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ORIGINAL ARTICLE

Description of the behavioural contexts of underwater sound production in juvenile green turtles *Chelonia mydas*

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Abstract

Green sea turtles *Chelonia mydas* have the ability to hear and produce sounds under water, with some of them potentially involved in social communication. To investigate the potential biological function of these sounds, we used a combination of acoustic, video and multi-sensor recordings of 23 free-ranging juvenile green turtles and we examined the co-occurrences of sounds with behaviours or external events. Our study revealed that most of the sounds were produced when the sea turtles were resting or swimming. However, four sound types were produced in more specific contexts. Long sequences of rumbles were recorded after sunset and mainly during resting. All these rumbles appear to have been produced by several individuals recorded simultaneously, suggesting that rumbles may be used for social interactions. The frequency modulated sound was highly associated with scratching behaviour. The grunt that was produced occasionally when green turtles were vigilant or approaching a conspecific. The long squeak was produced significantly by a small number of individuals in the presence of humans. The grunt and the long squeak may be the first evidence of an alarm or warning signal for intra-specific communication in green turtles. Our results mark a significant milestone in advancing the understanding of sound production in the behavioural ecology of sea turtles. Further experimental investigations (i.e., playback experiments) are now required to test the hypotheses suggested by our findings. Warning signals could be used to prevent sea turtles of a danger and may contribute to their conservation.

Significance statement

Underwater sound production in Chelonioidea is yet not well documented. We investigated the contexts of sound production in green sea turtles. Our results show that juvenile green sea turtles produced at least 4 identified sounds in specific contexts. This is a crucial step, as it will provide a solid basis for understanding the acoustic behaviour of green sea turtles and for improving current conservation methods. To date, the lack of knowledge on sea turtle behavioural ecology and acoustic communication hinders the implementation of mitigation measures to effectively reduce mortality and disturbance from human activities. Our findings offer the possibility of using species-specific sounds in a deterrent system to prevent them from potentially dangerous areas, including areas where seismic surveys, construction work, or areas with fishing activities (fishing

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nets) occurs with the aim of reducing the risk of temporary or permanent hearing damage or accidental by-catch.

Keywords Behaviour · *Chelonia mydas* · Chelonians · Juveniles · Underwater sound production

Introduction

Intraspecific communication plays a crucial role in social interactions such as finding a mate, interacting within social partners (particularly during foraging or alerting to the presence of a predator), and providing care to offspring (Bradbury and Vehrencamp 2011). There are many ways of conveying information, with acoustic signals being among the most widely recognised and studied signals (Bradbury and Vehrencamp 2011). Among vertebrates, sound production has been well studied in birds, mammals and anurans but much less is known about non-avian reptiles which are regarded to produce sounds relatively rarely in comparison (Vergne et al. 2009; Jerem and Mathews 2021; Russell and Bauer 2021). Several studies have been conducted on freshwater turtles, but little is known about sea turtle sound production.

Sound production in freshwater turtles (in air and under water) and acoustic communication has recently been demonstrated (Ferrara et al. 2013, 2014b, 2017; Papale et al. 2020; Jorgewich-Cohen et al. 2022), suggesting that the produced sounds could be involved in social behaviour (e.g. oblong turtle *Chelodina oblonga*, Giles et al. 2009; arrau turtle *Podocnemis expansa*, Ferrara et al. 2014c, d). These findings marked the initial phase of challenging prevailing concepts regarding chelonian sound production and social behaviours (Charrier et al. 2022). Until the early 2000s, sea turtles were considered a ‘silent group’ (Campbell and Evans 1972).

Additionally, due to the absence of a visible tympanum in sea turtles (possessing only the middle and inner ear without an external ear, Bartol and Musick 2002), they have historically been considered as deaf. However, behavioural and electrophysiological studies have shown their hearing abilities in air and under water (DeRuiter and Larbi Doukara 2012; Lavender et al. 2014). Hearing seems to be well adapted to their underwater environment, as the subtympanic fatty tissue of sea turtles has a density similar to that of water, which reduces sound attenuation and optimises sound transmission to the inner ear (Ketten 2008). The juvenile sea turtles’ underwater hearing ability ranges between 50 and 1600 Hz with maximum sensitivity between 200 and 400 Hz for green *Chelonia mydas* (Piniak et al. 2016), 50 and 1100 Hz with maximum sensitivity between 100 and 400 Hz for loggerhead *Caretta caretta* (Lavender et al. 2014), 100 and 500 Hz with maximum sensitivity between 100 and 200 Hz for Kemp’s ridley *Lepidochelys kempii* (Bartol and Ketten 2006) and 50 and 1200 Hz with maximum sensitivity between 100 and 400 Hz for hatchlings leatherback *Dermochelys coriacea* (Piniak et al. 2012).

Airborne sound production was observed and characterised in nesting female sea turtles, such as the leatherback (Carr 1952; Mrosovsky 1972; Lutcavage and Lutz 1996; Cook and Forrest 2005). Additionally, sound production was demonstrated in embryos and hatchlings of several sea turtles species, such as hawksbill *Eretmochelys imbricata* (Monteiro et al. 2019), Kemp’s ridley (Ferrara et al. 2019), green (Ferrara et al. 2014a, b), olive ridley *Lepidochelys olivacea* (Ferrara et al. 2014b; McKenna et al. 2019), and leatherback (Ferrara et al. 2014b, c). However, the biological function and sound production mechanisms are not well understood, and further studies are required to draw conclusions regarding the occurrence of acoustic communication in these species (McKenna et al. 2019). Studies carried out on other hatching non-avian reptiles have demonstrated sound production in crocodilians, such as the Spectacled caiman *Caiman crocodilus* and American alligator *Alligator mississipiensis* (Garrick and Garrick 1978; Britton 2001; Higgs et al. 2002; Vergne et al. 2009). In the Nile crocodile *Crocodylus niloticus*, it was shown that sounds produced by the embryos can synchronise hatching, aiding their emergence from the nest (Vergne and Mathevon 2008). Nevertheless, the sounds produced by sea turtle embryos do not appear to synchronise hatchlings in olive ridley, green and leatherback sea turtles (McKenna et al. 2019; Nishizawa et al. 2021).

Underwater sound production in sea turtles has been neglected likely due to the difficulties to record sea turtles in their natural environment. The development of multisensory tags with hydrophone has opened new research questions including the study of underwater acoustic production of free-ranging wild sea turtles (Charrier et al. 2022). The first underwater sounds described in juvenile green sea turtles (Charrier et al. 2022) exhibited similarities with the general acoustic structure of the underwater sounds produced by the oblong turtle and Kemp’s ridley sea turtle hatchlings (Giles et al. 2009; Ferrara et al. 2019). However, both frequency and temporal features varied across these studies, attributable to size differences between hatchlings and juveniles. In each of the three species studied (i.e. oblong, Kemp’s ridley and green), sound production ranged from simple pulses to more complex sounds endowed with a harmonic structure and a frequency modulation pattern. The source of sounds described in Charrier et al. (2022) was supported by control recordings carried out in the green turtle natural habitat, but without the presence of green turtles nearby. Indeed, recordings showed that while some detected sounds were similar in their main structure, the frequency and/or temporal characteristics were different from the sounds produced by green sea turtles. These variations suggest that some of these sounds were likely produced by other marine species, such as crustaceans or fishes, present in the green turtle's habitat. Although the biological function of sound production is not fully understood, Charrier et al. (2022) demonstrated that turtles' squeaks were individual-specific and could potentially be used for individual recognition. Furthermore, all recorded individuals produced sounds at frequencies within the hearing range of green turtles, suggesting potential implications for social communication. Other sounds in their repertoire, such as the rumble, the toc and the Frequency Modulated Sound (FMS) are within the best auditory sensitivity of juvenile green turtles (the frequency of the highest energy of these sounds ranging from 200 to 400 Hz), but they did not show any individual identity. These sounds may thus be involved in intraspecific communication, but are probably not involved in individual recognition processes.

The aim of the present study was to investigate the behavioural contexts during which free-ranging juvenile green turtles, equipped with a biologger CATS Cam (Customized Animal Tracking Solution, Germany), a multi-sensor tag associated with a video camera and one hydrophone, produced sounds, thereby providing insights into their associated biological functions. To automatically identify their behaviour, we used a deep learning algorithm (Jeantet et al. 2021), trained to predict the observed behaviour of green turtles from data recorded by the CATS Cams device (from the accelerometer, gyroscope and depth).

METHODS

Study Site and Data Collection from Free-ranging Green turtles

This study was carried out from May 2018 to May 2022 in coastal waters of Grande Anse d'Arlet (14°30.158' N, 61°5.271' W), Anse Noire (14°31.683' N, 61°5.320' W) and Anse Dufour (14°31.562'N, 61°5.425'W), Martinique island (French West Indies), where juvenile green turtles recruit. They originate from various Caribbean and Atlantic nesting sites (Chambault et al. 2018). There they spend several years, feeding on seagrass beds located in shallow sheltered bays (Siegwalt et al. 2020; Lelong et al. 2024). Once they reach a size close to sexual maturity (i.e. at around 80 cm curved carapace length), they embark on a major post-developmental migration and they join Caribbean and Atlantic adult feeding grounds (Chambault et al. 2018). Juvenile green turtles were captured along the coast by freedivers at various sites with depths up to 25 m. The capture of each turtle was performed by up to three freedivers when the turtle was static (i.e. resting or feeding on the sea floor). The freediver silently dived towards the turtle to avoid detection and once close enough and above the animal, seized the nuchal shell and pygales plate. The freediver then positioned the turtle against his chest with the hind flippers against his breastplate and rose to the surface. A second diver held the fore flippers and helped to lift the turtle on to the deck of the boat for measurements and tagging (Nivière et al. 2018; Bonola et al. 2019). Once on a boat, each individual was identified by scanning its Passive Integrated Transponder (PIT) or tagged with a new PIT if it was unknown, as described in Siegwalt et al. (2020) and Lelong et al. (2024). Identifying individuals with PIT tags enables the population demography to be monitored, particularly during Capture-Mark-Recapture campaigns in these areas. The CATS Cams device was attached to the carapace using four suction cups, as described in Jeantet et al. (2020). This suction cup attachment method avoids the use of glue on the carapace. Air was manually expelled from the cups, which were held in place by the use of a galvanic timed-release system, used to limit the duration of the deployment. The dissolving of galvanic timed-release system by seawater and the slightly positive buoyancy of the device (23.3 × 13.5 × 4 cm for 785 g) led to the remote release of the device with the removal of the suction cups from the shell several hours to two days later, thus avoiding the need to recapture the turtle and minimising the stress associated with a second capture to recover the device. A CATS Cams device included a video-recorder (1920 × 1080 pixels at 30 frames.s^{-1}, viewing angle of 100°) combined with a tri-axial accelerometer, a tri-axial gyroscope, a tri-axial magnetometer, time-depth recorder, hydrophone (HTI 96 min, frequency response: 2 Hz to 30 kHz, sensitivity: -165 dB re 1 V/mPa), thermometer, luminosity and a GPS tracker. All auxiliary data were sampled at 20 Hz. Devices were recovered using a goniometer (RXG-134, CLS, France) by geolocation of an Argos SPOT-363 A tag (MK10, Wildlife Computers Redmond, WA, USA), glued to the CATS Cams device. Due to low light conditions after sunset, the cameras were programmed to record from 05:00 to 19:00, but others sensors are still recording. CATS Cams devices were deployed on 23 juvenile green turtles (8 in 2018 were included in the study by Charrier et al. 2022, p. 10 in 2021 and 5 in 2022). Due to the different configurations between 2018 and the following years, or the early release of the device, only 12 of the 23 devices were recording after sunset. A total of 247 h of recorded tag data (sound, video and accelerometer) were investigated, with an average duration of recording of 10h44 (range: 3h24–18h37, $n = 23$), Recording started at 7:45 am at the earliest and stopped at 03:23 am next day at the latest. However, the retained part of the deployments for the analyses (data usable without uncertainty, i.e. no behaviour could be identified from the accelerometer data) lasted 207 h in total.

All data were collected in the wild from free-ranging animals, thus it was not possible to use blinded methods.

Acoustic recordings and analyses

CATS Cams device recorded acoustic data in mono at a frequency sampling rate of 24 kHz (16 bit). Listening and spectrogram labelling of sound files were performed using Avisoft SASlab Pro (Avisoft Bioacoustics, Version 5.3.01, 14 May 2022). A label starts at the beginning of the sound (turtle sounds or boat noise) and stops at its end. To improve visualisation of the sounds on spectrograms (Hamming, Fast Fourier Transform [FFT] size 1024 pts), all sound files were down sampled at 22 kHz, as there was no energy for frequencies above 10 kHz.

Sounds, behaviours and external events labelling

Eleven sound types were considered in the present analysis (Table 1). Ten of which (mono, doublet, triplet, multipulse, toc, croak, rumble, FMS, short squeak and long squeak) have been described in the juvenile green turtle sound repertoire in Charrier et al. (2022). They were classified into four main sound categories: pulse, Low Amplitude Call (LAC), FMS and squeak. The grunt is a new sound type and a new sound category not previously described (see Fig. S1 in the Supplementary Information for spectrograms of the eleven sounds type).

We defined six main behavioural categories (feeding, gliding, resting, scratching, swimming and surface activity, Table 1; see Jeantet et al. 2020; for the behavioural definitions). For data collected in 2018, behaviours were visually analysed and defined using the software VLC media player (version 3.0.18 Vetinari, 13 October 2022; VideoLAN, Paris, France). For the analysis of data collected in 2021 and 2022, we used a deep learning algorithm coded in custom Python scripts to automatically identify the behaviours from the accelerometer, gyroscope and depth (Jeantet et al. 2021). The algorithm was trained on the behaviour dataset labelled from the visual analysis of the 2018 video files. Details on this algorithm can be found in Jeantet et al. (2021). The behaviours obtained with this method included different variants and were pooled into five behavioural categories (feeding, gliding, resting, scratching, and swimming). In the same manner, the sixth behaviour labelled surface activity, included all activities (e.g. breathing, basking) occurring between 0 and 0.3 m depth (depth data was collected from the CATS Cams device). With this method, surface activity is not exclusive, and occurs at the same time as the turtle is swimming, as in the study by Jeantet et al. (2020). Similar to sound labelling, a label started at the beginning of the behaviour and stopped at its end.

In addition to monitoring behaviour, three external events (boat noise and presence of conspecifics or humans, Table 1) were recorded to assess their potential impact on sound production of the turtles. All video files were processed using the software VLC media player so that the timing of each external event of interest was recorded, using slow motion and frame-by-frame modes if necessary. External events, including the presence of a conspecific or a human, were considered if at least one turtle other than the equipped turtle or at least one human was visible in the camera field with direct interaction (e.g. touching, smelling, biting and intimidating for turtles; following and touching the turtle for humans) or without (e.g. resting, swimming, feeding for turtles; being in the water, swimming, snorkelling for humans). If the conspecific or the human left the camera's field of view and then can be observed again at a later stage (i.e., beyond the next two minutes), then the label ended at the end of the first observation, and the second observation was considered as a new observation and a new label was thus created. Indeed, during the "blind period", we cannot be sure that the same individual stayed in the vicinity of the equipped green turtle. Finally, the boat noise events (i.e. boat motor noise) were detected on the audio recordings.

Since the different loggers could start in a non-synchronous way, the behaviours detected from the accelerometer data using the automatic classification algorithm (Jeantet et al. 2021) were synchronised with the sound data using external events (e.g. breathing at surface).

Dummy Coding Procedure

To assess the behavioural context of underwater sound production in juvenile green turtles, we investigated the co-occurrence of sounds with behaviours and external events.

Table 1 List of the labels for the sounds, behaviours and external events (see fig. S1 in the supplementary information for spectrograms of sounds type)

Sounds				Behaviour	External Events
Pulse	1. Mono	Grunt	7. Grunt	I. Feeding	A. Boat noise
	2. Doublet	LAC	8. Croak	II. Gliding	B. Conspecific
	3. Triplet		9. Rumble	III. Resting	C. Human
	4. Multipulse	Squeak	10. Long Squeak	IV. Scratching	
	5. Toc		11. Short Squeak	V. Surface activity	
FMS	6. FMS			VI. Swimming	

Table 2 Descriptive data on individuals with sound production (for a total of 20 666 sound 1-s bins)

	Mono	Doublet	Triplet	Multipulse	Toc	Croak	Rumble	FMS	Grunt	Short Squeak	Long Squeak
Number of individuals	18	21	18	12	18	17	20	11	21	17	19
Number of 1-s bins	341	435	825	94	1024	185	14 560	171	347	1096	1588

To do this, each recording day and all label durations were split into 1-second bin (1-s bin), using a "Dummy coding" method coded in R. Basically, the occurrence of a sound or a behaviour or an external event at a given time took the value of 1. If absent, it took the value of 0. This method quantified the number of 1-s bins of a given sound that co-occurred with the 1-s bins of a given behaviour or an external event. Only sounds occurring during an identified behaviour or an external event were considered.

To assess if co-occurrences were significantly different from chance, we performed a Monte Carlo simulation on the percentage of each co-occurrence (i.e. the number of 1-s bins of a given sound co-occurring with a behaviour or an external event, divided by the total of 1-s bins of this sound). Each co-occurrence was simulated 10 000 times by randomly assigning 1-s bins of sounds with behaviours and external events, while maintaining the same total number of 1-s bins for each sound. To obtain an empirical P value from Monte Carlo simulation, we use the formula $(r+1)/(n+1)$, where r is the number of these replicates that produce a test statistic greater than or equal to that calculated for the actual data and n is the number of replicate samples that have been simulated ($n = 10\ 000$) (Davison and Hinkley 1997). Monte Carlo simulations estimate significance but do not measure it (North et al. 2002).

Since a sound can occur during 1-s bins of two different external events, it was included in both external events as they are not mutually exclusive (e.g. boat noise can occur in the presence of a human or a conspecific) and it is therefore not possible to calculate their detection rate. To estimate the total sound production (Fig. 1) and the behavioural budget (Fig. 2) of green turtles, we calculated the percentage of 1-s bins for each sound and behaviour types. All dummy coding procedures and Monte Carlo simulation were performed in RStudio (version 4.3.0, 2023-04-21).

RESULTS

The behavioural contexts of underwater sound production of 23 juvenile green turtles were investigated. From the dataset of recorded tag data, 20 666 sound 1-s bins (representing approximately 6 h of sound recordings), 746 382 behaviour 1-s bins (~ 207 h) and 92 549 external event 1-s bins (~ 26 h) were identified (see Table S2 in the Supplementary Information for the full dataset). Individual produce sounds for 0.15–14.14% of the time they were recorded.

Sound production

Among the eleven recorded sounds, the rumble was the most produced. It accounted for 70.5% of total sound production (Table 2; Fig. 1a). The remaining 29.5% of the total sound production was distributed among the other ten sound categories. Among these, the pulse and the squeak categories were the most represented, each accounting for 13.3% and 13% of the total sound production, respectively (Table 2; Fig. 1b). In contrast, the FMS category represented only

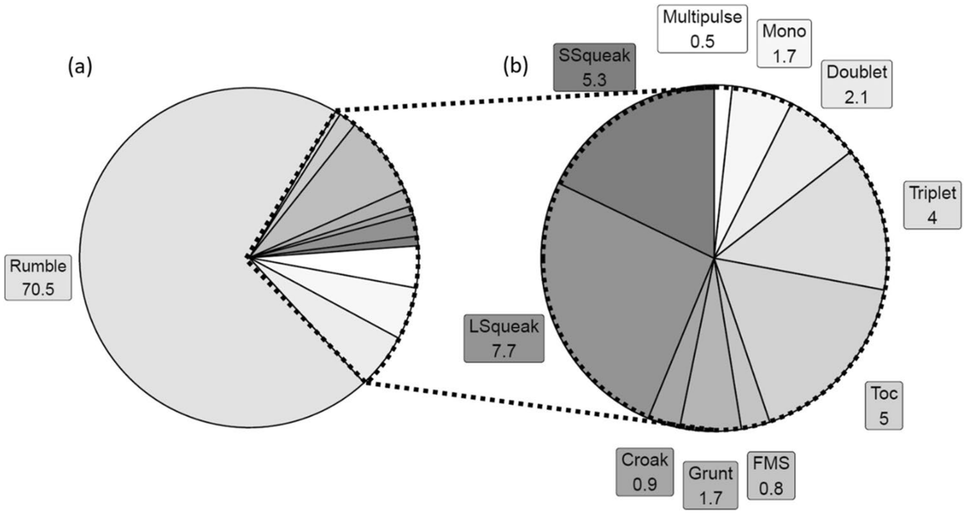

Fig. 1 Pie charts of (a) total sound production and (b) sound production without rumble (the remaining 29.5% of total sounds production). The pulse category includes Mono, Doublet, Triplet, Multipulse and Toc. The LAC category includes Croak and Rumble. The Squeak category includes Short and Long Squeak

Table 3 Descriptive data on individuals with behaviour budget (for a total of 746 382 behaviour 1-s bins)

	Feeding	Gliding	Resting	Scratching	Swimming	Surface activity
Number of individuals	22	23	23	21	23	23
Number of 1-s bins	41 861	17 521	368 847	18 178	299 975	47 659

0.8% of the total sound production (Table 2; Fig. 1b). The LAC category (including the croak and the rumble) was the most produced sound category, with rumble contributing to the large majority of it. Additionally, 99.2% of rumbles 1-s bins were recorded after sunset.

Behavioural Budget and External Event occurrences

Among the six defined behaviours, resting and swimming were the most observed, each accounting for 49.4% and 37.8% of total behaviour budget, respectively (Table 3; Fig. 2).

Among the three external events, the boat noise was the most observed (Table 4). The interaction of the tagged turtle with a conspecific was much more frequent than with human (Table 4).

Co-Occurrences of Sounds with Behaviours

Ten of the eleven types of sound described (excluding FMS) were all generally produced during resting and swimming (Fig. 3a, b, d, e). The five sound types of the pulse category and the rumble were mostly produced during resting (all of them are significantly different from chance with $p < 0.05$, Table 5a), with 74.9% of rumbles were produced during resting ($p = 0.0001$, Table 5a). Rumbles were mostly recorded in three individuals whose showed an intense rumble production after sunset, mainly during resting (Fig. 4a, b): 881 1-s bins from 20:11 to 21:27, 6 753 1-s bins from 18:44 to 21:41 and 6 783 1-s bins from 18:41 to 21:31. However, only 12 out of 23 individuals were recorded after sunset.

The grunt and the two sound types of the squeak category were mostly produced during swimming (all of them are significantly different from chance with $p < 0.001$, Table 5a), with 68.9% of grunts were produced during swimming ($p = 0.0001$, Table 5a).

The FMS was quite rare (171 1-s bins recorded in total on 11 individuals, Table 2) as well as the scratching behaviour (accounting for 2.4% of the total behavioural budget, Fig. 2). However, the FMS was highly associated with this scratching behaviour (Fig. 3c), with 89.5% of FMS were produced during scratching (11 individuals, $p = 0.0001$, Table 5a).

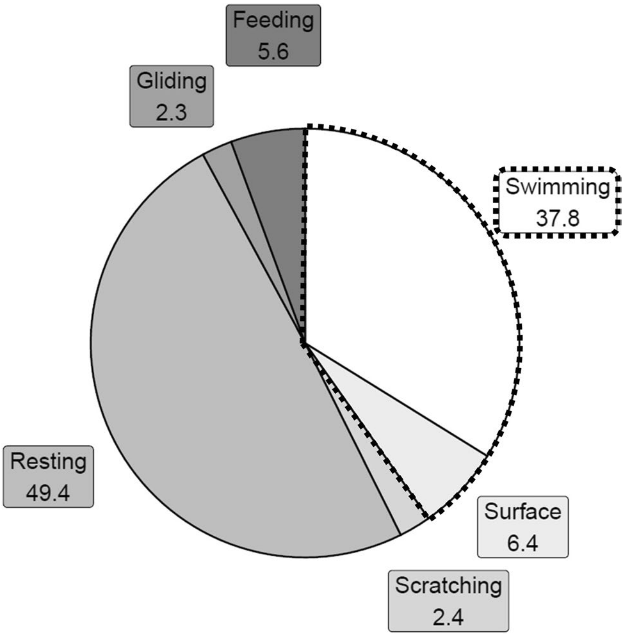

Fig. 2 Pie chart of total behavioural budget. As turtles were always swimming during surface activity, its budget was included in the swimming behaviour. It accounted for 6.4% of the total behavioural budget and always co-occurred with swimming

Table 4 Descriptive data on individuals with external event production (for a total of 92 549 external event 1-s bins)

	Human	Conspecific	Boat noise
Number of individuals	15	22	23
Number of 1-s bins	955	14 765	76 829

Co-occurrence of sounds with external events

Very few sounds were heard during external event-driven contexts except during boat noise (mono and croak were produced significantly differently from chance with $p < 0.01$, Table 5b). Only FMS and long squeak were produced in the presence of humans ($p < 0.05$, Table 5b), whereas eight sound types were produced in the presence of conspecifics in the camera's field of view (four sound types, including grunt, were produced significantly differently from chance with $p < 0.05$, Table 5b). However,

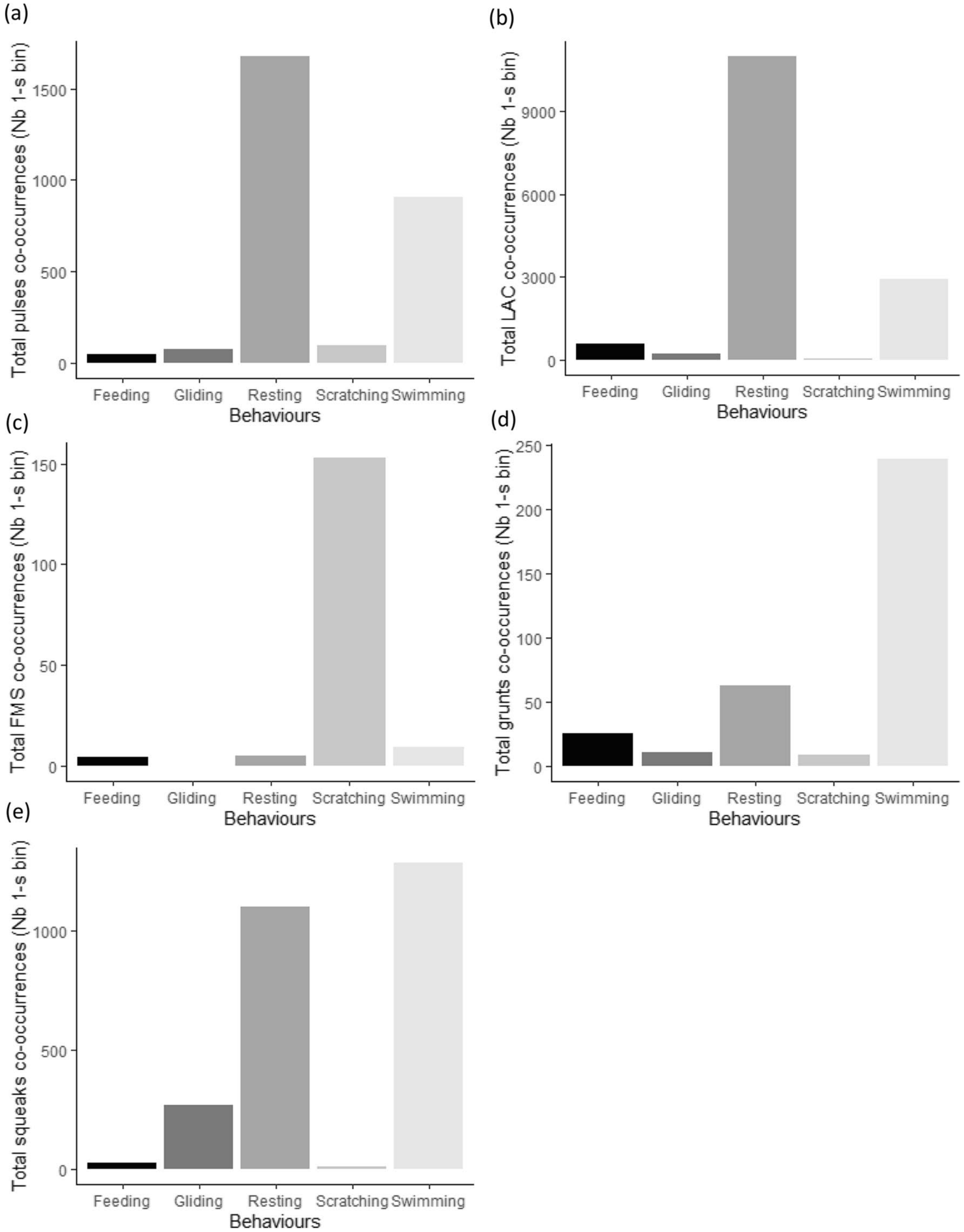

Fig. 3 Barplots of total co-occurrences of (a) pulses, (b) LAC, (c) FMS, (d) grunts and (e) squeaks with juvenile green turtle behaviours

the long squeak production in the presence of human was significantly different from chance ($p = 0.0001$, Table 5b). This is the sound heard the most during such event (10 1-s bins).

DISCUSSION

This study provides new knowledge on the acoustic behaviour of green sea turtles based on a multi-year research program investigation focusing on immature green turtle

Table 5 Co-occurrence of sounds with (a) behaviours and (b) external events. For each cell, the first line corresponds to the number of individuals in which the co-occurrence happened (n ind), the second line is the number of 1-s bins of sounds co-occurring with (a) behaviours or (b) external events, and the third line is the percentages of 1-s bins of sounds, co-occurring with (a) behaviours or (b) external events. A Monte Carlo simulation was performed to assess if the percentage of a given co-occurrence was significantly different from the one obtained randomly (* indicate $p < 0.05$, ** indicate $p < 0.01$, *** indicate $p < 0.001$; see table S3 in the supplementary information for p-values)

(a)			Feeding	Gliding	Resting	Scratching	Swimming	Surface activity
Pulse	Mono	n ind	1	5	12	2	17	5
		Total of 1-s bins	1	15	190	2	133	9
		1-s bins rate	0.3%	4.4% **	55.7% **	0.6%	39%	2.6%
	Doublet	n ind	1	3	15	1	17	4
		Total of 1-s bins	1	7	256	2	169	11
		1-s bins rate	0.2%	1.6%	58.9% ***	0.5%	38.9%	2.5%
	Triplet	n ind	2	4	13	1	15	8
		Total of 1-s bins	2	12	522	2	287	20
		1-s bins rate	0.2%	1.5%	63.3% ***	0.2%	34.8%	2.4%
	Multipulse	n ind	No co-occurrence	1	3	No co-occurrence	12	4
		Total of 1-s bins		2	57		35	5
		1-s bins rate		2.1%	60.6% *		37.2%	5.3%
	Toc	n ind	5	4	15	3	15	2
		Total of 1-s bins	22	32	636	73	261	2
		1-s bins rate	2.1%	3.1%	62.1% ***	7.1% ***	25.5%	0.2%
LAC	Croak	n ind	2	1	10	2	13	5
		Total of 1-s bins	4	2	94	15	70	6
		1-s bins rate	2.2%	1.1%	50.8%	8.1% ***	37.8%	3.2%
	Rumble	n ind	5	7	18	2	14	3
		Total of 1-s bins	564	195	10 911	21	2869	236
		1-s bins rate	3.9%	1.3%	74.9% ***	0.1%	19.7%	1.6%
FMS		n ind	3	No co-occurrence	2	11	6	No co-occurrence
		Total of 1-s bins	4		5	153	9	
		1-s bins rate	2.3%		2.9%	89.5% ***	5.3%	
Grunt		n ind	8	5	17	5	20	4
		Total of 1-s bins	25	11	63	9	239	24
		1-s bins rate	7.2%	3.2%	18.2%	2.6%	**68.9%** ***	6.9%
Squeak	Short Squeak	n ind	2	9	10	2	15	11
		Total of 1-s bins	6	83	447	2	558	29
		1-s bins rate	0.5%	7.6% ***	40.8%	0.2%	**50.9%** ***	2.6%
	Long Squeak	n ind	4	7	6	2	16	11
		Total of 1-s bins	19	185	653	7	724	30
		1-s bins rate	1.2%	11.6% ***	41.1%	0.4%	**45.6%** ***	1.9%
(b)			Human	Conspecific	Boat noise			
Pulse	Mono	n ind	No co-occurrence	3	8			
		Total of 1-s bins		17	51			
		1-s bins rate		**5 %** ***	**15 %** **			
	Doublet	n ind	No co-occurrence	2	8			
		Total of 1-s bins		8	54			
		1-s bins rate		1.8 %	12.4 %			
	Triplet	n ind	No co-occurrence	2	9			
		Total of 1-s bins		7	88			
		1-s bins rate		0.8 %	10.7 %			
	Multipulse	n ind	No co-occurrence	2	4			
		Total of 1-s bins		4	14			
		1-s bins rate		**4.3 %** *	14.9 %			
	Toc	n ind	No co-occurrence	3	4			
		Total of 1-s bins		14	42			
		1-s bins rate		1.4 %	4.1 %			

Table 5 (continued)

LAC	Croak	n ind	No co-occurrence	2	6
		Total of 1-s bins		10	31
		1-s bins rate		**5.4 %** **	**16.8 %** **
	Rumble	n ind	No co-occurrence	2	6
		Total of 1-s bins		3	45
		1-s bins rate		0 %	0.3 %
FMS		n ind	1	No co-occurrence	4
		Total of 1-s bins	1		17
		1-s bins rate	**0.6 %** *		9.9 %
Grunt		n ind	No co-occurrence	4	6
		Total of 1-s bins		11	21
		1-s bins rate		**3.2%** *	6.1 %
Squeak	Short Squeak	n ind	No co-occurrence	No co-occurrence	7
		Total of 1-s bins			111
		1-s bins rate			10.1 %
	Long Squeak	n ind	3	No co-occurrence	6
		Total of 1-s bins	10		73
		1-s bins rate	**0.6 %** ***		4.6 %

Significant values (marked with one, two or three *) are in bold

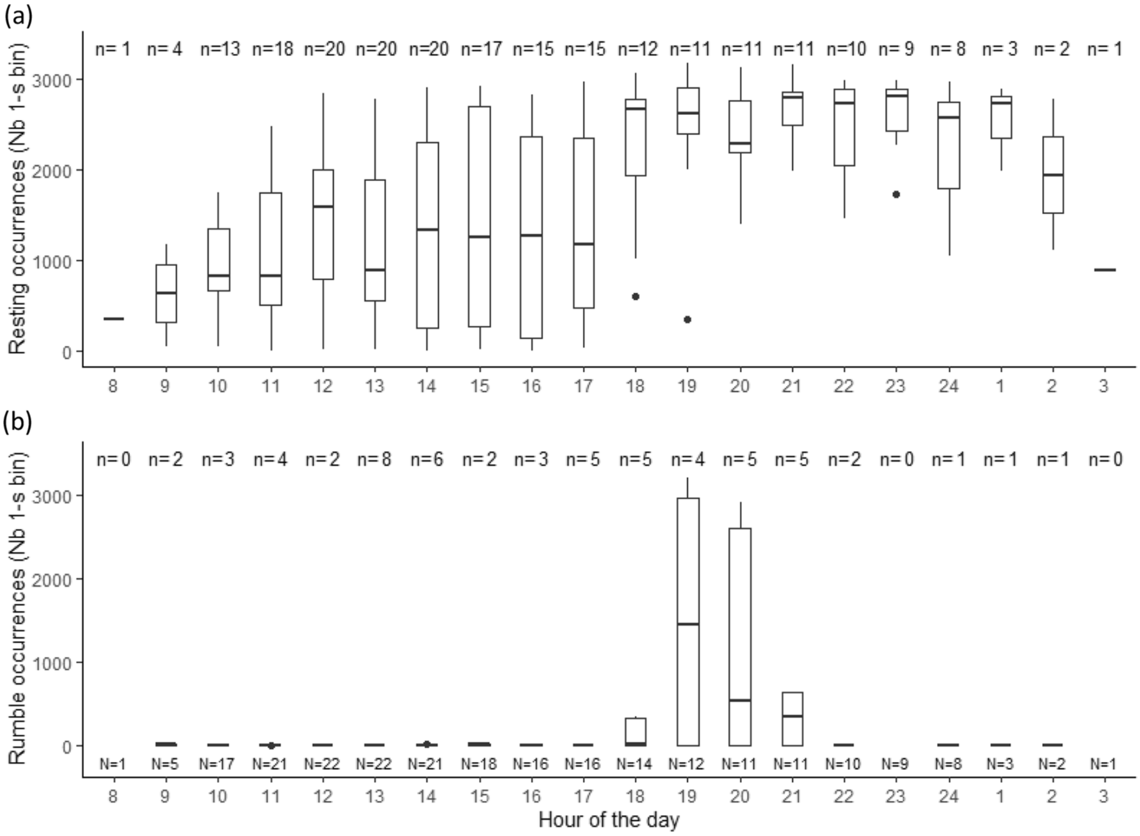

Fig. 4 Boxplots of occurrences of (a) resting behaviour and (b) rumbles produced at each hour of the day. Boxes indicate the inter quartile range, with the central line depicting the median and the whiskers extending to min and max values and outliers. For each hour, the N corresponds to the number of individuals recorded for more than twenty minutes in each time slot, and the n corresponds to the number of sampled* individuals resting (a) or producing a rumble (b) at least once in each time slot. No sea turtles were recorded before 8am and after 3am. * Individuals with a tag that was recording data

population in the Lesser Antilles. The investigations on the co-occurrences of sounds and behaviours of juveniles at their foraging grounds are key to understanding the potential importance of acoustic communication in this endangered species. Altogether, these findings offer new and innovative perspectives for improving sea turtle conservation.

Our first finding revealed a highly variable production rate within the sound repertoire of the green turtle. Doublet, grunt and rumble were the sounds most commonly produced among juvenile green turtles ($n \geq 20$ individuals). However, doublets and grunts were produced far less than the rumble. Indeed, the doublet and the grunt accounted for 2.1% and 1.7% of the total sound production, respectively, while the rumble accounted for 70.5% of the total sound production. In contrast, the FMS and the Multipulse were the sounds produced least commonly among individuals ($n \leq 12$ individuals) and accounted for 0.8% and 0.5% of the total sound production, respectively. The croak was also little produced, accounting for 0.9% of the total sound production. However, since the tags recorded for short amounts of time (i.e. less than 24 h at a time and not on several successive days), it is likely that all sounds, behaviours and external events could not be sampled for each individual within a recording session.

This study provided the first investigation focusing on the relationship between behaviours, external events and underwater sounds produced by juvenile green turtles. The pulse, the LAC, the grunt and the squeak categories were generally produced while juvenile green turtles were resting or swimming. These prevailing co-occurrences can be attributed to their predominant activity patterns during the tag deployment which was mainly resting and swimming. As seven out of the eleven described sounds types (mono, doublet, triplet, multipulse, toc, croak and short squeak), were not produced in a specific context, it is not possible to suggest any biological function or to conclude on the absence of function for these seven sounds types. Thus, we cannot confirm whether these sound types are used for communication. Furthermore, as no sound was recorded during physical interactions between conspecifics (affiliative or agonistic), we suggest that sound may not be the medium used for direct social interaction, as sight or smell remain effective at close range (Bartol and Musick 2002). However, we found some sounds produced by a small number of turtles while in presence of conspecifics (without physical contact).

Among the context-specific sound productions, the FMS was mostly produced during scratching behaviour (Fig. 3c). Both FMS and scratching are individually rare compare to others sounds and behaviours (Tables 2 and 3). However, the average percentage of co-occurrence is very high (83.9%, Table 5a). The FMS was generally produced when sea turtles seem to be alone and undisturbed. However, we are not able to assess any biological function for this sound.

Grunts were found to be commonly produced during resting and mostly during swimming. However, when watching the behaviour of the green turtles producing grunts, we found a stereotyped retreat head movement coinciding with the production of grunts, which suggests a potential link between this sound and a specific behavioural response in green turtles. Indeed, few grunts were produced in the presence of conspecifics ($p = 0.0443$) during an intimidation interaction (i.e. two conspecifics swimming around each other, which is considered swimming behaviour in the results, $p = 0.0001$). Thus, such head movement could be a visual agonistic component analogous to aggressive threat signals observed in others species, such as lizard waving their tails at approaching predators (Bradbury and Vehrencamp 2011). Given that grunts were also produced when sea turtles exhibited a vigilance posture (head up, looking around, leaning on its front legs) while swimming or feeding or when approaching conspecifics, we suggest that grunts could function as warning signals, playing a role in intra-specific acoustic communication among juvenile green turtles.

We previously assessed that the squeak might be a good candidate for intra-specific communication due to its individual stereotypy (i.e., individual-specific) (Charrier et al. 2022). Our recordings show that long squeaks were recorded for three individuals during human avoidance events. Two produced long squeaks just after being released from the tagging boat and one produced a long squeak while swimming away from three swimmers. Long squeaks were also observed on one other individual after the sunset. The data from the hydrophone, the pressure logger and the 3D-accelerometer showed that the green turtle was about to surface, stopped, then dove rapidly after producing such sound, suggesting an avoidance behaviour. The observation of long squeaks produced by green turtles during avoidance behaviour (which is considered swimming behaviour in the results, $p = 0.0001$) in the presence of humans ($p = 0.0001$) provides interesting insights into the potential link between this sound in response to perceived threats and anti-predator or avoidance behaviour. The limitations of the camera's field of view (100°) highlight the possibility that important contextual cues, such as the presence of conspecifics or another potential threats (animal or a human), may not have been captured, thus complicating the interpretation of behavioural responses. Indeed, we often saw that the turtle was vigilant and looking around, but we could not explain why it remained alert. The long squeak may thus constitute a first evidence of an alarm acoustic signal in juvenile green turtles, used to alert conspecifics from a threat. While evidence of alarm acoustic signals has been shown in other non-avian reptile species (e.g. leopard lizard *Gambelia wislizenii*, Wever et al. 1966; fossorial snakes, Young et al. 2013), confirmation of the alarm function of the long squeak in green turtles would require experimental validation using playback experiments.

We recorded long sequences of rumbles after sunset and during resting behaviour. The overlapping and varied amplitude levels of these rumbles suggest that several individuals in the vicinity may contribute to these long-lasting acoustic interactions, potentially engaging in some form of coordinated sound production. It may thus constitute first evidence of a social acoustic communication among juvenile green turtles during night-time resting periods. Similar production, called choruses, are observed in other taxa like birds, insects frogs and fishes (Farina and Ceraulo 2017). It highlights the potential for social communication and coordination among green turtles during night-time resting periods. The only example is the Travancore tortoise *Indotestudo travancorica*, in which several individuals called together, with individual sound productions appearing to be regularly spaced, at night (Campbell and Evans 1972). While chorusing behaviour is well documented among insects, fishes, frogs and birds and has associated with diverse ecological functions (e.g. energetic and behavioural matters in birds, Farina and Ceraulo 2017), its occurrence in non-avian reptiles, particularly Chelonians, remains relatively unknown.

Although we did not examine the sound level of the boat noise we recorded, our findings show there is no specific sound produced, nor any behaviour that stopped during boat noise events. This suggests that juvenile green turtles may not alter their acoustic behaviour in direct response to boat activities, as it was reported in diamondback terrapins *Malaclemys terrapin* (Lester et al. 2013). However, the absence of change in behaviour through their sound production or behaviour does not mean that boat activities do not induce physiological stress or cause hearing loss (e.g. red-eared slider *Trachemys scripta elegans*, Salas et al. 2023). Although green turtles have not altered their sound production in response to boat noise, they appear to surface less often to breathe (LM, unpubl. data). This alteration in surfacing behaviour may indicate a potential physiological response to the presence of boats and associated noise, suggesting a possible impact on their respiratory patterns or diving behaviour. A comparable behavioural response has previously been observed in a juvenile green turtle, wherein it appears to remain stationary on or near the sea floor when ships pass nearby (Tyson et al. 2017). Most studies of sea turtle responses to boat noise have focused on exposure to high-intensity seismic airguns in a closed or semi-closed environment, which limits the ability to assess the behaviour of free-ranging turtles exposed to different boat noises (O'Hara and Wilcox 1990; Moein et al. 1994; McCauley et al. 2000). The rare studies on free-ranging turtles exposed to seismic airgun surveys reported highly variable behavioural responses of turtles. Indeed, DeRuiter and Larbi Doukara (2012) reported that loggerhead turtles dived immediately following an airgun shot, while Weir (2007) reported that 83% of sea turtles (including olive ridley, leatherback and loggerhead turtles) continued to bask at the surface during airguns exposure and as the vessel and towed equipment moved past. The variability of behavioural responses to a noisy event is highly complex in many species including non-avian reptiles. For example, freezing is a typical stress response in non-avian reptiles, as in the Eastern blue tongued lizard *Tiliqua scincoides* when exposed to the noise of mining machinery (Mancera Alarcon 2016). Given impact of anthropogenic noise on non-avian reptile behaviour remains relatively understudied compared to other taxa (Simmons and Narins 2018; Jerem and Mathews 2021), the interpretation of the results regarding the effect of boat noise on the behaviour of juvenile green turtles is constrained. Further research is required to compare the behaviour of green turtles occurring in areas with low and high-levels of boat traffic.

The four sounds types, rumble, FMS, grunt and long squeak were the only ones produced by juvenile green turtles in specific behavioural contexts. Such findings could potentially contribute to sea turtle conservation. Indeed, our findings highlight intra-specific social interactions, but also alert or vigilance sounds. It provides a strong baseline to test free-ranging green turtle with playback experiments using the long squeak, the grunt or the rumble to assess if we can elicit a behavioural reaction of the tested individuals. It has been shown that some non-avian reptiles are sensitive to heterospecific calls and can adapt their behavioural response from threat signals (marine iguana *Amblyrhynchus cristatus*, Vitousek et al. 2007; e.g. brown anoles *Anolis sagrei*, Cantwell and Forrest 2013). Some of these sounds could be used in deterrent systems aiming to reduce by-catch of sea turtles by preventing them from being entangled in fishing nets (Chevallier et al. 2024).

Indeed, the use of acoustic pingers on harbour porpoise *Phocoena phocoena* for instance has shown that acoustic signals can reduce the occurrence of by-catches (Kraus et al. 1997; Trippel et al. 1999; Gearin et al. 2000). As part of the TOPASE program (Martinique-Guadeloupe) aiming to reduce by-catch of sea turtles in fishing nets, recent investigations based on the findings of this present study has been carried out. Selected green turtle sounds (squeaks and rumbles) were used in playback experiments on free-ranging green turtles during their foraging activities in Martinique (Chevallier et al. 2024). Encouragingly, the playback tests showed that a majority of green turtles responded to these sounds by exhibiting behavioural alertness. Further investigations are now required to confirm such findings. Specifically, attention can be directed towards examining specific sounds such as the grunt and the long squeak to confirm their role in avoiding danger from conspecifics or humans and to explore the biological function of the rumble in social interactions and social grouping pattern during night-time.

Finally, to gain a deeper understanding of the biological function of these sounds, it would be valuable to perform similar recordings using animal-borne tags on adult green turtles. By comparing the sound repertoire of juvenile to those of adult green turtles, we could potentially highlight any variations in acoustic parameters and reveal ontogenetic information regarding the development of sound-producing organs. Moreover, this approach could reveal new sound productions used only during the breeding period, providing further insights into the acoustic behaviour of adult green turtles.

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Author contributions DC, IC and LM designed research; DC, NA, OB, LJ, NL, FL, PL, ML, JM and SR performed data collection; LM and CH designed the code of the Dummy Coding method; LM, IC, LJ and DC analysed data; DC acquired funding; LM wrote the original version of the paper; IC, DC and CH edited the paper.

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Data availability All datasets generated or analysed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval Fieldwork was performed in accordance with the French legal and ethical requirements. Specifically, the protocol was approved by the Conseil National de la Protection de la Nature and the French Ministry for Ecology (permit numbers: 201710-0005 and R02-2020-08-10-006) and followed the recommendations of the Police Prefecture of Martinique. Fieldwork was carried out under the certification of DC (prefectural authorisations' owner) under strict compliance of the Police of Martinique's recommendations to minimize animal disturbance. Indeed, the capture, although stressful for the animal, respects the safety conditions for the divers as well as for the sea turtle. The handling time on the boat did not exceed 10 min in order to minimise the stress associated with capture. The use of suction cups instead of glue makes the attachment system much less invasive. The slightly positive buoyancy and hydrodynamics of the camera ensure that the turtle's movements are not constrained when diving or surfacing. The automatic release of the device after a maximum of two days avoids the stress of a second capture.

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