment-specific changes in activity level and swimming kinematics from morning to afternoon observation. Therefore, the presence of external telemetry packages altered the kinematics, activity levels and swimming performance of small young-of-the-year *N. brevirostris* and these data may therefore be relevant to other similar-sized juveniles of other shark species.

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Key words: accelerometer; biologging; buoyancy; dynamic body acceleration; tag attachment.

INTRODUCTION

As the technology behind external telemetry packages has improved to accommodate miniaturized devices, there is an increased opportunity for applying biotelemetry and biologging studies to juvenile sharks (Ropert-Coudert & Wilson, 2005; Wilson *et al.*, 2008; Whitney *et al.*, 2012; Jones *et al.*, 2013). External tag packages, however, are subject to miniaturization constraints (battery and memory capacity) and may still represent a larger percentage of a smaller animal's surface area and submerged weight

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relative to larger individuals (Wilson *et al.*, 2008). Therefore, compensating for hydrodynamic drag (Methling *et al.*, 2011) and regulating buoyancy (Lefrançois *et al.*, 2001; Grusha & Patterson, 2005) may become problematic over short or long deployments for small juvenile sharks.

Because external telemetry packages may influence the swimming of tag-bearing individuals, data recorded on these devices may not be authentic. Validation studies should, therefore, be conducted to account for any interference from tag-bearing on deriving ecological conclusions from results (Jones *et al.*, 2013; Jepsen *et al.*, 2015). The effects of external telemetry packages on juvenile sharks include changes in swimming performance (Lowe, 1996), energy expenditure (Scharold & Gruber, 1991; Lowe *et al.*, 1998) and growth rates (Manire & Gruber, 1991). Studies have found no changes in activity levels and kinematics (Bullock *et al.*, 2015) or energy expenditure (Lynch *et al.*, 2017), however, for juveniles of several shark species. While studies in teleosts have additionally documented delayed maturity (McFarlane & Beamish, 1990), reductions in foraging efficiency (Ross & McCormick, 1981; Wilson *et al.*, 1986; Thorstad *et al.*, 2001) and reduced ability to escape predation (Ross & McCormick, 1981; McFarlane & Beamish, 1990; Feltham & MacLean, 1996; Jones *et al.*, 2013), these data do not exist for juvenile sharks. Therefore, there is a need to quantify how external telemetry packages may influence swimming in juvenile sharks.

Guidelines for external telemetry packages are not ubiquitous across aquatic taxa or life history stage, including sharks (Wilson *et al.*, 2008; Jones *et al.*, 2013; Jepsen *et al.*, 2015). Acceptable ratios of frontal cross-sectional area of tags to animals are not clearly defined and appear species specific (Jones *et al.*, 2013; Jepsen *et al.*, 2015). Tag-mass-to-animal-mass ratios (*c.* 1.3–4.0%, or the 2% rule) have been a standard for neglecting tag-borne effects (Ross & McCormick, 1981; Blaylock, 1990; Lowe *et al.*, 1998; Lowe, 2002; Steinhausen *et al.*, 2006), yet guidelines for drag generated by tags are rare (Jones *et al.*, 2013; Lynch *et al.*, 2017). Furthermore, tags with similar masses may have differential effects on an animal's buoyancy (Grusha & Patterson, 2005; Lynch *et al.*, 2017). Thus, identifying thresholds of acceptable submerged weights and frontal cross-sectional area is important, because small-bodied sharks are more likely to approach or exceed those thresholds than larger conspecifics or species by virtue of their size.

The purpose of this study was to define the effect of increasing submerged weight and frontal cross-sectional area of an external telemetry package on the activity levels, kinematics and swimming performance of a small-bodied juvenile shark. Juvenile lemon sharks *Negaprion brevirostris* (Poey 1868) were selected as a model species because they are the target of a substantial body of telemetry work (Sundström *et al.*, 2001) and their small size and morphology are characteristic of small-bodied carcharhinid sharks (Webb & Keyes, 1982). Miniaturized acceleration biologgers (accelerometers) were selected as the external telemetry package because accelerometers are becoming popular among fish telemetry studies (Brown *et al.*, 2013; Metcalfe *et al.*, 2016) with few validation studies to date (Bullock *et al.*, 2015). Furthermore, *N. brevirostris* have proven to be effective study subjects for validating the use of accelerometry for behavioural and energetics studies of sharks (Shepard *et al.*, 2008a, b; Gleiss *et al.*, 2009; Bullock *et al.*, 2015; Wilson *et al.*, 2015; Lear *et al.*, 2016; Bouyoucos *et al.*, 2017).

MATERIALS AND METHODS

ANIMAL COLLECTION AND HUSBANDRY

Five male and five female juvenile *N. brevirostris* were collected in September 2014 from tidal creeks at Cape Eleuthera, The Bahamas (24° 49' 46.43" N; 76° 19' 41.49" W) using block seining. *Negaprion brevirostris* were measured (curvilinear total length, L_T) and tagged with passive integrated transponders (PIT) for individual identification (Feldheim *et al.*, 2002). Body width and depth were measured to calculate frontal cross-sectional area following the methods of Bell & Terhune (1970). The 10 individuals were (mean \pm s.d.) 70.4 \pm 6.6 cm L_T , 38.2 \pm 5.4 cm² in frontal cross-sectional area and weighed 1.4 \pm 0.3 kg in air.

Transport to the Cape Eleuthera Institute's wet-laboratory facility occurred within 45 min post-capture. Water changes occurred during transit whereby half of the water in 200 l containers was replenished every 5 min (Brooks *et al.*, 2011). Upon arrival at the wet-laboratory, *N. brevirostris* were moved to 13 000 l (3.7 m diameter by 1.3 m depth) flow-through holding tanks continuously supplied with fresh sea water. The Cape Eleuthera Institute's wet-laboratory is a covered, open-sided outdoor facility, exposing fishes to ambient water conditions and natural photoperiod (25° N). *Negaprion brevirostris* were fed a daily ration of commercially available thawed Spanish sardines *Sardinella aurita* Valenciennes 1847.

Experimental treatments were conducted between 26 September and 9 October 2014 in a 4000 m² saltwater pond (mesocosm), consisting of silt substratum, red mangroves *Rhizophora mangle*, exposure to natural photoperiod and water depth of 0.5–1.0 m. The mesocosm is continuously supplied with sea water from the adjacent wet-laboratory. *Negaprion brevirostris* were released into a penned-off 250 m² area of the mesocosm for 3 day observation periods and fed a daily ration of *S. aurita*. Temperature, salinity and dissolved oxygen (mg l⁻¹) were monitored at a peripheral location of the mesocosm three times daily in the morning (0700–0800 hours), mid-day (1200–1300 hours) and afternoon (1600–1700 hours) with a YSI Pro2030 portable water quality meter (YSI Inc.; www.ysi.com).

EXPERIMENTAL TREATMENTS

Experimental treatments included swimming without an accelerometer [Fig. 1(a)], swimming with a dorsal fin-mounted accelerometer [Fig. 1(b)] and swimming with an accelerometer counterweighted on the opposite side of the dorsal fin [Fig. 1(c)]. These treatments were referred to as untagged, single-tagged and double-tagged, respectively. Single-tagged configurations represented 1.2% of the mass and 8.5% of the frontal cross-sectional area of *N. brevirostris* used in this study and double-tagged configurations represented 2.4 and 17.0% of a given *N. brevirostris*' mass and frontal cross-sectional area, respectively. All 10 *N. brevirostris* were used for the untagged and double-tagged accelerometer treatments, but only eight could be used for the single-tagged treatment due to a weakened dorsal fin precluding a second deployment. To identify individual animals, accelerometers were colour-coded.

To define swimming performance, a 6.0 m \times 6.0 m grid (for reference) constructed from PVC pipe was placed in the mesocosm. The grid was subdivided every 0.5 m by braided nylon grid lines. *Negaprion brevirostris* could swim above or below the grid, which was placed 0.2 m off the substratum in 0.5 m of water and still be observed from the surface. Trials were filmed with a GoPro Hero 3 Silver digital video camera (Woodman Labs Inc.; www.gopro.com) mounted 3.0 m above the grid and recording at 30 frames s⁻¹, 720 or 1080 p resolution.

Individual *N. brevirostris* were haphazardly assigned an order of three treatments with a minimum 2 day recovery period between trials. *Negaprion brevirostris* were randomly divided into two groups of five that were alternated in the mesocosm over 3 day periods. Each group was given 24 h to acclimate and overcome tagging and handling stress. Video observation occurred only during the second day and *N. brevirostris* were filmed in the morning (0800–1200 hours) and afternoon (1300–1700 hours). *Negaprion brevirostris* were removed from the mesocosm on the third day and replaced with the other alternating group. This process was repeated until all 10 *N. brevirostris* were run through all three experimental treatments once, which required three deployments in the mesocosm per group.

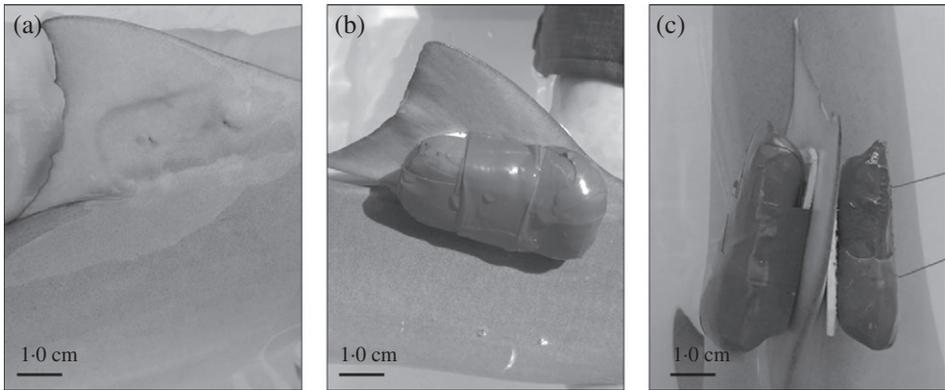


FIG. 1. External accelerometer configurations. (a) Untagged *Negaprion brevirostris* experienced minimal chafe to the dorsal fin from accelerometers. (b) Single-tagged accelerometers represented a 1.2 and 8.5% increase in mass and frontal cross-sectional area, respectively. (c) Double-tagged configurations included an identical dummy tag on the left side of the dorsal fin to serve as a counterweight to accelerometers, and represented 2.4% of animal mass and 17.0% of the cross-sectional area.

VIDEO-DERIVED KINEMATIC METRICS

Tail-beat frequency (F_{TB}), stride length (S_L) and relative swimming speed (U_{rel}) were derived from video footage (Lowe, 1996). Tail-beat frequency was measured by counting the number of complete tail-beat cycles over the duration that a *N. brevirostris* passed over the grid. A pass was defined as the period of time starting when the tip of the caudal fin entered the grid and lasted until the last complete tail-beat cycle prior to exiting the grid. Absolute swimming speed (U , $m\ s^{-1}$) over the grid was calculated using an open source freeware tracking programme (Kinovea; www.kinovea.org; Charmant, 2014). Kinovea allows for manual tracking, whereby tracks are manually affixed to an animal every time it enters the field of view. Absolute swimming speeds were then converted to relative swimming speed (U_{rel}) by dividing U by curvilinear L_T (cm) and U_{rel} is measured in body lengths per second ($L_B\ s^{-1}$). Stride length, measured in body lengths travelled per tail beat, was calculated as U_{rel} divided by F_{TB} . Metrics were calculated for all individuals in all treatments for the first 20 passes over the grid during morning and afternoon measurement periods, yielding 40 passes per *N. brevirostris* per treatment.

ACCELEROMETER-DERIVED METRICS

The use of external data-logging accelerometers made it possible to define an acceleration-based metric of activity level for *N. brevirostris* across single-tagged and double-tagged treatments (Whitney *et al.*, 2012). Accelerometers (X8M-3 and X16-mini, Gulf Coast Data Concepts; www.gcdadataconcepts.com) were prepared for deployment in the mesocosm following Wilson *et al.* (2015). Briefly, both types of accelerometer (5.1 cm \times 2.5 cm \times 1.3 cm, 17.0 g mass in air, 4.6 g submerged) were encased in a low-density, waterproof coating (Plasti Dip International; www.plastidip.com; density 0.8 $g\ l^{-1}$) and firmly taped to a plastic backing plate (c. 4.5 cm \times 2.0 cm \times 0.1 cm) around 36 kg break-strength braided Dacron line. Two holes were punched c. 2.5 cm apart laterally through the first dorsal fin *via* 16 gauge 3.8 cm needles to allow the line to be threaded through and tied across a plastic backing plate on the other side of the fin [Fig. 1(c)] (Wilson *et al.*, 2015). In double-tagged treatments, a passive dummy tag of the same dimensions and mass was attached opposite the accelerometer [Fig. 1(b)]. Accelerometers were mounted on the right side of the fin (Gleiss *et al.*, 2009, 2010) and uniformly oriented so that accelerometers logged consistently across individuals.

The authors acknowledge that these accelerometers were negatively buoyant and poorly streamlined, although the *N. brevirostris* used for this study were too small to allow accelerometers to be encased in a larger streamlined or neutrally buoyant housing (Methling *et al.*, 2011;

Whitmore *et al.*, 2016). The effect of single and double-tagged treatments on *N. brevirostris* buoyancy was estimated as an increase in the submerged weight of juvenile *N. brevirostris*. The submerged weight of *N. brevirostris* for this study was assumed to be 4.1% of their mass, which is the ratio between submerged weight and mass of adult *N. brevirostris* reported in Baldrige (1970). Thus, using the mean mass of *N. brevirostris* for this study, a 1400 g *N. brevirostris* was estimated to weigh 57.1 g in sea water. Single and double-tag packages increased the submerged weight of juvenile *N. brevirostris* by 4.6 and 9.2 g, respectively. Therefore, single-tagged and double-tagged configurations were estimated to increase the negative buoyancy (increase the submerged weight) of *N. brevirostris* by 8.1 and 16.1%, respectively.

Prior to deployment, accelerometers were individually calibrated by slowly rotating tags through each axis (Gleiss *et al.*, 2010; Brownscombe *et al.*, 2014). Accelerometers were set to record at 25 Hz (Wilson *et al.*, 2015). A smoothing interval of 2 s (Bullock *et al.*, 2015; Wilson *et al.*, 2015) was applied to total acceleration data logged by tags (in units of standard gravity; $1 g = 9.8 \text{ m s}^{-2}$), yielding static acceleration (Wilson *et al.*, 2006; Shepard *et al.*, 2008a). Static acceleration was subtracted from total acceleration to produce dynamic acceleration for each axis and the absolute values of dynamic acceleration were summed, yielding overall dynamic body acceleration (A_{ODB} ; Wilson *et al.*, 2006), which can be used as a proxy for energy expenditure in juvenile sharks (Gleiss *et al.*, 2009, 2010; Lear *et al.*, 2016). Estimates of body acceleration were derived from total acceleration data using Igor Pro 6.3.3.5 (WaveMetrics, Inc.; www.wavemetrics.com).

STATISTICAL ANALYSES

Kinematic (F_{TB} and S_{L}) and activity (U_{rel} and A_{ODB}) metrics were analysed individually using linear mixed effects models to determine if *N. brevirostris* with different tag configurations responded differently throughout the day. Treatment (untagged, single-tagged and double-tagged) and time of day (morning and afternoon) were entered into models as fixed effects, along with their interaction. Individual *N. brevirostris* identification number, nested within treatment, was also entered into models to account for the fact that the same *N. brevirostris* was used in multiple treatments such that data might not be independent across treatments and swimming metrics might be correlated within an animal (Laird & Ware, 1982; Lindstrom & Bates, 1990). Lastly, sex and L_{T} were included in the model as additional fixed effects because sex and L_{T} have previously been found to influence activity levels of juvenile *N. brevirostris* at Cape Eleuthera (Wilson *et al.*, 2015). *Post hoc* multiple comparisons were run with Tukey's HSD for models of U_{rel} , S_{L} and F_{TB} if one main effect or the interaction term were significant and *post hoc t*-tests were used to separate means for the model of A_{ODB} . Where L_{T} was a significant fixed effect, linear regression was run between L_{T} and the swimming performance metric.

To determine if swimming performance was affected, the relationships between kinematic and activity metrics were compared exclusively across treatments (Lowe, 1996). Specifically, activity metrics (U_{rel} and A_{ODB}) were fit with linear mixed effects models with F_{TB} as a continuous covariate, treatment as a fixed effect and the interaction of F_{TB} and treatment. Stride length (S_{L}) was excluded from analysis because U_{rel} is used in the calculation of S_{L} . Individual *N. brevirostris* identification was nested in treatment and included as a random effect. Type I error rate for all tests was $\alpha = 0.05$. All data were analysed using JMP 10.0.0 (SAS Institute Inc.; www.jmp.com).

RESULTS

VIDEO-DERIVED KINEMATIC METRICS

As a portion of the mesocosm was out of frame, all *N. brevirostris* were not represented for each treatment during each time of day. Morning measurements comprised 480 passes (untagged = 180, double tagged = 140, single tagged = 160) and afternoon comprised 460 passes (untagged = 200, double tagged = 140, single tagged = 120).

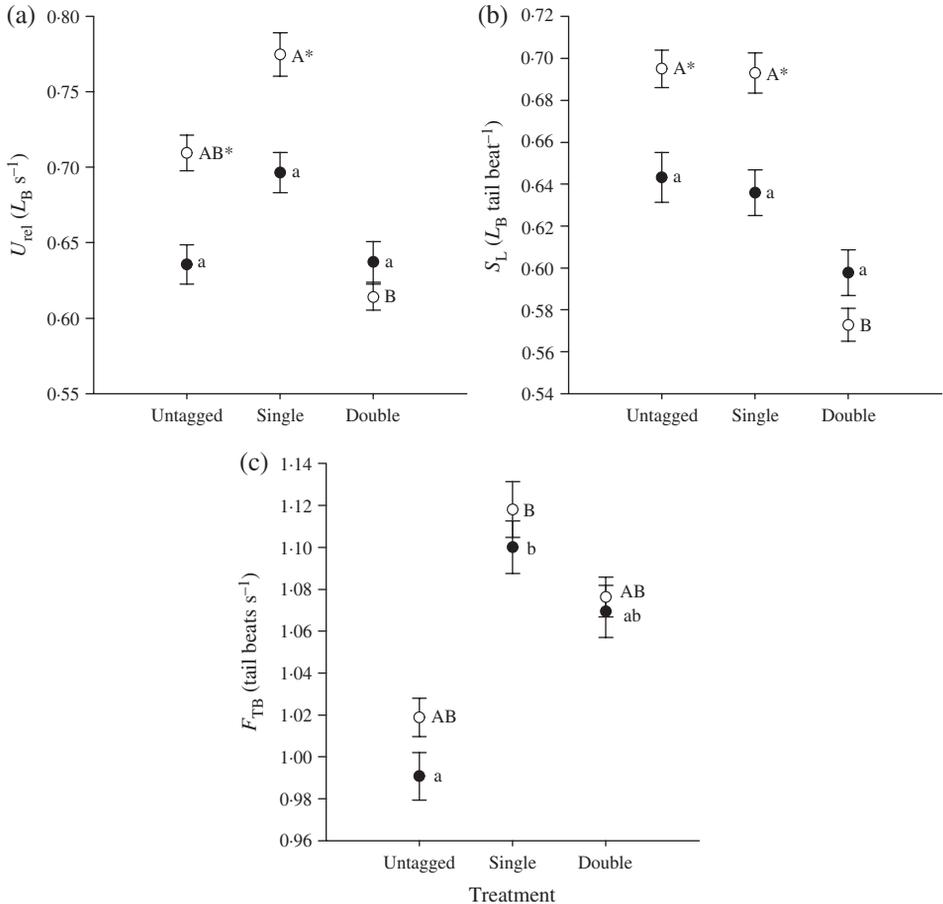


FIG. 2. Effects of treatment and time of day on (a) relative swimming speed (U_{rel} , in body lengths; L_B), (b) stride length (S_L) and (c) tail-beat frequency (F_{TB}). Treatment refers to *Negaprion brevirostris* without an accelerometer (untagged), *N. brevirostris* with an accelerometer mounted on the right side of the first dorsal fin (single) and *N. brevirostris* with an accelerometer and a counterweight on either side of the dorsal fin (double) (see Fig. 1). ○, Measurements (\pm s.e.) made during the morning (0700–0900 hours); ●, measurements (\pm s.e.) made during the afternoon (1300–1500 hours). Different letters indicate statistically significant differences between treatments, where uppercase letters refer to morning measurements and lowercase letters refer to afternoon measurements (Tukey's HSD, $P < 0.05$). *Statistically significant differences within treatments across time of day (Tukey's HSD, $P < 0.05$).

Untagged and single-tagged *N. brevirostris* decreased U_{rel} [Fig. 2(a)] from morning to afternoon. Conversely, double-tagged *N. brevirostris* exhibited no change in U_{rel} between morning and afternoon. During the morning, single-tagged *N. brevirostris* swam faster than double-tagged *N. brevirostris*, but neither tagged group swam faster nor slower than untagged *N. brevirostris*. There were no changes in U_{rel} between treatments by the afternoon. Relative swimming speed was not influenced by sex or L_T [Table I and Fig. 2(a)].

Untagged and single-tagged *N. brevirostris* both decreased in S_L [Fig. 2(b)] from morning to afternoon. Stride length of double-tagged *N. brevirostris* did not differ

TABLE I. Summary of fixed effects from linear mixed effects models on relative swimming speed (U_{rel}), stride length (S_L), tail-beat frequency (F_{TB}) and overall dynamic body acceleration (A_{ODB}) of juvenile *Negaprion brevirostris* in relation to time of day

| Model | Effect | Estimate (95% c.i.) | t | d.f. | P | |
|---|---|---|----------------------|-------|--------|--------|
| U_{rel} | Treatment: double tagged | -0.06 (-0.11, -0.01) | -2.37 | 20 | <0.05 | |
| | Treatment: untagged | -0.02 (-0.05, 0.03) | -0.48 | 20 | >0.05 | |
| | Time of day: midday | -0.02 (-0.03, -0.01) | -3.32 | 922 | <0.001 | |
| | Treatment × time of day: double tagged × midday | 0.03 (0.01, 0.04) | 4.03 | 917 | <0.001 | |
| | Treatment × time of day: untagged × midday | -0.02 (-0.03, -0.00) | -2.59 | 922 | <0.01 | |
| | Sex: female | 0.00 (-0.03, 0.03) | 0.19 | 20 | >0.05 | |
| | L_T | -0.01 (-0.01, 0.00) | -1.94 | 20 | >0.05 | |
| | Treatment: double tagged | -0.05 (-0.09, -0.02) | -3.15 | 20 | <0.01 | |
| | Treatment: untagged | 0.03 (0.00, 0.06) | 1.98 | 20 | >0.05 | |
| | Time of day: midday | -0.02 (-0.02, -0.01) | -3.66 | 926 | <0.001 | |
| S_L | Treatment × time of day: double tagged × midday | 0.03 (0.02, 0.04) | 4.70 | 920 | <0.001 | |
| | Treatment × time of day: untagged × midday | -0.01 (-0.02, 0.00) | -1.94 | 926 | >0.05 | |
| | Sex: female | 0.00 (-0.02, 0.02) | 0.05 | 20 | >0.05 | |
| | L_T | 0.00 (-0.00, 0.01) | 1.04 | 20 | >0.05 | |
| | Treatment: double tagged | -0.00 (-0.04, 0.04) | -0.03 | 19 | >0.05 | |
| | Treatment: untagged | -0.07 (-0.10, -0.03) | -3.63 | 19 | <0.01 | |
| | Time of day: midday | 0.00 (-0.01, 0.01) | 0.38 | 922 | >0.05 | |
| | Treatment × time of day: double tagged × midday | -0.00 (-0.02, 0.01) | -0.86 | 917 | >0.05 | |
| | Treatment × time of day: untagged × midday | -0.01 (-0.02, 0.00) | -1.78 | 922 | >0.05 | |
| | Sex: female | 0.00 (-0.03, 0.03) | 0.07 | 19 | >0.05 | |
| F_{TB} | L_T | -0.01 (-0.02, -0.01) | -4.96 | 19 | <0.001 | |
| | Treatment: double tagged | 0.02 (0.01, 0.01) | 3.70 | 8 | <0.01 | |
| | Time of day: midday | -0.00 (-0.01, -0.00) | -5.00 | 466 | <0.001 | |
| | Treatment × time of day: double tagged × midday | -0.00 (-0.00, 0.00) | -0.63 | 466 | >0.05 | |
| | Sex: female | -0.01 (-0.02, 0.01) | -0.89 | 8 | >0.05 | |
| | L_T | -0.00 (-0.00, 0.00) | -0.37 | 9 | >0.05 | |
| | A_{ODB} | Treatment: double tagged | -0.01 (-0.02, -0.01) | -4.96 | 19 | <0.001 |
| | | Time of day: midday | 0.02 (0.01, 0.01) | 3.70 | 8 | <0.01 |
| | | Treatment × time of day: double tagged × midday | -0.00 (-0.01, -0.00) | -5.00 | 466 | <0.001 |
| | | Sex: female | -0.00 (-0.00, 0.00) | -0.63 | 466 | >0.05 |
| L_T | | -0.01 (-0.02, 0.01) | -0.89 | 8 | >0.05 | |
| Treatment × time of day: double tagged × midday | | -0.00 (-0.00, 0.00) | -0.37 | 9 | >0.05 | |

L_T , total curvilinear length.

TABLE II. Summary of fixed effects from linear mixed effects models on relative swimming speed (U_{rel}) and overall dynamic body acceleration (A_{ODB}) in relation to swimming performance

| Model | Effect | Estimate (95% C.I.) | t | d.f. | P |
|-----------|--|-----------------------|-------|------|--------|
| U_{rel} | Treatment: double tagged | -0.06 (-0.07, -0.04)) | -3.53 | 21 | <0.01 |
| | Treatment: untagged | 0.02 (0.01, 0.03) | 1.58 | 22 | >0.05 |
| | F_{TB} | 0.57 (0.53, 0.60) | 16.37 | 861 | <0.001 |
| | $F_{TB} \times$ treatment: double tagged | -0.05 (-0.10, 0.00) | -1.07 | 904 | >0.05 |
| | $F_{TB} \times$ treatment: untagged | 0.04 (-0.01, 0.08) | 0.81 | 841 | >0.05 |
| A_{ODB} | Treatment: double tagged | 0.02 (0.01, 0.02) | 3.80 | 11 | <0.01 |
| | F_{TB} | 0.01 (0.00, 0.02) | -0.18 | 473 | >0.05 |
| | $F_{TB} \times$ treatment: double tagged | -0.00 (-0.01, 0.01) | 0.79 | 473 | >0.05 |

F_{TB} , tail-beat frequency.

between morning and afternoon. Untagged and single-tagged *N. brevirostris* had equal S_L during the morning, which were longer than for double-tagged *N. brevirostris*. There were no differences in S_L in the afternoon between any treatments and sex and L_T did not influence S_L [Table I and Fig. 2(b)].

Negaprion brevirostris in all treatments had relatively constant F_{TB} [Fig. 2(c)] between morning and afternoon. In both the morning and afternoon, single-tagged *N. brevirostris* exhibited higher F_{TB} than untagged *N. brevirostris*, but neither had different F_{TB} from double-tagged *N. brevirostris*. Lastly, F_{TB} varied with L_T , where larger *N. brevirostris* generally had lower F_{TB} (linear regression, $R^2 = 0.14$, $F_{1,938} = 154.3$, $P < 0.001$). Tail-beat frequency did not vary with sex [Table I and Fig. 2(c)].

From the swimming performance model addressing variation in U_{rel} with F_{TB} across treatments, U_{rel} varied across treatments and with F_{TB} (Table II). The linear relationship between F_{TB} and U_{rel} , however, was not significantly different across treatments (Table II).

ACCELEROMETER-DERIVED METRICS

Not all *N. brevirostris* were represented for double-tagged and single-tagged treatments at each time of day, because acceleration data were only analysed when *N. brevirostris* were observed on video. Across measurement periods, A_{ODB} was higher in double-tagged *N. brevirostris* than for single-tagged *N. brevirostris* (t -test, $t = -16.71$, d.f. = 260, $P < 0.001$), and, across both treatments, A_{ODB} was higher in the morning relative to the afternoon (t -test, $t = 2.47$, d.f. = 460, $P < 0.01$) (Fig. 3). Lastly, A_{ODB} was not influenced by F_{TB} , and, therefore, there was no significant variation in the linear relationship between F_{TB} and A_{ODB} between single and double-tagged *N. brevirostris* (Table II).

DISCUSSION

A combination of accelerometer weight and frontal area influenced the swimming kinematics, activity levels and swimming performance of juvenile *N. brevirostris*, despite adhering to published standards for tag-mass-to-animal-mass ratios.

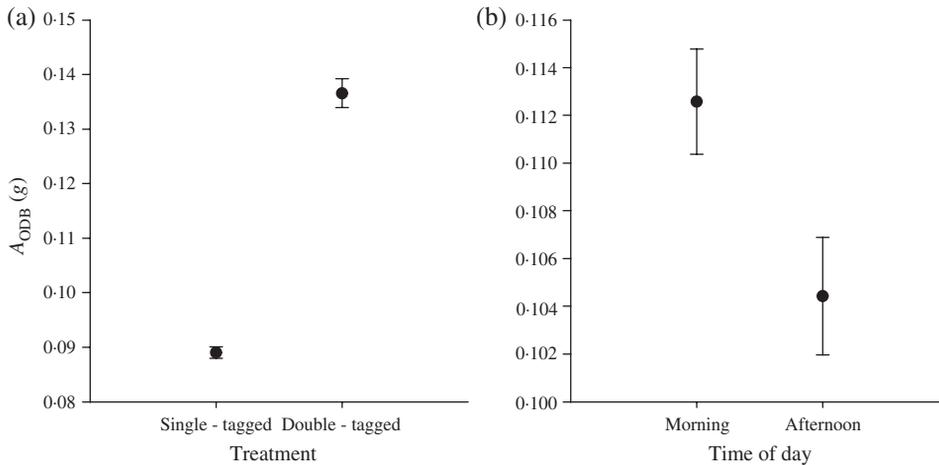


FIG. 3. Differences in overall dynamic body acceleration (A_{ODB}) of *Negaprion brevirostris* when (a) tagged with accelerometer only (single) or accelerometer and dummy tag (double) and (b) time of day. Overall dynamic body acceleration was greater in double-tagged *Negaprion brevirostris* (mean \pm S.E. = 0.14 ± 0.01 g) than for single-tagged *N. brevirostris* (0.09 ± 0.01 g), and both treatments had greater A_{ODB} in the morning (0.12 ± 0.01 g) than in the afternoon (0.11 ± 0.01 g).

Although tag-mass-to-animal-mass ratios for this study were 1.2–2.4%, Coughlin & Frost (1999) also observed reductions in critical swimming speeds in white sturgeon *Acipenser transmontanus* Richardson 1837 despite adhering to a 1.3% tag-mass-to-animal-mass ratio. Conversely, Bullock *et al.* (2015) did not observe alterations in swimming speeds and F_{TB} of juvenile *N. brevirostris* from miniaturized external accelerometer packages (CEFAS Technologies Ltd; www.cefas.co.uk), although *N. brevirostris* in that study were considerably larger (97–135 cm L_T , >4.3 kg) and external accelerometer packages were relatively smaller (<0.5% tag-mass-to-animal-mass ratio). Thus, tag mass alone was not a suitable metric of the suitability of external telemetry packages for small-bodied sharks.

The presence of an external telemetry package altered swimming kinematics and increased activity levels of juvenile *N. brevirostris*. Both accelerometer configurations potentially increased energy expenditure relative to untagged *N. brevirostris*, because A_{ODB} increased with increasing submerged weight and frontal cross-sectional area of accelerometers. Altered activity levels and increases in energy expenditure were probably due to increases in negative buoyancy (8.1 and 16.1% for single and double-tagged *N. brevirostris*, respectively) and hydrodynamic drag afforded by both accelerometer configurations (Scharold & Gruber, 1991; Lowe *et al.*, 1998). Double-tagged *N. brevirostris* exhibited equal F_{TB} as untagged *N. brevirostris* to travel less distance (lower S_L) during the morning and single-tagged *N. brevirostris* exhibited higher F_{TB} than untagged *N. brevirostris* to travel the same distance (equal S_L) in the morning and afternoon. Single-tagged *N. brevirostris* swam faster than double-tagged *N. brevirostris* and had longer S_L at comparable F_{TB} , which supports the finding of a difference in swimming performance between these treatments $S_L = U_{rel} F_{TB}^{-1}$. Thus, differences in how sharks modulated tail-beat amplitude and the portion of the body generating propulsion may explain differences in dynamic body acceleration, U_{rel} and S_L observed at identical

F_{TB} (Webb & Keyes, 1982). For short-term deployments, alterations in swimming kinematics may affect fishes if alterations reduce foraging efficiency or the ability to escape interactions with predators. For long-term deployments, alterations in activity levels may affect fishes if relatively more energy is allocated to activity metabolism over production of somatic or gonadal tissues. Therefore, the external telemetry packages used in this study altered the swimming kinematics and activity levels of small-bodied neonate *N. brevirostris*.

Swimming performance of juvenile *N. brevirostris* was affected by the presence of external telemetry packages. The linear relationship between U_{rel} and F_{TB} was not different for untagged, single-tagged and double-tagged *N. brevirostris* and no relationship was observed between F_{TB} and A_{ODB} . The relationship between U_{rel} and F_{TB} of juvenile scalloped hammerhead sharks *Sphyrna lewini* (Griffith & Smith 1834) swum in a flume was affected by the presence of an external telemetry package relative to untagged individuals, although this may be attributable to considerable differences in fin dimensions of *S. lewini* or restricted swimming in a flume (Lowe, 1996; Payne *et al.*, 2016). Furthermore, the lack of a linear relationship between A_{ODB} and F_{TB} was unexpected given that it has been previously documented for free-swimming *N. brevirostris*, but a lack of a relationship between swimming speed and A_{ODB} has also been demonstrated (Gleiss *et al.*, 2009; Bouyoucos *et al.*, 2017). While relationships between activity metrics and F_{TB} did not indicate changes in swimming performance, sharks can modify a combination of F_{TB} , tail-beat amplitude and the propulsive wavelength of the body to change speed (Webb & Keyes, 1982). It is possible, therefore, that changes in activity levels across time of day at constant F_{TB} were a result of *N. brevirostris* modulating tail-beat amplitude or propulsive wavelength, although it was not possible to measure accurately these variables from video. Changes in tail-beat amplitude can be approximated from acceleration data as changes in the amplitude of the acceleration signal used to derive F_{TB} and changes in A_{ODB} observed at constant F_{TB} strongly suggests that juvenile *N. brevirostris* modulated tail-beat amplitude (Gleiss *et al.*, 2009, 2011; Whitney *et al.*, 2012). Furthermore, differences in U_{rel} and S_L between single and double-tagged *N. brevirostris* at comparable F_{TB} suggest greater performance in single-tagged *N. brevirostris* and differential modulation of an additional kinematic variable (tail-beat amplitude) to confer greater performance. Thus, F_{TB} is not appropriate as a standalone metric of swimming performance for *N. brevirostris* because it ignores the complexity of fish swimming. Therefore, single-tagged and double-tagged juvenile *N. brevirostris* exhibited altered swimming performance and *N. brevirostris* probably experienced changes in performance related to a kinematic variable other than F_{TB} (tail-beat amplitude).

Negaprion brevirostris in the mesocosm exhibited treatment-specific changes in kinematics and activity across time of day. Specifically, untagged and single-tagged *N. brevirostris* exhibited altered U_{rel} and S_L across time of day and double-tagged *N. brevirostris* did not. Given that the current study documented treatment-specific differences in swimming kinematics and activity levels for only 1 day of testing, it is unclear whether observed differences reflected a treatment effect on some component of circadian activity levels or inter-individual variation in diel activity. Reductions in U_{rel} and S_L exhibited by untagged and single-tagged *N. brevirostris* and differences in A_{ODB} for both accelerometer treatments across time of day may be associated with a circadian component of *N. brevirostris* activity and metabolism (Nixon & Gruber, 1988; Sundström *et al.*, 2001). Conversely, Murchie *et al.* (2010) observed no diel activity

cycles for *N. brevirostris* from Cape Eleuthera and Wilson *et al.* (2015) documented diel changes in activity within this study's mesocosm tied to sex and sociality. Bullock *et al.* (2015) did not observe differences in various swimming speed and F_{TB} between tagged and untagged *N. brevirostris*, although these comparisons were made during 6 h of daylight. Lastly, Bouyoucos *et al.* (2017) observed a decrease in U_{rel} and F_{TB} in accelerometer-equipped juvenile *N. brevirostris* (using this study's single-tagged configuration in the same mesocosm) from day to night. Therefore, additional research is required to determine how external telemetry packages influence activity and kinematics across diel scales and whether circadian activity levels are affected.

In conclusion, this study's external telemetry packages, which increased negative buoyancy and frontal cross-sectional area, altered the swimming kinematics, activity levels and swimming performance of juvenile *N. brevirostris*. Given that the *N. brevirostris* used in this study were small neonate animals, these findings may not apply to larger or older juvenile *N. brevirostris*. Furthermore, the ability of juveniles to carry external telemetry packages may increase disproportionately with body size, which limits the applicability of these results strictly to similar-sized juvenile sharks, including shark species other than *N. brevirostris*. It is strongly recommended that validation is run as a part of external tagging studies to determine if tag-bearing biases swimming performance or has other consequences for animal welfare (Lowe & Goldman, 2001; Jepsen *et al.*, 2015). While the majority of tag validation studies to date have cited tag mass as a key determinant of tag suitability, studies ought to move away from this paradigm and provide systematic assessments of hydrodynamic drag and alterations to buoyancy, which are arguably more relevant to aquatic animals. Furthermore, buoyancy control represents a substantial energetic investment for elasmobranchs, including juveniles that are typically less buoyant than adults (Gleiss *et al.*, 2015; Iosilevskii & Papastamatiou, 2016). Therefore, small juvenile *N. brevirostris* experienced alterations in activity levels, swimming kinematics and swimming performance by carrying external telemetry packages.

All research was conducted in accordance with the University of Illinois Institutional Animal Care and Use Committee protocol #14163 and under permits MAMR/FIS/17 and MAMR/FIS/34 issued by the Bahamian Department of Marine Resources. Permission to capture sharks within the Bahamian Shark Sanctuary was established in accordance with Bahamian Department of Marine Resources Form 20A, Regulation 36D (3), permitting fishing, possession and exportation of sharks or shark parts. Partial funding was provided by an anonymous research gift to E.J.B. and J.W.M. I.A.B. would like to thank T. Nugent, B. Baker, D. Piersiak, H. Swain, G. Siegert, H. Paget-Brown and E. Schmidt. Lastly, the authors are grateful for the comments and advice from A. C. Gleiss and an anonymous reviewer who greatly improved the quality of this manuscript.

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