

9-28-2020

## First insights into the vertical habitat use of the whitespotted eagle ray *Aetobatus narinari* revealed by pop-up satellite archival tags

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Brewster LR, Cahill BV, Burton MN, Dougan C, Herr JS, Issac Norton L, McGuire SA, Pico M, Urban-Gedamke E, Bassos-Hull K, Tyminski JP, Hueter RE, Wetherbee BM, Shivji M, Burnie N, Ajemian MJ. First insights into the vertical habitat use of the whitespotted eagle ray *Aetobatus narinari* revealed by pop-up satellite archival tags. *J Fish Biol.* 2020 Sep 28. doi: 10.1111/jfb.14560. PMID: 32985701.

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1 **First insights into the vertical habitat use of the whitespotted eagle ray *Aetobatus narinari***  
2 **revealed by pop-up satellite archival tags**

3

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20

21 **Abstract**

22 The whitespotted eagle ray *Aetobatus narinari* is a tropical to warm-temperate benthopelagic  
23 batoid that ranges widely throughout the western Atlantic Ocean. Despite conservation concerns

24 for the species, its vertical habitat use and diving behaviour remain unknown. Patterns and drivers  
25 in depth distribution of *A. narinari* were investigated at two separate locations—western North  
26 Atlantic (Islands of Bermuda) and Eastern Gulf of Mexico (Sarasota, Florida, USA). Between  
27 2010 and 2014, seven pop-up satellite archival tags (PSATs) were attached to *A. narinari* using  
28 three methods: a through-tail suture; external tail-band; and through-wing attachment. Retention  
29 time ranged from 0–180 days, with tags attached via the through-tail method retained longest.  
30 Tagged rays spent the majority of time ( $82.85 \pm 12.17$  % S.D.) within the upper 10 m of the water  
31 column and, with one exception, no rays travelled deeper than ~26 m. One Bermuda ray recorded  
32 a maximum depth of 50.5 m suggesting that these animals make excursions off the fore-reef slope  
33 of the Bermuda Platform. Individuals occupied deeper depths ( $7.42 \pm 3.99$  m S.D.) during the day  
34 versus night ( $4.90 \pm 2.89$  m S.D), which may be explained by foraging and/or predator avoidance.  
35 Each individual experienced a significant difference in depth and temperature distributions over  
36 the diel cycle. There was evidence that mean hourly depth was best described by location and  
37 individual variation using a generalized additive mixed model approach. This is the first study to  
38 compare depth distributions of *A. narinari* from different locations and describe the thermal habitat  
39 for this species. Our study highlights the importance of region in describing *A. narinari* depth use,  
40 which may be important when developing management plans, whilst demonstrating that diel  
41 patterns appear to hold across individuals.

42

43 Keywords: Biotelemetry, Bermuda, Diel vertical migration, Elasmobranch, Gulf of Mexico,  
44 PSAT.

45

46 **1. Introduction**

47 Mobile marine species often exhibit complex horizontal and vertical movements. Understanding  
48 both movement patterns is critical to revealing a species' behaviour and ecology, including  
49 foraging, reproduction, habitat use and human interactions (Cooke *et al.*, 2012; Hays *et al.*, 2016).  
50 Whilst historically challenging to observe, the development of biologging and biotelemetry  
51 technology has offered great insight into how organisms use the marine environment (Hussey *et*  
52 *al.*, 2015; Hays *et al.*, 2016; Sequeira *et al.*, 2019). Data derived from these devices have provided  
53 opportunities to assess ecosystem connectivity and develop conservation and management  
54 practices (Cooke *et al.*, 2012; Braun *et al.*, 2014; Hays *et al.*, 2016). In particular, knowledge of a  
55 species' preferred location in the water column can help reduce vulnerability to human threats,  
56 such as fishing or boat strikes, and can promote a better understanding of its ecological role, for  
57 example in benthic-pelagic coupling (Cooke, 2008; Braun *et al.*, 2014).

58         Our understanding of pelagic batoid habitat use is relatively limited due to the transient  
59 nature of these species and the challenges associated with capturing and tagging them. Fortunately,  
60 recent applications of biologging and biotelemetry technology have facilitated some initial insights  
61 into the behaviour of these elusive species. For example, research on the reef manta ray *Manta*  
62 *alfredi* (Kreffft 1868), a planktivorous coastal-pelagic batoid, indicate that patterns of vertical  
63 movement vary by location. *M. alfredi* in the British Indian Ocean Territory exhibit diel vertical  
64 migration (DVM), occupying deeper mean diving depths during the day and moving up through  
65 the water column at night (Andrzejaczek *et al.*, 2019), whilst in the Red Sea and around the  
66 Seychelles, *M. Alfredi* remain closer to the surface during the day and dive deeper at night (Braun  
67 *et al.*, 2014; Peel *et al.*, 2020), a movement pattern known as reverse DVM. Both vertical  
68 movement strategies may be driven by foraging behaviour, with the contrasting patterns being  
69 attributed to regional oceanography affecting the distribution of their prey (Andrzejaczek *et al.*,

70 2020). DVM patterns have also been observed in more benthic batoids such as the short-tail  
71 stingray *Bathytoshia brevicaudata* (Hutton 1875) (Le Port *et al.*, 2008) and several skate species  
72 (Wearmouth & Sims, 2009; Humphries *et al.*, 2017). However, DVMs exhibited by benthic  
73 species may represent nektobenthic displacement (i.e. inshore/offshore movement along the  
74 substrate; Humphries *et al.*, 2017) rather than a change in position in the water column as observed  
75 in more pelagic animal DVMs. Nonetheless, foraging strategies are also thought to be a dominant  
76 driver for benthic species' DVMs (Le Port *et al.*, 2008; Wearmouth & Sims, 2009; Humphries *et*  
77 *al.*, 2017).

78 Not all batoids demonstrate diurnal patterns of vertical habitat use and other biotic and  
79 abiotic factors beyond foraging can explain dive behaviour. For example, the cownose ray  
80 *Rhinoptera bonasus* (Mitchill 1815), a benthopelagic schooling ray, exhibited no diel differences  
81 in depth or temperature but rather depth use varied between sexes and across seasons as feeding  
82 habitats changed with migration (Omori & Fisher, 2017). Temperature has been coined the  
83 “ecological master factor” that affects the physiology of aquatic ectotherms and consequently  
84 many fish, including the bat ray *Myliobatis californica* Gill 1865, behaviourally thermoregulate  
85 (Brett, 1971; Matern *et al.*, 2000). Lunar phase, due to its relationship with tides, illumination and  
86 changes in predator-prey distribution, has also been shown to influence the depth and habitat use  
87 of several elasmobranch species (Dewar *et al.*, 2008; Vianna *et al.*, 2013; Braun *et al.*, 2014;  
88 Whitty *et al.*, 2017), including *M. alfredi* (Braun *et al.*, 2014; Peel *et al.*, 2020). Additional  
89 investigation into the vertical movement of batoids and the reasons for these movements could  
90 shed light on potential interactions between species and trophic dynamics (Vaudo *et al.*, 2014).  
91 However, despite the importance of understanding vertical movements to elucidate the ecology of

92 a species, little is known about this behaviour in many large marine species, such as the  
93 whitespotted eagle ray *Aetobatus narinari* (Euphrasen 1790).

94 *Aetobatus narinari* is a large batoid ray inhabiting the subtropical and tropical coastal  
95 waters of the Western Atlantic Ocean (Richards *et al.*, 2009; White *et al.*, 2010; Naylor *et al.*,  
96 2012). There are conservation concerns for *A. narinari*; the International Union for the  
97 Conservation of Nature (IUCN), classifies the species as Near Threatened due to its life history  
98 characteristics, marketability and accessibility using inshore fishing gear (Kyne *et al.*, 2006). As  
99 such, the species is afforded protection in parts of its range, including Florida and Alabama state  
100 waters, around the Islands of Bermuda, the Maldives and the Great Barrier Reef, Australia. The  
101 species is highly mobile, with tagged individuals showing movements of 258.1 km ( $\pm 23.9$  S.E.;  
102 DeGroot, 2018), and has a demonstrated genetic link between populations in Florida and Cuba  
103 (Sellas *et al.*, 2015). Despite its migratory potential, *A. narinari* is known to exhibit high levels of  
104 multi-year philopatry (Ajemian *et al.*, 2012; Bassos-Hull *et al.*, 2014; Flowers *et al.*, 2017; Cerutti-  
105 Pereyra *et al.*, 2018; DeGroot, 2018). As a benthopelagic mesopredator, like *R. bonasus*, *A.*  
106 *narinari* forms an important link between benthic and pelagic environments (Ajemian *et al.*, 2012;  
107 Serrano-Flores *et al.*, 2019) and could play an important role in bioturbation (O'Shea *et al.*, 2012).

108 Vertical movements of *A. narinari* have only been described in a few short-term studies.  
109 In Bimini, Bahamas, diel movements were correlated with tidal phase; individuals aggregated to  
110 refuge in three deeper core areas during low tide (Silliman & Gruber, 1999). In Bermuda, Ajemian  
111 *et al.* (2012) identified diel patterns in depth use by *A. narinari* in Harrington Sound, a semi-  
112 enclosed inshore lagoon accessible to the open ocean via a single inlet. Similar movement patterns  
113 on the surrounding reef were inferred from Smart Positioning and Temperature (SPOT) satellite  
114 tag transmissions (Ajemian & Powers, 2014). However, taken together, these studies were unable

115 to provide fine-scale depth data outside of Harrington Sound, limiting our understanding of how  
116 *A. narinari* uses deeper habitats beyond inshore sounds of the Bermuda Islands.

117 The goals of this study were to use pop-up satellite archival tags (PSATs) to 1) quantify *A.*  
118 *narinari* vertical habitat use, 2) investigate the influence of environmental drivers known to affect  
119 depth use in other batoids, and 3) examine the effect of two different locations—Florida, USA and  
120 the Islands of Bermuda—with different habitat characteristics (continental shelf and bay/insular  
121 shelf respectively). Knowledge of the vertical movement patterns of *A. narinari* will help provide  
122 a more cohesive understanding of overall habitat use and behavioural trends, which can be used to  
123 inform future management in countries where this species remains vulnerable to human threats.

124

## 125 **2. METHODS**

### 126 *2.1 Capture and Tagging Techniques:*

127 Seven *A. narinari* were fitted with PSATs (Table 1), five near Sarasota, FL, USA (Fig. 1) with  
128 Standard rate X-Tags (Microwave Telemetry, Inc., Columbia, MD, USA; 122 x 33 mm, weight in  
129 air = 46 g), and two near Bermuda (Fig. 1) with MiniPAT tags (Wildlife Computers Inc., Redmond,  
130 WA, USA; 124 x 38 mm, weight in air = 60 g). Programmed tag detachment ranged 120–270  
131 days (Table 1). All Sarasota tags had an archived and transmitted sampling rate of 2 min and 15  
132 min, respectively. The animals in Sarasota were captured and tagged in September of 2010,  
133 October of 2010 and May of 2013. The Bermuda rays had an archived and transmitted sampling  
134 rate of 5 sec and 5 min, respectively. Animals in Bermuda were caught and tagged in August of  
135 2014.

136 Rays were caught with either a 500 x 4 m nylon seine net in Sarasota or a 100 x 5 m purse  
137 seine net in Bermuda. Capture involved visually spotting a ray in shallow water (< 4 m), encircling



138 with the respective nets, reducing net compass size and using a smaller scoop net to transfer the  
139 animal onto the boat. For rays caught in Sarasota, each individual was placed into a livewell on  
140 the boat with a free-flowing bilge pump supplying ambient, oxygenated seawater. Animals from  
141 Sarasota were sampled and tagged while in the livewell. For the individuals caught in Bermuda,  
142 each ray was placed on the deck of the boat with a hose into the buccal cavity to actively pump  
143 water over the gills. A towel was placed over the eyes to minimize stress during transit back to the  
144 Bermuda Aquarium for tagging. For the tagging procedure, the ray was transferred to a land-based  
145 clove oil bath for sedation (25 mg/L) (Grusha, 2005). At both tagging locations, rays were  
146 measured (disc width; cm), sexed and fitted with a PSAT; however, tag attachment varied among  
147 individuals (Table 1).

148         The absence of prominent structures and strong tissue in rays can make the attachment and  
149 retention of animal-borne devices difficult (Ward *et al.*, 2019); a problem that may be further  
150 aggravated for batoids like *A. narinari* that breach (Silliman & Gruber, 1999). Consequently, in  
151 this study three techniques were explored for PSAT attachment (Table 1; Fig. 2). The first  
152 technique was the through-wing method (Fig. 2a) which involved inserting a hollow tagging  
153 needle (cleaned with 70 % alcohol) from the ventral side through the caudal part of the pectoral  
154 fin. Monofilament (136 kg test), looped through the base of the PSAT, was passed into the hollow  
155 needle from the anterior side and both the needle and monofilament were pulled back through to  
156 the ventral side. The monofilament was secured with a steel fishing crimp on either side of the  
157 wing. To provide a more secure attachment point and reduce abrasion from the crimp, a soft, tear  
158 resistant pad (made of polyester reinforced PVC pool liner bonded with 1/8" inch neoprene) was  
159 placed between the animal and the crimp, on either side of the wing. Excess monofilament on the  
160 ventral side was trimmed prior to release. This attachment method was used to tag two Sarasota

161 rays (S1 and S3; Table 1). The second technique was the tail-band method (Fig. 2b) which was  
162 applied for Sarasota rays S2 and S4. The tail-band was constructed using a plastic cable tie encased  
163 in plastic tubing that was large enough to fit around the widest part of the base of the tail. The tail-  
164 band contained a small loop to pass a second small cable tie through to connect to the PSAT. The  
165 third technique, the through-tail suture, was used for the final Sarasota ray (S5) and both Bermuda  
166 rays. The through-tail method involved using a stainless steel needle (cleaned with 70 % alcohol)  
167 to pass either a wire tie in black poly-tubing (S5), or aircraft cable encased in silastic tubing (40.8  
168 kg test; Bermuda rays), through the musculature at the base of the tail and crimping it back on  
169 itself on the dorsal side, creating a bridle to which the PSAT was attached (Fig. 2c; see Le Port *et*  
170 *al.*, 2008). Heat-shrink tubing was heated over the crimps to minimize abrasion and the possibility  
171 of predation from the reflective metal acting like a fishing lure.

172         Following tag attachment, Bermuda rays were moved from the anaesthesia tank to a  
173 recovery tank with ambient seawater to assess their health prior to release at the Bermuda  
174 Aquarium dock. Time from capture to release for these rays was 55–65 min. Sarasota rays were  
175 assessed in the livewell on the boat and released close to the capture location. The approximate  
176 times between capture and release were XX for Sarasota animals tagged using the tail-band  
177 method, XX for the through-wing method and XX for the through-tail method.

178

## 179 *2.2 Ethical Statement:*

180 All animal handling procedures were approved through Mote Marine Laboratory's IACUC permits  
181 #10-03-PH1 and 13-02-PH1, FWC Special Activity License (SAL-10-1140-SRP and SAL-13-  
182 1140-SRP) and Bermuda Department of Conservation Services permit #14-06-15-06.

183

## 184 *2.3 Data Analyses:*

185 Satellite-transmitted data were downloaded through a CLS America portal. In the event a tag was  
186 physically recovered, the archived data were processed using WC-DAP 3.0 (MiniPATs) or  
187 returned to Microwave Telemetry (X-Tags) for download (Table 1). Data were inspected for a  
188 constant depth value, indicating the tag had detached from the animal (i.e. the end of the retention  
189 period; Table 1) and data including and subsequent to that constant depth point were discarded.  
190 All vertical movement analyses were conducted in R (Version 4.0.0). To analyse the horizontal  
191 movement of the rays, geolocation analysis was performed for each deployment except S4 because  
192 of the short deployment duration. To create maximum likelihood tracks for the Bermuda rays, the  
193 MiniPAT data were processed in the Wildlife Computers GPE3 software. The program uses the  
194 tag data, sea surface temperature (SST) and bathymetric constraints to generate a hidden Markov  
195 model that estimates the most likely position of the animal. The model also provides a probability  
196 distribution that indicates the quality of the location estimate. To obtain the most probable track  
197 for the Microwave Telemetry X-Tag fitted to S5, the data were processed in R using a state-space  
198 unscented Kalman filter in the ‘UKFSST’ package (Nielson *et al.*, 2009) along with the Reynolds  
199 Optimally Interpolated sea surface temperatures (SST) Data. Following state-space estimation, we  
200 used the ‘analyzepsat’ package to apply a secondary bathymetric correction that constrained  
201 estimated locations based on the daily maximum depths that the ray achieved (Galuardi, 2012).

202 To assess whether depth and ambient temperature (as measured by the tag) distribution  
203 varied between night and day for each ray, we conducted Kolmogorov-Smirnov (K-S) tests ( $p <$   
204 0.001). The data were identified as ‘day’ or ‘night’ based on sunrise and sunset times obtained  
205 from the ‘suncalc’ package (Thieurmel & Elmarhraoui, 2019) at each animal’s release location.

206 To determine the effect of abiotic factors on *A. narinari*, we aggregated the data to calculate  
207 hourly means and built a Generalized Additive Mixed Model (GAMM) with a gamma distribution,

208 to describe mean hourly depth (m). The GAMM was built using the ‘mgcv’ package (Wood, 2006).  
209 GAMMs are a semi-parametric approach used for modelling effects in response to a variety of  
210 predictor variables simultaneously and can account for repeated measures and serial correlation  
211 (Hastie & Tibshirani, 1990). Abiotic factors considered included: tagging location  
212 (Sarasota/Bermuda), hour of the day, month, moon phase and sea surface temperature (SST, °C).  
213 Moon phase (0.0–1.0; representing new moon, waxing crescent, first quarter, waxing gibbous, full  
214 moon [0.5], waning gibbous, last quarter and waning crescent) was extracted using the ‘suncalc’  
215 package. Hourly SST was derived as the mean temperature when the animal was within 5 m of the  
216 surface (Andrzejaczek *et al.*, 2018). As part of data exploration prior to model development, we  
217 plotted the response variable against each covariate, investigated potential interactions and  
218 assessed collinearity between covariates using conditional boxplots and generalized variance-  
219 inflation factor (GVIF) scores; covariates yielding GVIF values higher than 3 were removed and  
220 scores were recalculated (Zuur *et al.*, 2009, 2010). Circular smoothers were applied to hour of the  
221 day and moon phase. Smoothing splines were automatically optimized using cross-validation in  
222 the ‘mgcv’ package (Wood, 2006). Ray ID was added to the model as a random effect to avoid  
223 pseudo-replication and account for individual variation. An auto-correlation plot was used to  
224 assess if there was serial correlation between residuals where a value at time  $t$  is a linear function  
225 of the value at  $t-1$  (Zuur *et al.*, 2009). The auto-correlation plot indicated temporal correlation was  
226 evident in the initial model residuals and thus an auto-regressive process of order 1 was included.  
227 To balance model fit with model size, Akaike Information Criterion (AIC; Akaike, 1973) scores  
228 were used for optimal model selection. The model with the lowest AIC score was selected, unless  
229 a more parsimonious model had an AIC value within two of the lowest score (Burnham &

230 Anderson, 2002). Models were validated by examining routine diagnostics (Q-Q plots, histograms  
231 of residuals, response versus fitted values and linear predictors versus residuals).

232

### 233 3. RESULTS

234 Four of the seven deployed tags successfully transmitted and/or archived data (Table 1). S1 and  
235 S3 did not report, and one tag (S2) was recovered after washing ashore. S2 demonstrated regular  
236 vertical movements for approximately 2 h, at which point the tag was either ensnared at depth (and  
237 detached) or the animal died and sank to the bottom (tag remaining attached). Of the remaining  
238 four *A. narinari*, tag retention periods varied between 4 days (S4) up to the programmed duration  
239 of 180 days (B1; Table 1). Early detachment of the tags from S4 and B2 occurred because the tag's  
240 constant depth release mechanism was triggered. Examination of the tag's tether revealed that a  
241 slipped crimp caused the early release from S5. All four tags transmitted data via the ARGOS  
242 satellites; two of these were recovered and the full datasets accessed (B2 and S5). The Sarasota  
243 rays' (S4 and S5) distance between release locations and first satellite transmissions were 101 and  
244 72 km, respectively (Fig. 1). Similarly, for the Bermuda *A. narinari* (B2), the first transmitted  
245 detection was within close proximity to the release location; however, the other Bermuda ray (B1)  
246 first transmitted ~990 km away from its release location, 107 days after the tag release from the  
247 animal (Fig. 1).

248 The results of the geolocation analyses for S5, B1 and B2 were considered unrepresentative  
249 of the horizontal movements exhibited by the three rays and are consequently not presented.  
250 Typical geolocation accuracy for both the X-Tag and MiniPAT are  $\pm 1^\circ$  latitude,  $\pm 0.5^\circ$  longitude  
251 but PSAT estimates of geolocation using light-based methods can be associated with large margins  
252 of error in cases where there is not much overall tag displacement (Brunnschweiler *et al.*, 2010;  
253 Braun *et al.*, 2015; Omori & Fisher, 2017; Hueter *et al.*, 2018), as was the case for B2 and S5. For

254 B1, although it clearly moved over deep water (see below), the late report confounded the pop-off  
255 location and thus confidence in the track was low.

256

### 257 *3.1 Depth Distribution*

258 Bermuda *A. narinari* experienced a wider range of depths than those tagged off Sarasota, with one  
259 ray reaching a maximum depth of 50.5 m. The two Sarasota rays were found at depths < 25 m for  
260 the entire tracking period (Table 2; Fig. 3). Bermuda rays also occupied a deeper mean depth  
261 (Table 2). All rays spent the majority of the time ( $82.85 \pm 12.17$  % S.D.) within 10 m of the surface  
262 but demonstrated oscillatory diving behaviour throughout the diel cycle (Fig. 4). The depth  
263 distribution of each individual was significantly different between night and day (B1:  $D=0.19$ ,  $P$   
264  $< 0.001$ ; B2:  $D=0.41$ ,  $P < 0.001$ ; S4:  $D=0.34$ ,  $P < 0.001$ ; S5  $D=0.19$ ,  $P < 0.001$ ), with rays  
265 consistently occupying shallower mean depths at night (collectively mean day depth =  $7.42 \pm 3.99$   
266 m S.D. versus mean night depth =  $4.90 \pm 2.89$  m S.D; Table 2; Fig. 4). There was variability in  
267 depth distribution across individuals, but all individuals spent the largest proportion of nighttime  
268 in the top 10 m of the water column (B1 73.00 %; B2 83.07 %; S4 100.00 %; S5 93.84 %).

269 Apart from one dive to 31 m on 24 August 2014, B1 did not reach depths greater than 25 m  
270 until 20 November 2014, approximately halfway through the deployment, when surface  
271 temperatures dropped below 23 °C (Fig. 3a). B1 spent 7.41 % of the deployment at depths below  
272 the 26 m maximum depth obtained by B2. For B2 in particular, depth use was bimodal (Fig. 4b).  
273 It regularly dove to depths exceeding 20 m throughout the deployment, except during September  
274 when water temperature was warmest (Fig. 3b). S5 exhibited a similar pattern of shallower depth  
275 use (< 10 m) with warmer temperatures during late June–early July 2013 (Fig. 3d). The deployment  
276 of S4 was too short to see discernible changes in depth use over time (Fig. 3c).

277 During data exploration for modelling mean hourly depth using the GAMM, covariates month  
278 and SST were found to be collinear and thus month was omitted from model development. Data  
279 exploration indicated a potential interaction between SST and location; however, when including  
280 this interaction, the models failed to converge and thus the term was omitted from the analysis.  
281 Models were built with and without S4 to determine sensitivity of model results to the short  
282 deployment duration. Excluding this individual did not influence overall model results, and thus it  
283 was kept in the final model. Although the saturated model showed all fixed covariates were  
284 significant, model selection indicated the mean hourly depth of the animal was best explained by  
285 location and individual random effect (Table 3). Unfortunately, there is no established way to  
286 calculate the variance explained for individual covariates in GAMMs (Wood, 2006; Zuur *et al.*,  
287 2009). However, model selection on an exploratory model without a random effect highlighted  
288 that all covariates should be retained, thus indicating the random effect accounts for most of the  
289 model variance. There was substantial evidence for location and individual random effect ( $\Delta AIC$   
290 = 78.09) as the optimal model over alternative GAMMs with other fixed covariates (Table 4).

291 The K-S test indicated depth distribution was significantly different between day and night for  
292 each animal, with individuals spending a higher proportion of time in deeper water during the day  
293 (Fig. 4) and depth distribution contracting for B1, B2 and S5 during night hours (Supporting  
294 Information Fig. 1). Whilst SST—like moon phase and hour of the day—was not included in the  
295 optimal model, there was a trend (particularly for the Bermuda rays) towards occupying shallower  
296 depths as temperatures rose (Supporting Information Fig. 1). The relationship between depth and  
297 moon phase was less clear than that of depth and hour of the day, with no clear trend across  
298 individuals (Supporting Information Fig. 3).

299

300 *3.2 Temperature Distributions:*

301 Collectively, *A. narinari* experienced a temperature range of 18.10–32.86 °C (Table 2; Fig 4). B1  
302 experienced the widest temperature range spanning 14.40 °C, encompassing the 10.5 °C range  
303 obtained by B2 (Table 2). The warmest temperature (32.86 °C) was experienced by S5; there was  
304 no overlap in temperature range between S4 and S5 (Table 2). Rays experienced cooler  
305 temperatures at night, with a collective mean nighttime temperature of 26.03 °C ( $\pm 2.38$  S.D) versus  
306 26.30 °C ( $\pm 2.22$  S.D) during the day; mean night-day temperature differences ranged 0.06–0.63  
307 °C across individuals (Table 2; Fig. 4). The K-S tests showed statistical differences between day  
308 and night temperature distributions for each individual (B1:  $D=0.11$ ,  $P < 0.001$ ; B2:  $D=0.09$ ,  $P <$   
309  $0.001$ ; S4:  $D=0.27$ ,  $P < 0.001$ ; S5  $D=0.06$ ,  $P < 0.001$ ). Seasonal shifts in water temperature were  
310 particularly evident in the longer deployments (Fig. 3); SSTs cooled from 32.50 °C at the  
311 beginning of the deployment on B1, to 18.90 °C at the end; 32.00–23.20 °C for B2 and warmed  
312 from 28.02 °C to 31.65 °C for S5.

#### 313 314 **4. DISCUSSION**

315  
316 Off the coast of Sarasota, Florida, and surrounding Bermuda, *A. narinari* show similar diel  
317 behavioural patterns in vertical habitat use (Fig. 3; Supporting Information Fig. 1). In both  
318 locations, the rays spent the majority of their time in the upper 10 m of the water column (Fig. 4;  
319 Supporting Information Fig. 1). This is consistent with previous studies in Harrington Sound  
320 indicating that *A. narinari* prefers shallow ( $< 10$  m) habitats (Ajemian *et al.*, 2012). The average  
321 depth of Sarasota Bay is ~2 m and the 10 m depth contour occurs approximately 9 km offshore  
322 (Fig. 1). Of the four rays monitored in the study, both rays from Sarasota and one of the rays from  
323 Bermuda (B2) remained above 26 m for the entire deployment (Table 2). These rays were released  
324 in relatively shallow water, either on the continental shelf on the west coast of Florida, or in  
325 Harrington Sound, Bermuda (Fig. 1; Fig 2). Ray B1 recorded a maximum depth of 50.5 m,



326 substantially deeper than any of the other rays (Table 2). Ray B1 was released in Harrington Sound;  
327 however, the attached PSAT first transmitted from the open ocean southwest of Bermuda, where  
328 the depth is approximately 4,000 m (Fig. 1). For unknown reasons, the tag transmitted late—107  
329 days after it was released from the animal—and thus is not a reliable indicator of animal location.

330         There is a high likelihood that in areas with shallow bathymetry, the deepest extent of a  
331 ray's dive correlates to the sea floor in that location. Harrington Sound, the capture site of the two  
332 Bermuda rays, is a 4.8 km<sup>2</sup> lagoon with a mean depth of 14.5 m and a maximum depth of ~26 m  
333 at Devil's Hole, a remnant sink hole in the south-southeast corner of the sound (Bates, 2017; Fig  
334 2). The maximum depth obtained by B2 coincides with that of Devil's Hole and was reached on  
335 57.73 % of the monitoring days. Typically between October–May, the dissolved oxygen in Devil's  
336 Hole is similar to that at the surface; however, during the summer the bottom 3 m of Devil's Hole  
337 usually becomes hypoxic with anoxia occurring in September (Bates, 2017). Based on the capture  
338 and first transmission locations, in tandem with the depth profile of the animal, we suspect B2 may  
339 have remained within Harrington Sound throughout the deployment but did not access the deeper  
340 depths of Devil's Hole during September when dissolved oxygen concentrations were low. B1  
341 displayed similar depth use patterns as B2 until halfway through the deployment where it must  
342 have made forays off the main terrace (< 20 m), onto the fore-reef slope (< 50 m) of the Bermuda  
343 Platform and beyond. While a previous study tracking this species using SPOT tags found that *A.*  
344 *narinari* travels outside of Harrington Sound to the outer reefs of the platform, this species was  
345 not previously observed moving off the Bermuda platform as B1 must have done here in order to  
346 obtain its depth of 50.5 m (Table 2; Fig. 1a; Ajemian & Powers, 2014). Dives to the 40–50 m depth  
347 range occurred repeatedly between late November–February, suggesting that individuals may  
348 move offshore during this period when surface water temperatures are below 23 °C.

349           The optimal model indicated that the depth of *A. narinari* was best described by location  
350 and individual variation, with the Bermuda animals occupying significantly deeper mean hourly  
351 depths than those tagged off Sarasota (Table 3). This may be explained by the difference in  
352 bathymetry of the two locations. Sarasota is located along the Gulf of Mexico coast of Florida  
353 where the continental shelf is wide (up to 320 km), while Bermuda is in the Atlantic Ocean far  
354 from the continental shelf (Wilhelm & Ewing, 1972). The Bermuda Islands' unique  
355 geomorphology includes a volcanic pedestal of three topographic highs that include offshore banks  
356 and seamounts within relatively close proximity (50 km) to inshore sounds and lagoons of the  
357 Bermuda platform (Vacher & Rowe, 1997). Thus, deeper depths are more readily accessible to the  
358 Bermuda animals than the Sarasota rays. However, it should be noted that as the location of the  
359 individuals were unknown, the depth of the water column at any given depth recording cannot be  
360 determined and we cannot confirm that rays were occupying the entirety of the water column  
361 available to them.

362           Although hour of the day was not selected in the optimal model to explain mean hourly  
363 depth, in both locations *A. narinari* exhibited a diel pattern of vertical habitat use, spending more  
364 time at depth during the day while remaining closer to the surface at night (Fig. 4; Supporting  
365 Information Fig. 1). However, this was not mutually exclusive, and rays could be found near the  
366 surface and at depth during both diel periods. These results are consistent with previous studies.  
367 In the Indian River Lagoon, FL, USA active acoustic tracking revealed individuals spent more  
368 time in deeper channels during the day and occupied shallower habitats at night (DeGroot *et al.*,  
369 2020). In Harrington Sound, Bermuda, *A. narinari* was observed predominantly in the upper 10 m  
370 of the water column and exhibited a diel shift to deeper waters during the day (Ajemian *et al.*,  
371 2012). In a later study involving SPOT tags at the same site (Ajemian & Powers, 2014),

372 transmissions from these tags correlated both to the diel depth patterns noted in the earlier acoustic  
373 study, and to the patterns noted in this PSAT study.

374         This pattern of DVM is also in line with other batoid species. For example, *B. brevicaudata*  
375 was found to have a similar diel movement pattern, thought to be related to foraging (Le Port *et*  
376 *al.*, 2008). A possible explanation for the behaviour noted in this study is that *A. narinari*, as a  
377 benthic predator known to consume bivalves and gastropods (Ajemian *et al.*, 2012; Serrano-Flores  
378 *et al.* 2019), forages in shallow water at night. These prey prefer shallow water (< 2 m) (Arnold *et*  
379 *al.*, 1991) and some species are known to exhibit increased nocturnal activity which may make  
380 them easier to detect (Robson *et al.*, 2010). Whilst foraging during the day can confer an advantage  
381 to visual predators like white sharks *Carcharodon carcharias* (Linnaeus 1758) (Huveneers *et al.*,  
382 2015), *Aetobatus narinari* may be able to detect buried prey such as bivalves just as easily using  
383 other sensory organs, under any light conditions. Smith & Merriner (1985) hypothesized that *R.*  
384 *bonasus* could detect the bioelectric fields mollusks produce, using the ampullae of Lorenzini, or  
385 the stream of excurrent water from burrowing bivalves. *B. brevicaudata* is known to detect  
386 excurrent water jets from worm burrows and clams to find prey (Montgomery & Skipworth, 1997).  
387 Research focused on acquiring direct behavioural observations of *A. narinari*, via animal-borne  
388 cameras or acceleration data loggers, could be beneficial to clarify whether spatiotemporal patterns  
389 in diving observed herein are foraging-related (Hays, 2015).

390         Alternative explanations for patterns of DVM often include predator avoidance and  
391 behavioural thermoregulation (Matern *et al.*, 2000). *A. narinari* has several known predators that  
392 frequent the Gulf of Mexico and Bermuda (e.g., the tiger shark *Galeocerdo cuvier* (Péron &  
393 Lesueur 1822) and the great hammerhead shark *Sphyrna mokarran* (Rüppell 1837) (Simpfendorfer  
394 *et al.*, 2001; Chapman & Gruber, 2002)). *A. narinari* may be exhibiting nektobenthic displacement,

395 occupying deeper depths during the day when they can visually detect these predators, and moving  
396 to shallower habitats at night to seek refuge and forage. The results of this study suggest that  
397 vertical movements are not due to behavioural thermoregulation because mean temperatures were  
398 similar between night and day (Table 1). Currently, the thermal sensitivity of *A. narinari* is  
399 unknown; further research is needed to determine the importance of temperature on the  
400 physiological performance and behaviour of this species.

401         There were some limitations with the modelling process; currently there is no established  
402 way to estimate model fit for GAMMS, preventing quantification of the variance explained by  
403 each model term (i.e. individual and location) (Wood, 2006; Zuur *et al.*, 2009). Whilst the  
404 autocorrelation structure implemented here largely corrected for the temporal autocorrelation, it is  
405 not ideal for handling irregularly spaced data which can occur with satellite tags when not all data  
406 is relayed (e.g. B1; Fig. 3a). As such, there is the possibility that temporal autocorrelation for this  
407 animal may have been underestimated. Additionally, an increased sample size would allow for  
408 more explanatory variables to be considered in the model, such as animal size and sex. There is  
409 evidence in other fishes, including for the batoid *M. californica*, that depth and temperature  
410 preferences change with ontogeny (Hopkins & Cech, 2003) whilst sex has been demonstrated to  
411 significantly influence the depth and temperature distribution of *R. bonasus* whereas diel period  
412 did not (Omori & Fisher, 2017). Nevertheless, whilst the sample size is small (n=4) our data  
413 indicate the importance of location and individual variation in describing the depth use of *A.*  
414 *narinari* whilst showing that diel patterns may hold across individuals.

415         The most effective PSAT attachment technique was the through-tail method (Fig. 2a). All  
416 through-tail tags were retained longer than tags attached by other methods, including one (B1),  
417 which popped-up after the pre-programmed 180 days but reported late (Table 1). Examination of the

418 tag's tether from S5 revealed that a slipped crimp was the breaking point suggesting that the  
419 attachment method to the ray itself was adequate. This method provides a robust mounting point  
420 for tagging to reduce drag without interfering with normal behaviours (e.g., males biting the  
421 female's pectoral fins during pre-copulation (McCallister *et al.*, 2020)). Its success in similar  
422 species, *B. brevicaudata*, indicated its potential for *A. narinari* (Le Port *et al.*, 2008).

423         Despite its role in the marine food web and designated status as “Near Threatened” by the  
424 IUCN, *A. narinari* remains a seldom studied species (Kyne *et al.*, 2006; Cuevas-Zimbrón *et al.*,  
425 2011; Tagliafico *et al.*, 2012; Ajemian & Powers, 2014). As this species has a range that spans  
426 several countries, each with fisheries management policies with varying levels of protection,  
427 information on the large-scale movement of this mobile ray and position in the water column is  
428 important in planning conservation efforts (Ajemian & Powers, 2014; Serrano-Flores *et al.*, 2019).  
429 This study provides the first insights into the vertical habitat use of *A. narinari* in both the Gulf of  
430 Mexico and western North Atlantic. It indicates the importance of recognizing that individual  
431 variation and location can influence behaviour when determining effective management of this  
432 species. Further, it demonstrates that the through-tail method of attaching PSATs to *A. narinari*  
433 can yield retention times conducive to quantifying their large-scale movements and migration  
434 patterns. To better resolve horizontal movement patterns, future studies could combine passive  
435 acoustic telemetry with PSAT technology. Inclusion of acoustic tagging data can reduce the error  
436 associated with geolocation estimates (Peel *et al.*, 2020) and provide insight into more fine-scale  
437 horizontal movement patterns. Future studies should focus on expanding tagging efforts further  
438 south in the Gulf of Mexico and the Caribbean. These areas have fewer protections for *A. narinari*  
439 and local fisheries exploit the species (Cuevas-Zimbrón *et al.*, 2011; Bassos-Hull *et al.*, 2014;  
440 Serrano-Flores *et al.*, 2019). Movement data in these areas will enable researchers to develop

441 management plans that cater to regional movement patterns, as well as to evaluate connectivity  
442 between these exploited regions and protected areas to the north.

443

#### 444 *Acknowledgements*

445 We dedicate this study to the late Dr. Neil Burnie, who provided his unwavering passion  
446 and guidance to the work carried out in Bermuda. Funding for the Bermuda component  
447 was provided by a grant from the Bermuda Zoological Society to MJA as well as the Guy  
448 Harvey Ocean Foundation. Field operations were supported by C. Aming, C. Flook, D.  
449 Ward, C. Bridgewater, A. Smith, J. Singleton and L. Rheinin. Additional logistical support  
450 was coordinated by the Harte Research Institute for Gulf of Mexico Studies and Florida  
451 Atlantic University's Harbor Branch Oceanographic Institute (FAU-HBOI). We thank  
452 Mote Marine Laboratory field operations staff P. Hull, D. Dougherty, G. Byrd, K.  
453 Wilkinson and J. Morris for their assistance with this work. Funding for the Sarasota  
454 component was provided by Georgia Aquarium, National Aquarium, Disney Conservation  
455 Fund and Save Our Seas Foundation. This paper is the product of the 2020 spring semester  
456 graduate class, "Introduction to Biologging and Biotelemetry" (BSC 6936-004), taught by  
457 MJA and LRB at FAU.

#### 458 *Supporting Information*

459

#### 460 *Contributions*

461 LRB and MJA conceived the study. KB-H, REH, MJA, BMW, MS obtained funding. MJA,  
462 CA, NB, KB-H, REH conducted fieldwork. LRB, JPT, MJA, BVC, MNB, CD, JSH, LIN,  
463 SAM, MP, and EU-G conducted analysis and helped to write the manuscript. All authors  
464 provided manuscript edits.

465 *Significance Statement (max. 75 words)*

466 *Aetobatus narinari* is a seldom studied benthopelagic batoid that is designated as “near  
467 threatened” by the International Union for Conservation of Nature. Understanding its  
468 vertical movement patterns can help elucidate the ecological role of the species and assess  
469 vulnerability to human threats. This is the first study to compare vertical movement of *A.*  
470 *narinari* from different locations. Our study highlights the importance of region and  
471 individual variation in describing this species’ depth use.

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