Evidence and description of a nursery habitat for the recently reclassified stingray *Styracura schmardae* from The Bahamas

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ABSTRACT: While definitions of elasmobranch nurseries remain fluid within the literature, the identification and description of nursery habitats for batoids remain relatively scarce. The Atlantic chupare stingray *Styracura schmardae*, a large-bodied demersal ray that was recently described from The Bahamas, is considered Data Deficient by the International Union for the Conservation of Nature. Using a combination of mark–recapture and benthic habitat surveying, we describe long-term site fidelity of *S. schmardae* for the first time, and provide evidence and characteristics of a nursery environment for this species in South Eleuthera, The Bahamas. Overall, 190 capture events were recorded from 86 tagged individuals from April 2014 to August 2017 (1222 d), with 51% of individuals recaptured at least once, 36% at least twice and 2% 6 times. Most (95%) of the captured rays were considered immature (mean disc width 553.5 mm) and had a mean ± SD residence time of 243 ± 177 d. Residence time did not differ among sites, sex or size (disc width) of individual rays at time of capture. Of 4 creeks sampled, Deep Creek had the highest prevalence of captures and recaptures, and correspondingly the highest values for soft sediment cover and sediment depth among sites, suggesting these habitat characteristics in particular may be important in supporting populations of juvenile *S. schmardae*. Results of this study will better inform effective management and conservation efforts for *S. schmardae,* including concentrating localised conservation efforts on these ecosystems.

KEY WORDS: Atlantic chupare · Mark–recapture · Refugia · Batoid · Mangrove creek · Juvenile

1. INTRODUCTION

Coastal and nearshore ecosystems of the tropics are a highly diverse mosaic of interconnected habitats, characterized by high productivity, that provide refugia for a number of species (Shulman 1985, Beck et al. 2001, Dale et al. 2011). Many of these environments are considered to be nursery habitats, supporting juvenile fishes over extended periods of time by offering abundant resources such as increased prey avail-

ability and protection against predators (Springer 1967). These traits may aid in the mitigation of early life mortality (Branstetter 1990, Heupel & Simpfendorfer 2002, Yokota & Lessa 2006), thereby regulating overall population size (Heppell et al. 1999). This is particularly relevant for *K*-selected species that may be more vulnerable to extrinsic pressure, such as elasmobranch fishes.

Definitions of elasmobranch nurseries remain fluid within the literature, yet many contemporary studies

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regard criteria published by Heupel et al. (2007) as the fundamental benchmark for assessing these habitats. Specifically, these criteria include (1) that individuals of a species are encountered with higher frequency relative to other areas, (2) individuals have a tendency to remain or return for extended periods, and (3) the area or habitat is used repeatedly across years.

However, recent additions to the literature have cautioned against the delineation of what is considered an elasmobranch nursery without proper application, undermining effective management and conservation efforts (Heupel et al. 2019). It is therefore critical to focus attention on the identification and parameters that underpin accurate perceptions of what constitutes a nursery habitat, particularly for rare or cryptic species that offer increased challenges to effective management. Batoids are one such group that are considered vulnerable to exploitation considering their ubiquitous abundance in tropical nearshore ecosystems and have received less attention in the literature, with fewer than 6% of recognised species being the focus of studies pertaining to nurseries (Martins et al. 2018).

The Atlantic chupare stingray *Styracura schmardae* (Werner 1904) (also known as the Caribbean whiptail stingray) is a large-bodied demersal ray recorded from the western-central and southwest Atlantic from Brazil to the Gulf of Campeche (Last et al. 2016). It has been reported in small-scale subsistence fisheries and noted as possible bycatch in larger-scale fisheries (Charvet-Almeida & de Almeida 2006). However, it is considered Data Deficient by the International Union for the Conservation of Nature (IUCN) and is rare throughout its known range (Nunes & Nunes 2020). Virtually all aspects of its life history are unknown, and its taxonomic resolution remains obscure, having recently been reclassified to the Potamotrygonidae (de Carvalho et al. 2016), which includes the neo-tropical freshwater river rays of South America. However, it has been proposed that the genus *Styracura* may belong to its own family, since *S. schmardae* and its Pacific counterpart *S. pacifica* are marine species (Last et al. 2016, Nunes & Nunes 2020). Currently, the largest described population of *S. schmardae* is from The Bahamas (O'Shea et al. 2017, Nunes & Nunes 2020), where its contemporary distribution was only reported relatively recently (O'Shea et al. 2017) and is currently the focus of several ongoing studies. This species has been recorded as a resident of tidal mangrove creek systems throughout the island of Eleuthera, the Exuma Cays and Great Exuma Island in The Bahamas (O'Shea et al. 2017).

The Bahamas Archipelago represents the largest shallow tropical ecosystem in the western Atlantic, with a total marine estate in excess of 640 000 km^2 and comprising over 3000 islands, cays and islets (Buchan 2000), creating fragmented and often discontinuous habitats with deep oceanic basins separating some of the larger outer islands. Providing realistic frameworks for the effective management of these environments is often exacerbated by limited resources and poorly defined protection for critical habitats and the species they support. Further, there is a need to address deficits in local economic needs as they pertain to the exploitation of these habitats that may be critical in the early life history of ecologically and economically important species. Historically, investigations into batoid nurseries and descriptions of physical or biological characteristics to describe them have been a source of high variability in the literature. For example, descriptions of nursery habitats have included coastal sandbanks and the occurrence of neonates, juveniles and pregnant females (e.g. Yokota & Lessa 2006); sandy, muddy or rocky benthic habitat correlated with egg density and distribution (for oviparous species) (e.g. Hoff 2008, 2009, Love et al. 2008, Martins et al. 2018); and high abundances of juveniles in reef lagoons with soft sediment substrates and patchy reefs (e.g. Cerutti-Pereyra et al. 2014).

The overall objective of this study was to describe the long-term site fidelity of *S. schmardae* that occupy specific size classes indicative of their life-history stage, and to provide evidence for a well-defined nursery environment for the species. Specifically, we aimed to (1) demonstrate the persistence of *S. schmardae* over time in a mangrove creek system in South Eleuthera, The Bahamas, through mark–recapture methods, (2) compare the physical benthic characteristics of this creek and 3 other creeks where this species was sampled and (3) provide additional empirical evidence to support the nursery habitat concept for *S. schmardae* in other creek systems in South Eleuthera, based on presence and shared physical features among creek systems with and without *S. schmardae* captures.

2. MATERIALS AND METHODS

2.1. Study sites

Eleuthera (25.2873° N, 76.3332° W) is a low-profile limestone island occupying the northeastern boundary of the Great Bahama Bank in the Family Islands

of The Bahamas. Shallow soft sediment habitats run along the western portion of the island, with deeper neritic habitats giving way to the Atlantic Ocean along the east (Fig. 1). South Eleuthera is characterized by shallow patch reefs, soft sediment expanses and tidal creek systems with close proximity to pelagic environments. We surveyed 4 creek systems of South Eleuthera with superficially homogeneous physical features; Deep Creek (24.770° N, 76.275° W), Wemyss Bight Creek (24.722° N, 76.220° W), Kemps Creek (24.810° N, 76.309° W) and Starved Creek (24.813° N, 76.186° W) (Fig. 2). Deep Creek (Fig. 2A) and Wemyss Bight Creek (Fig. 2B) both occupy the southern boundary of South Eleuthera, and are in close proximity to Exuma Sound, a deep-water inlet of the Atlantic Ocean (2.3 and 3.8 km, respectively). Kemps Creek is on the north side of Cape Eleuthera, approximately 8 km from Exuma Sound (Fig. 2C), and Starved Creek occupies an area that is immediately adjacent to the Great Bahama Bank, situated approximately 21 km east of Exuma Sound (Fig. 2D). For the purpose of this study, we concentrated our focus on Deep Creek as the largest of these systems, to use in our hypotheses of a model system for an early life history nursery for *Styracura schmardae*. Total sampling time among all creeks was 168.5 d (1011 h) based on 6 h field sampling periods constituting '1 day'. Of this, 120.5 d (723 h) were spent in Deep Creek, 24.5 d (147 h) in Kemps Creek, 17 d (102 h) in Wemyss Bight Creek and 6.5 d (39 h) in Starved Creek.

Deep Creek covers an area of approximately 34 km² and forms part of a larger, continuous mangrove ecosystem running parallel to shore for almost 19 km in a NW–SE orientation. The demarcation of Deep Creek, and several other individual creek systems along this trajectory (including Wemyss Bight Creek), are governed by the establishment of roads and culverts, separating what was 1 large system, into what is now considered 7 separate creek systems, although the high tide reconnects many of these systems. Deep Creek is fringed with large expanses of red mangrove *Rhizophora mangle* and is further characterized by large expanses of soft sediments. At high tide, mean water depth is <1 m, and at low tide, approximately 70% of benthic habitat is exposed, with a smaller, deeper channel (<3 m) near its mouth that generally retains water throughout the year. Its northern margin borders a small urban settlement named for this creek system, and runs approximately 5 km in the same orientation. Four kilometres to the southwest lies Exuma Sound, with a shallow (<30 m) neritic zone separating the two.
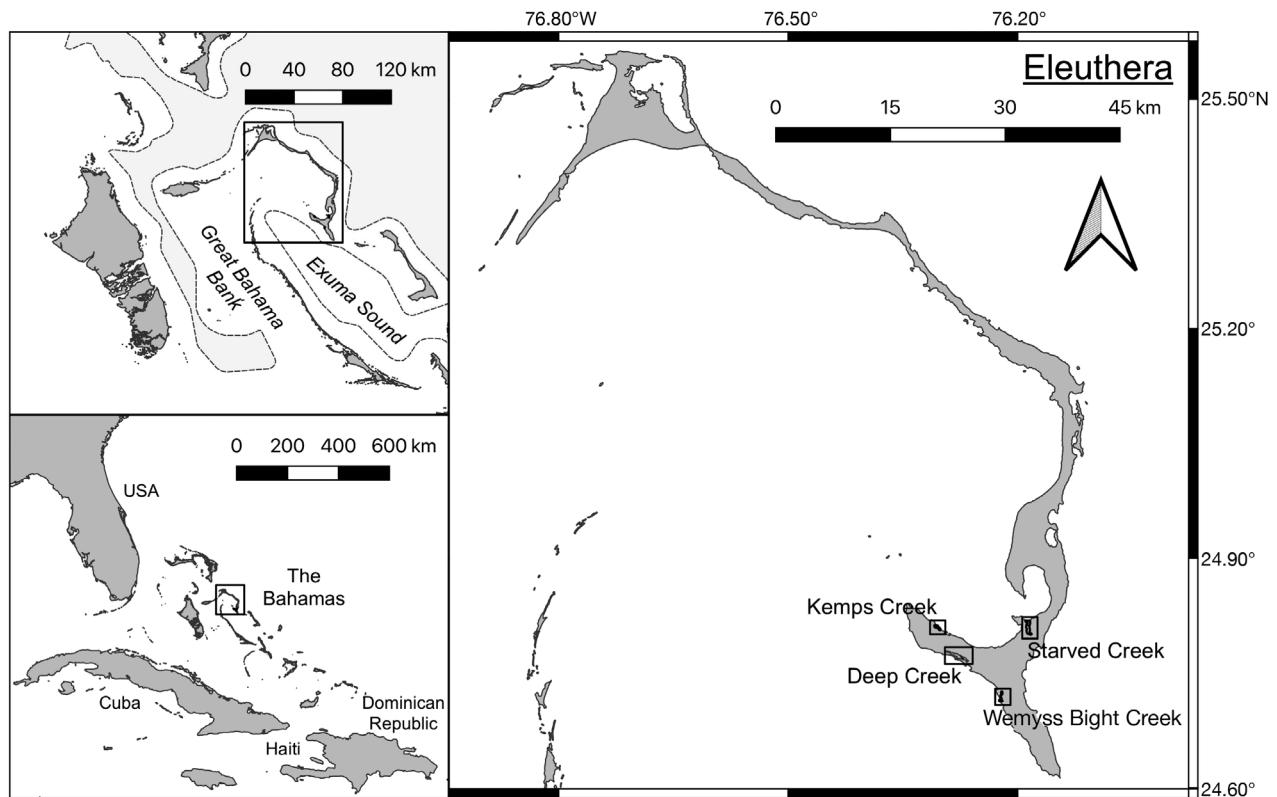

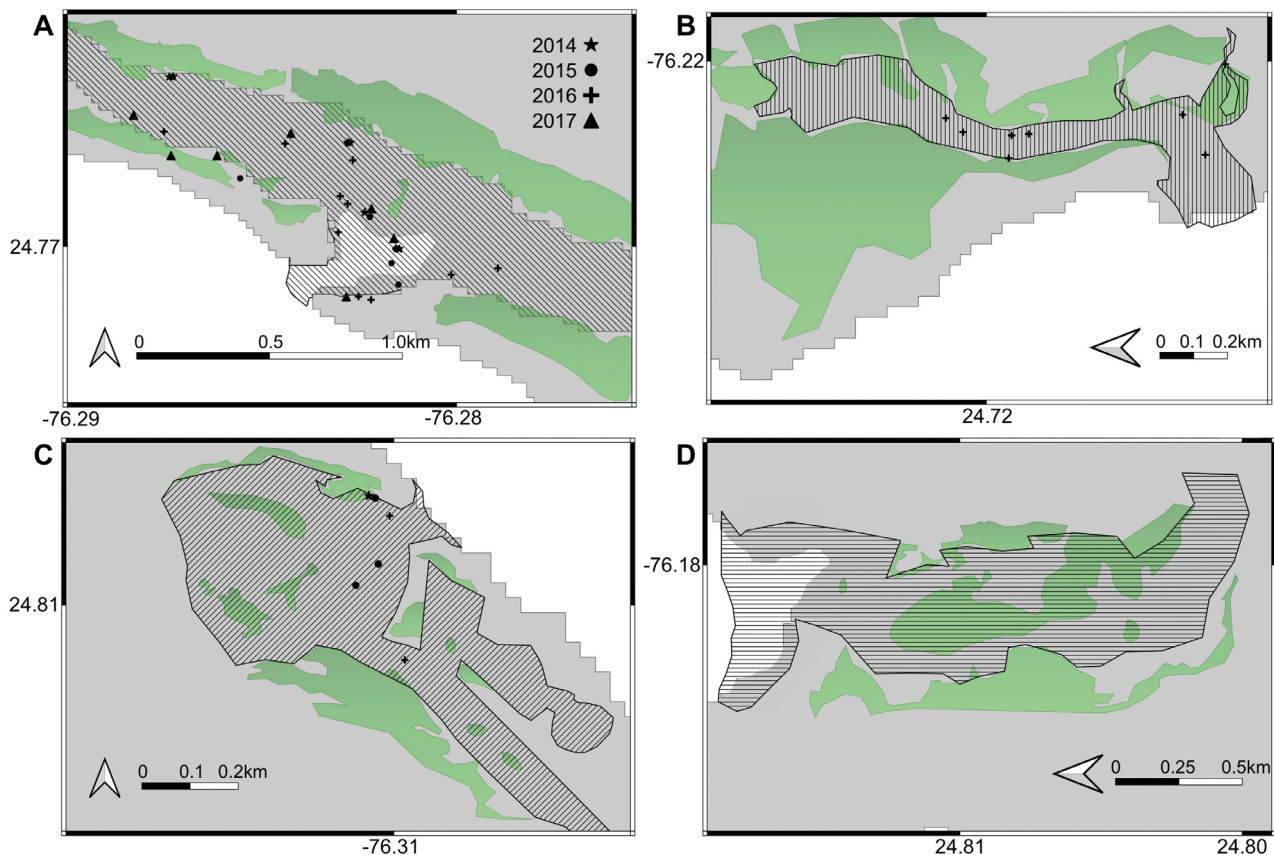Fig. 1. Eleuthera, The Bahamas, in relation to the wider Caribbean region and study site locations from South Eleuthera

Fig. 2. Initial capture and tagging locations of *Styracura schmardae* in (A) Deep Creek (n = 69), (B) Wemyss Bight Creek (n = 9), (C) Kemps Creek (n = 8) and (D) Starved Creek (n = 0), Eleuthera, The Bahamas, for 2014 (star), 2015 (circle), 2016 (cross) and 2017 (triangle). Shaded green area represents mangrove cover, hatched areas represent soft sediment, light gray shading represents tidal mediated shallow areas, and white areas represent subtidal channel water at the mouth. Note: Some stingray captures occurred at the same location and thus are hidden by overlapping capture points. All recaptured individuals were sampled from the creeks of original capture

2.2. Mark–recapture of *S. schmardae*

S. schmardae were caught using methods outlined by O'Shea et al. (2017) between April 2014 and August 2017. Briefly, rays were located through visual census before being herded into a barrier net controlled by 2 people on foot. Once the ray swam into the net, a smaller dip net was used to collect the animal safely. Venomous barbs were secured by a wet cotton cloth wrapped around the tail and held in place with Velcro straps. Surgical gloves were worn throughout any handling, and animals remained submerged in water for the duration. Upon capture, sex was determined by the presence or absence of claspers, and size was recorded by measuring disc width (W_D, mm). External dart tags (www.hallprint. com) were attached to the left-hand side pectoral fin in an area closest to the main body to ensure enough musculature was available to maintain the tag considering the small size classes of individuals sampled

(Fig. 3). Secondary to this, a passive integrated transponder (PIT) tag was injected under the skin in close proximity to the external tag. The combination of tags ensured that recaptured animals could be identified by sight, as well as by PIT tag should the external tag be lost. Serial numbers and unique identifying codes of each tag were recorded, and rays were released at the same site of capture less than 10 min after being caught.

2.3. Estimating maturity

Published estimates for size at maturity in this species remain absent from the literature, so we used a combination of empirical observations and literature sources to propose the first estimate of this metric for *S. schmardae*. Firstly, maturity in males was assessed by the calcification state of the claspers, and individuals sampled here up to 830 mm W_D were considered

Fig. 3. Juvenile *Styracura schmardae* demonstrating tag placement and size
(disc width of this individual = 254 mm)

were recorded at low tide, with sub-tidal points photographed via snorkelling and analysed *ex situ*. Finally, mangrove cover was calculated using Google Earth Pro V7.3.3.7786 (www.google.com/earth). Sediment depths were determined from 28 random points from each creek sampled, by inserting a 1.8 m wooden stake, marked at 10 cm increments into the sediments and recording the depth where the probe reached bedrock.

2.5. Calculations and statistical analyses

Residence times of individual rays were calculated by summing the day duration between the first date of capture and subsequent recaptures. Proportional cover for detritus, limestone, mangrove mud, sand, 'fuzzy finger' algae *Dasycladus vermicularis*, shoal grass *Halodule wrightii*, 'mermaid's shaving brush' *Penicillus dumetosus*, red mangrove prop roots and turtle grass *Thalassia testudinum* was calculated by dividing the percentage cover of each habitat type by the total percentage habitat cover and multiplying by 100 for each quadrat. An ANCOVA was used to determine if there was a significant effect of location, sex or W_D on residence time. A 1-way ANOVA was used to determine if there was a significant effect of location on detritus, limestone, mangrove mud, sand, *D. vermicularis*, *H. wrightii*, *P. dumetosus*, *R. mangle*, *T. testudinum* cover or sediment depth. If a significant location effect was found, we used Tukey's post hoc analysis to assess statistical differences ($p < 0.05$) among locations. All analyses were conducted using RStudio Desktop v.3.5.2 (RStudio Team 2019).

immature. This is supported by Last et al. (2016), who reported males were immature at 600 mm W_D, and O'Shea et al. (2017), who showed males (n = 28) were immature at mean ± SE W_D of 560 ± 33 mm. More recently, O'Shea et al. (2020) provided evidence for a potential ontogenetic shift in diet for this species based on increases in $\delta^{13}C$ at 815 mm W_D and in $\delta^{15}N$ at 911 mm W_D from a sample size of n = 94 which included individuals sampled here. Considering males and females in this species attain similar sizes throughout maturation periods (O'Shea et al. 2017), we therefore propose size at maturity in this species to be at approximately 850 mm W_D.

2.4. Benthic habitat surveys

Habitat surveys took place between June and September 2016. Firstly, using GIS software (www.arcgis.com), a polygon was generated to delineate the sampling area and a single transect line was positioned through the centre of the creek longitudinally. Secondly, points were generated every 200 m along this central axis, and from here, 3 additional random points were generated to the north, and then repeated to the south of this central line. At each of these subsequent points, a 1 m² quadrat was placed on the benthos and percentage cover was recorded for all biotic and abiotic components. This was then repeated on the other side of this sampling point, resulting in 2 quadrats per point, equating to a total of 192 replicate surveys for Deep Creek, 36 each for Wemyss Bight and Kemps Creek and 80 for Starved Creek. All data

3. RESULTS

3.1. Mark−recapture of *Styracura schmardae* across South Eleuthera creek systems

Three of the 4 creek systems sampled across South Eleuthera had captures and recaptures of at least 1 *S. schmardae*, with Starved Creek being the only site with no captures (Fig. 4A). In total, there were 190 capture events of 86 tagged individual rays (42 females and 44 males). Of the 86 tagged individuals,
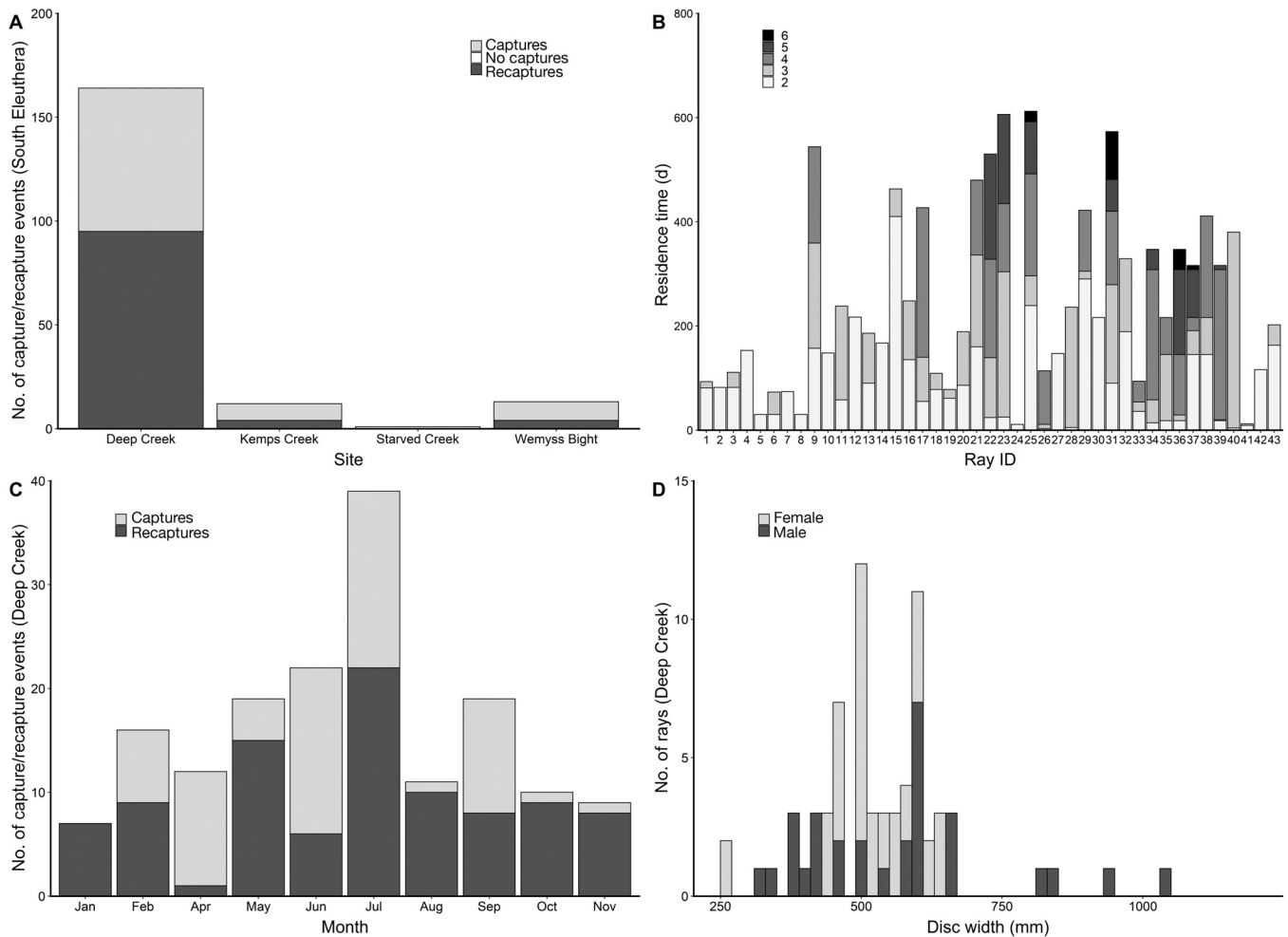
Fig. 4. Number of capture and recapture events and residence time for *Styracura schmardae* in relation to (A,B) the 4 study sites (Deep Creek, Kemps Creek, Starved Creek and Wemyss Bight Creek) in South Eleuthera, The Bahamas, creek systems (n = 86 individuals tagged, with 43 individuals recaptured at least once) and (C,D) the Deep Creek system (n = 69 individuals), by location (A), ray identification (B), month (C) and disc width (binned by 20 mm intervals) of individual rays at initial capture and tagging (D). Note: the 2 largest rays in panel (D) were mature males

51% were recaptured at least once, 36% at least twice and 2% 6 times between April 2014 and August 2017 (Fig. 4B). All recaptures occurred in the same creek system in which individuals were originally tagged, with the Deep Creek system having the highest prevalence of captures and recaptures (n = 164; Fig. 4A). Mean ± SD residency of all recaptured individuals was 243 ± 177 d, and did not differ among sites ($F_{2,38} = 0.82$, p = 0.45), sex ($F_{1,38} = 0.98$, p = 0.33) or W_D at time of original capture ($F_{1,38} = 0.004$, p = 0.95). Most (95%) of the rays were classified as immature and had a mean ± SD W_D of 553.9 ± 153.8 mm at time of capture (females = 515.1 ± 84.5 mm, males = 590.9 ± 192.5 mm).

3.2. Mark–recapture of *S. schmardae* in Deep Creek

Of the 190 total capture events among the 4 South Eleuthera creek systems sampled, 164 (86%) occurred specifically in the Deep Creek system. In total, 69 individual rays were tagged (39 females and 30 males) in Deep Creek, with 57% recaptured at least once, 40% at least twice and 3% 6 times between April 2014 and August 2017. All capture events in 2017 were recaptures. Capture events were highest in July and occurred across all months, except March (Fig. 4C). However, little to no sampling occurred during this month. Mean ± SD resi-

dence time of recaptured individuals was 253 ± 179 d. Almost all (97%) of the rays caught in Deep Creek were classified as immature (39 females and 27 males) and had a mean ± SD W_D of 538.2 ± 132.4 mm (females = 517.9 ± 85.8 mm; males = 564.6 ± 173.7 mm; Fig. 4D).

3.3. Habitat characteristics

There was a significant effect of location for limestone ($F_{3,339}$ = 18.02, p < 0.001), mangrove mud ($F_{3,339}$ = 46.95, p < 0.001), sand ($F_{3,339}$ = 62.74, p < 0.001), *Dasycladus vermicularis* ($F_{3,339}$ = 23.68, p < 0.001), *Halodule wrightii* ($F_{3,339}$ = 9.23, p < 0.001), *Rhizophora mangle* ($F_{3,339}$ = 3.14, p = 0.03), *Thalassia testudinum* ($F_{3,339}$ = 11.15, p < 0.001) and sediment depth ($F_{3,70}$ = 39.66, p < 0.001) (Table 1, Fig. 5). However, Deep Creek, the site with the highest prevalence of captures and recaptures, only differed by having the highest sand cover and deepest mean sediment depth (Table 1, Fig. 5A,C). Additionally, Starved Creek, the site with no captures of *S. schmardae*, was the only site with limestone cover and had the shallowest sediment depth among sites (Table 1, Fig. 5A,C).

Table 1. Statistical summary of the various dependent variables used in an ANOVA to test for the effect of location. A Tukey post hoc analysis was used to assess statistical differences (*p < 0.05) among locations. **Bold** text indicates dependent variables that were either different between Deep Creek, which had the highest prevalence of captures and recaptures of *Styracura schmardae,* and all other locations, or between all locations where *S. schmardae* were captured and Starved Creek, where no *S. schmardae* were captured

Benthic habitat	Dependent variable	Explanatory variable	Tukey post hoc comparison	df	F	Diff.	p
Abiotic	Detritus	~Site		3, 339	0.22		0.880
Abiotic	**Limestone**	**~Site**		**3, 339**	**18.02**		**<0.001***
			Kemps Creek–Deep Creek			**0.00**	**1.000**
			Starved Creek–Deep Creek			**9.80**	**<0.001***
			Wemyss Bight–Deep Creek			**0.00**	**1.000**
			Starved Creek–Kemps Creek			**9.80**	**<0.001***
			Wemyss Bight–Kemps Creek			**0.00**	**1.000**
			Wemyss Bight–Starved Creek			**9.80**	**<0.001***
Abiotic	Mangrove mud	~Site		3, 339	46.95		<0.001*
			Kemps Creek–Deep Creek			42.51	<0.001*
			Starved Creek–Deep Creek			13.66	<0.001*
			Wemyss Bight–Deep Creek			1.60	0.970
			Starved Creek–Kemps Creek			−28.85	<0.001*
			Wemyss Bight–Kemps Creek			−40.91	<0.001*
			Wemyss Bight–Starved Creek			−12.06	0.02*
Abiotic	**Sand**	**~Site**		**3, 339**	**62.74**		**<0.001***
			Kemps Creek–Deep Creek			**−56.34**	**<0.001***
			Starved Creek–Deep Creek			**−33.43**	**<0.001***
			Wemyss Bight–Deep Creek			**−18.52**	**<0.001***
			Starved Creek–Kemps Creek			**22.90**	**<0.001***
			Wemyss Bight–Kemps Creek			**37.81**	**<0.001***
			Wemyss Bight–Starved Creek			**14.90**	**0.03***
Abiotic	**Sediment depth**	**~Site**		**3, 70**	**39.66**		**<0.001***
			Kemps Creek–Deep Creek			**−55.23**	**<0.001***
			Starved Creek–Deep Creek			**−80.77**	**<0.001***
			Wemyss Bight–Deep Creek			**−27.87**	**0.003**
			Starved Creek–Kemps Creek			**−25.53**	**0.010**
			Wemyss Bight–Kemps Creek			**27.36**	**0.006**
			Wemyss Bight–Starved Creek			**52.90**	**<0.001***
Biotic	*Dasycladus vermicularis*	~Site		3, 339	23.68		<0.001*
			Kemps Creek–Deep Creek			16.00	<0.001*
			Starved Creek–Deep Creek			9.65	<0.001*
			Wemyss Bight–Deep Creek			4.40	0.200
			Starved Creek–Kemps Creek			−6.35	0.05*
			Wemyss Bight–Kemps Creek			−11.59	<0.001*
			Wemyss Bight–Starved Creek			−5.24	0.150

Table 1 (continued)

| Benthic habitat	Dependent variable	Explanatory variable	Tukey post hoc comparison	df	F	Diff.	p
Biotic	*Halodule wrightii*	~Site		3, 339	9.23		<0.001*
			Kemps Creek–Deep Creek			−0.29	0.990
			Starved Creek–Deep Creek			2.59	0.03*
			Wemyss Bight–Deep Creek			5.97	<0.001*
			Starved Creek–Kemps Creek			2.89	0.160
			Wemyss Bight–Kemps Creek			6.26	<0.001*
			Wemyss Bight–Starved Creek			3.38	0.070
Biotic	*Penicillus dumetosus*	~Site		3, 339	2.16		0.090
Biotic	*Rhizophora mangle*	~Site		3, 339	3.14		0.03*
			Kemps Creek–Deep Creek			−1.12	0.820
			Starved Creek–Deep Creek			−2.59	0.030
			Wemyss Bight–Deep Creek			−2.51	0.210
			Starved Creek–Kemps Creek			−1.48	0.730
			Wemyss Bight–Kemps Creek			−1.39	0.840
			Wemyss Bight–Starved Creek			0.08	1.000
Biotic	*Thalassia testudinum*	~Site		3, 339	11.15		<0.001*
			Kemps Creek–Deep Creek			−0.05	1.000
			Starved Creek–Deep Creek			−0.60	0.920
			Wemyss Bight–Deep Creek			7.11	<0.001*
			Starved Creek–Kemps Creek			−0.55	0.980
			Wemyss Bight–Kemps Creek			7.16	<0.001*
			Wemyss Bight–Starved Creek			7.71	<0.001*
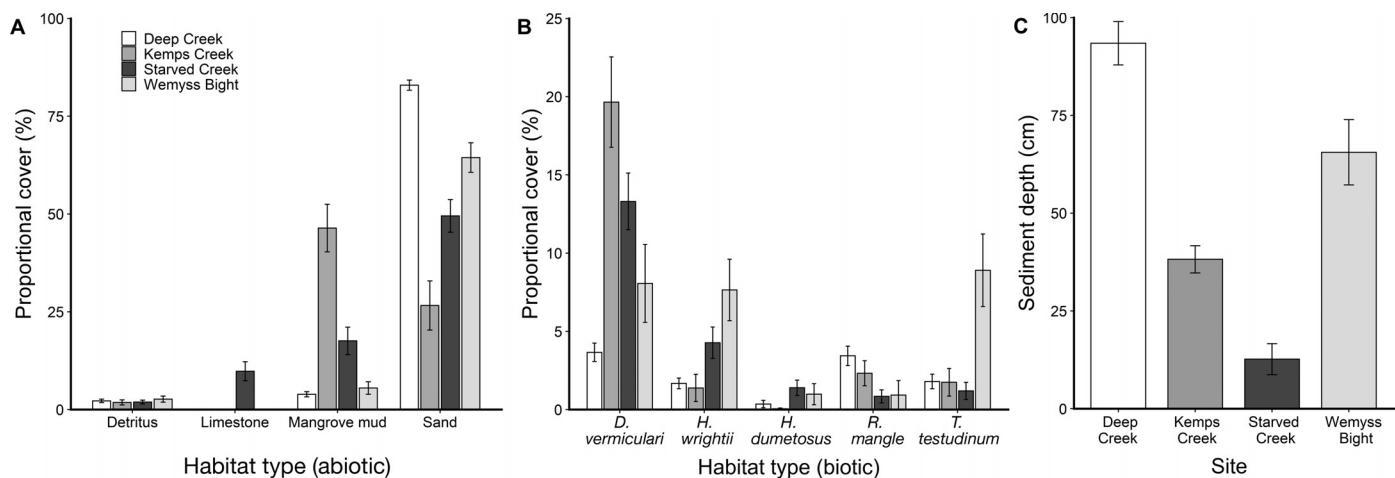
Fig. 5. Mean ± SE proportional cover of various (A) abiotic and (B) biotic benthic habitat types, and (C) sediment depths among 4 creek systems from South Eleuthera, The Bahamas (Deep Creek, Kemps Creek, Starved Creek and Wemyss Bight Creek). Species names listed in panel (B) are given in full in Table 1

4. DISCUSSION

Here, we describe for the first time the physical characteristics of coastal creek habitats that play a potentially critical role in the early life history of a rare and cryptic batoid from The Bahamas. In addition to mark–recapture methods, and following criteria published by Heupel et al. (2007), these data offer compelling evidence for the formal identification of the first batoid nursery in The Bahamas, and provides additional characteristics to define early life refugia for *Styracura schmardae*. Of the 4 creek systems sampled, Deep Creek is undeniably an important habitat for juveniles of this species, as supported by multiple recapture events of the same individuals over multiple years, and 97% of rays sampled in this

creek observed to be sexually immature. This notion is further supported by fulfilling criteria, in that (1) this species was encountered in higher abundance within this site relative to other sites, (2) individuals show persistent site fidelity over extended periods of time, and (3) this creek is used repeatedly among years, in this case, 1222 d (3 yr and 4 mo). Wemyss Bight and Kemps Creek also recorded this species for both capture and recapture events, whereas Starved Creek recorded a total absence of the species.

Deep Creek had the highest proportional cover and depth of soft sediment of all sites which correlated with the highest abundance of *S. schmardae* encountered and sampled. Despite fewer encounter rates of rays in Wemyss Bight and Kemps Creek, these locations should not be excluded as potential nursery habitats, and may also be acting as important refugia areas for early life individuals. Location was statistically non-significant for these 3 creeks where *S. schmardae* were observed, suggesting that homogeneous physical attributes indeed correlate to the presence and persistence of this species. Despite capture and recapture rates being lower than at Deep Creek, both Wemyss Bight and Kemps Creek recorded 9 individuals, of which 3 were recaptured over 3 periods up to and exceeding 1 yr. Based on this, we hypothesise that all 3 creeks are likely acting as nursery environments for the species. However, further work is required, especially greater sampling effort, to fully validate this hypothesis. This was exemplified by Froeschke et al. (2010), who tested 9 bays along the Texas coast using the same criteria from Heupel et al. (2007) to assess nursery habitats for young of the year (YOY) and juvenile bull sharks *Carcharhinus leucas*. While their results demonstrated that only 1 of these bays fulfilled all 3 criteria, it was certainly plausible that 1 or more of the other bays was acting as a nursery; nevertheless, the authors suggested that further considerations and investigations were required to definitively draw these conclusions. This was largely based on the abundance of YOY sharks being similar to the estimated mean population abundance. In our case, while Wemyss Bight and Kemps Creek are likely serving as early life-history refugia for *S. schmardae*, data presented here cannot definitively demonstrate this when considering these 3 criteria.

Nursey area concepts suggest that batoids will be drawn to these locations based on permutations of biotic and abiotic factors (Martins et al. 2018), and while these features will vary among species and locations, data presented here strongly indicate that soft sediment cover and sediment depth are impor-

tant drivers in the presence/absence of this species at our study sites. This was most apparent when considering that we made no observations of *S. schmardae* at Starved Creek, which was correlated with increased limestone cover within the benthoscape and further had the shallowest sediment depths of the 4 creeks sampled. The absence of *S. schmardae* at this site seems intuitive, considering the reliance of many batoids on soft sediment environments for feeding (O'Shea et al. 2012). Further, increased proportions of soft sediment allow for concealment from predators, increasing the survivorship of juvenile rays, which is postulated to be an important process when considering nursery habitats and their role in supporting adult populations through increased survival probability and the subsequent net export of individuals through ontogenetic migration (Beck et al. 2001).

Addressing the very few studies from the literature that describe elasmobranch nurseries, approximations can be made that align with specific characteristics presented here. For example, recurring features of elasmobranch nurseries include shallow water (Costa et al. 2015, Davy et al. 2015), soft sediment expanses (Yokota & Lessa 2006, Cerutti-Pereyra et al. 2014) or turbid water (Cerutti-Pereyra et al. 2014, Costa et al. 2015). Based on these descriptions, it seems that the most commonly accepted variables when defining nursery habitats are related to prey availability and protection from predators. However, given the scarcity of studies on the philopatry of juvenile batoids, it is important to consider the very strong taxonomic and habitat biases (Heupel et al. 2019), requiring further scrutiny to address the high variability of species-specific requirements. A habitat bias is certainly a possibility here, where during the course of our sampling, we encountered very few southern stingrays *Hypanus americanus* (n = 11), all of which were adults. Whilst our results imply that the physical parameters at our study site represented favourable conditions for *S. schmardae*, this may not have been the case for *H. americanus*, which are common and encountered in high abundance throughout South Eleuthera (Schwanck et al. 2020).

Therefore, based on site-specific characteristics and individual requirements, species may partition abiotic or biotic variables along some form of ecological gradient that will influence occupation of these nursery habitats. Davy et al. (2015) described tidal-mediated shifts in refuge habitat used by the mangrove whipray *Himantura granulata* from north Queensland, Australia, which at high tide sought structurally complex habitats such as the prop roots

of red mangroves, whereas at low tide, they sought refuge in coral reef habitats. While the creeks studied here do not entirely empty of water during low tide events, predictable aggregations were observed in deeper channels near the mouth at low tide, while at high tide, *S. schmardae* individuals would often be located among prop roots, especially in Deep Creek. Further, Dabruzzi et al. (2013) were able to demonstrate that juvenile ribbontail stingrays *Taeniura lymma* occupied a very specific thermal niche, allowing them to persist at a higher temperature relative to other species, possibly to exploit trophic resources or avoid predators.

Observations presented here address just 1 species of ray occupying these creek ecosystems, and therefore the sole occupancy by this species may represent partitioning of spatial resources, although further work would be needed to demonstrate this beyond speculation. Previous and current observations suggest that this species is social, with adults observed in mixed-sex aggregations of up to 17 individuals (O'Shea et al. 2017); here, individuals were typically encountered in loose, mixed-sex aggregations of several individuals. This leads us to postulate that there may be an as yet unknown factor driving the occupation of these creeks by *S. schmardae*, possibly a lack of predators and/or sympatric species of juvenile rays. Schwanck et al. (2020) recently described the genetic connectivity and sex-biased dispersal in *H. americanus* from 9 sites in South Eleuthera, including Deep and Kemps Creeks. Of the 200 individual rays sampled for their study, only 13 were caught in these creeks, including a single recapture from each site (Deep Creek n = 7, Kemps Creek n = 6); of these, 62% (n = 8) were immature and the 2 recaptured individuals were both mature. These results strongly suggest heterogeneous habitat requirements when compared to *S. schmardae*, and this was consistent throughout the assessment by O'Shea et al. (2017) of the contemporary distribution of the latter species in The Bahamas. That study sampled 32 sites across a spatial scale of 270 km and reported that size frequency distributions of *S. schmardae* were significantly correlated with habitat type, whereby individuals (n = 55) with a mean W_D of <572 mm were found exclusively in tidal mangrove creeks, and individuals with a mean W_D of 1168 mm were observed exclusively in sub-tidal, offshore locations (n = 15). This certainly supports the impression that tidal mangrove creek systems are serving as some kind of early life refugia for the species. However, an expanded and more rigorous assessment of these 32 sites would be required to definitively determine if they are acting as nurseries, following the criteria established by Heupel et al. (2007).

Finally, O'Shea et al. (2020) sampled 94 individual *S. schmardae,* from 23 sites along the same spatial gradient as O'Shea et al. (2017), and assessed the trophic ecology of this species through stable isotope analysis. Individual rays were caught from 3 habitat types; tidal mangrove creeks (including Deep Creek, Wemyss Bight and Kemps Creek), offshore yet within 200 m of tidal mangrove creeks and offshore subtidal sand flats and soft sediment expanses of the Great Bahama Bank. Results of a break-point analysis suggested that white muscle $\delta^{15}N$ was more enriched at 911 mm W_D (95% confidence interval [CI]: 770–1201 mm) by almost 2‰ compared to individuals <911 mm W_D, suggesting an increase in the trophic level at which they were foraging. Additionally, $\delta^{13}C$ increased in individuals by 2.14‰ at 815 mm W_D (95% CI: 745–1042 mm). These data are highly indicative of an ontogenetic shift in diet that is likely explained by foraging at increased spatial scales, suggesting it is at or around these sizes that they possibly leave the shelter of these creeks and make ontogenetic migrations to adult populations associated with more offshore habitats. This further supports the notion that *S. schmardae* are spending significant time up to a certain size in these creek habitats. This is likely to be the first size at maturity estimate for this species, certainly for The Bahamas, corroborated here by the persistence of size classes <850 mm W_D in these creek systems.

5. CONCLUSIONS

A high number of *Styracura schmardae* are located throughout the creek systems of South Eleuthera, and the evidence we present here strongly suggests that Deep Creek is serving as a nursery habitat for the species. Understanding parameters and environmental characteristics of similar habitats will underpin further research efforts to identify more of these areas, so effective management strategies can be implemented, particularly in areas close to urban environments which may experience higher levels of vulnerability due to anthropogenic activity. While data described here focussed on a single species, it corroborates important factors required for other species of batoids to propagate as juveniles in mangrove creek systems, and should be considered for future assessments of other tropical batoids.

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