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REPORT

The lunar cycle does not influence catch rates or foraging success of neonatal reef sharks in an amphidromic nursery system

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Abstract Elasmobranch (i.e. sharks, skates, and rays) behaviours have been found to align with moon phases; yet, it is not fully understood how the moon influences elasmobranchs' foraging habits. In coastal ecosystems, tidal changes are typically seen as the primary influence on the behavioural rhythms of fishes, which are linked to the lunar cycle. Sharks have been documented to synchronise behaviours, such as foraging patterns, with the phases of the moon, but studies have yet to clearly separate and identify the mechanisms by which the lunar phase affects these patterns. The island of Moorea, French Polynesia, serves as a nursery habitat for neonatal blacktip reef and sicklefin lemon sharks within the South Pacific amphidromic system, which experiences minimal tidal ranges (~ 0.2 m). This setting provides a unique opportunity to isolate the lunar cycle's effects from tidal influences. We compared catch rates of neonates of both shark species and foraging success, through stomach content analysis, of blacktip reef sharks across the lunar cycle. Our findings did not support the hypothesis of lunar-induced entrainment of foraging patterns for these neonatal reef sharks. However, understanding the environmental factors that shape the behavioural patterns and foraging strategies of neonatal reef sharks is becoming increasingly important against the backdrop of human disturbances.

Second language abstract (French) Les comportements des élasmobranches (les requins et les raies) peuvent être influencés par les phases de la lune. Cependant, on ne comprend pas entièrement comment la lune influence leurs habitudes alimentaires dans la recherche de nourriture. Dans les écosystèmes côtiers, les rythmes des marées sont généralement considérés comme le facteur principale modifiant les rythmes et les comportementaux des poissons, avec un effet confondant avec le cycle lunaire. Ainsi, les requins peuvent synchroniser leurs comportements, notamment leurs habitudes de recherche de nourriture, avec les phases de la lune, mais ces changements de comportements n'ont pas été bien étudiés chez les élasmobranches à ce jour. Les études menées n'ont pas encore clairement séparé et identifié les mécanismes par lesquels la phase lunaire affecte ces comportements. L'île de Moorea sert de lieu de nurserie pour les requins à pointe noire et les requins-citrons dans le système amphidromique du Pacifique Sud, avec des marées minimales (~0.2 m). Cette situation offre une opportunité exceptionnelle d'isoler les effets du cycle lunaire de l'influence des marées. Nous avons comparé les modèles d'activité en utilisant les données de capture des nouveau-nés des deux espèces de requins

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et leur succès quant à la recherche de nourriture en analysant le contenu de l'estomac des requins à pointes noires à travers le cycle lunaire. Nos résultats ne confirment pas l'hypothèse d'un entraînement de l'activité ou de la recherche de nourriture induit par la lune pour ces requins de récifs nouveau-nés. Comprendre les facteurs environnementaux qui façonnent les modèles d'activité et les stratégies de recherche de nourriture des requins de récifs néonataux devient de plus en plus important dans le contexte des perturbations humaines.

Keywords Carcharhinus melanopterus · Foraging behaviour · French Polynesia · Moon phase · Negaprion acutidens

Introduction

Synchronised behaviours of animals with the monthly phases of the moon have been demonstrated across a wide range of taxa (Grant et al. 2009; Lang et al. 2006; Naylor 2001; Prugh & Golden 2014; York et al. 2014), and the effects of the lunar cycle appear to be particularly important in the marine environment (Naylor 2001). Through both direct (e.g. light availability) and indirect effects (e.g. gravitational pull and geomagnetic activity), the celestial latitude of the moon can influence reproduction (Mercier & Hamel 2009; Mercier et al. 2011; Skov et al. 2005; Takemura et al. 2010), movement (Alldredge & King 1980; Benoit-Bird et al. 2009; Last et al. 2016; Lohmann & Willows 1987), foraging activity (Cruz et al. 2013; Payton & Tran 2019; Yamamoto et al. 2008), and predator–prey dynamics (Fallows et al. 2016) of marine organisms. Furthermore, several fisheries-dependent surveys reported increased shark catches around the full moon (e.g. raggedtooth sharks *Carcharias taurus* in South Africa [Wintner & Kerwath 2018]), new moon (e.g. several *Carcharhinus* spp. in Australia [Lee et al. 2018] and South Africa [Wintner & Kerwath 2018]; blue sharks *Prionace glauca* in Australia [Lowry et al. 2007]; and white sharks *C. carcharias* in Australia [Werry et al. 2012], California [Pyle et al. 1996], and South Africa [Weltz et al. 2013; Wintner & Kerwath 2018]) or bimonthly, around the first and third quarters (e.g. copper sharks *C. brachyurus* and tiger sharks *G. cuvier* in South Africa [Wintner & Kerwath 2018]).

In coastal ecosystems, tidal variation is often considered to be the major process entraining behavioural rhythms to the lunar cycle. Indeed, variation in tidal height can be an important factor influencing habitat decisions and the distribution of animals, particularly for intertidal species (Palmer 1995). Ebb and flow of the tide cause large nearshore areas to periodically switch between a terrestrial and marine habitat (Pugh & Woodworth 2014) allowing for a productive interface between the two ecosystems and often supporting and attracting a diverse range of species (Ray 1991). The shallow marine habitats adjoining the intertidal zone may consequently exhibit a temporally dynamic species composition (Robertson & Duke 1990). Submerged mangrove root habitats are, for example, often used by juvenile fishes at high tides as refuges from predators (Laegdsgaard & Johnson 2001; Nagelkerken et al. 2008), and juvenile elasmobranchs have been documented tracking the ebb and flow of the tide to remain in shallow waters, presumably to avoid predation (Davy et al. 2015; George et al. 2019; Guttridge et al. 2012; Weideli et al. 2023). On the other hand, adult reef sharks move from deeper lagoons onto shallower reef flats at high tides to exploit abundant prey resources (Lea et al. 2020).

Monthly changes in moonlight availability are a second major factor that can influence the movements and behaviour of marine animals. The effects of moonlight availability are believed to be most important in visual crepuscular and nocturnal animals (Lima & Dill 1990). Reef sharks are generally most active at twilight (Gruber et al. 1988; Hammerschlag et al. 2017; Nixon & Gruber 1988; Papastamatiou et al. 2015; Whitney et al. 2007) and have a well-developed visual system displaying a specialisation for scotopic (dim light) vision (Cohen 1990; Cohen et al. 1977; Gruber 1967; Lisney et al. 2012). Changes in moonlight availability may therefore provide periodic foraging opportunities for sharks and/or influence their capability to detect and evade predators—which is particularly important for mesopredatory sharks (e.g. neonates and juveniles)—and subsequently affect predator–prey dynamics. But whether moonlight availability affects mesopredatory sharks through variation in foraging success, variation in predation risk, or a combination of both remains unclear (Penteriani et al. 2013).

To date, no studies have successfully delineated the effects of the lunar phase to elucidate the mechanisms driving such patterns in sharks. The few studies that have investigated the effects of the lunar cycle on shark behaviour have mainly focussed on large, adult, often pelagic shark species (Hammerschlag et al. 2017), which frequently function as top-level predators in their ecosystem. Lunar-mediated effects on shark behaviour can, however, be highly specific to certain regions and environments and may vary considerably between and within species and across life stages (Hammerschlag et al. 2017; Spaet et al. 2020).

The island of Moorea in French Polynesia is located within the South Pacific amphidromic system and only experiences a very narrow tidal range (ca. 0.2 m; Hench et al. 2008), and as such, the effects of lunar-induced tidal variation are largely absent from the shallow reef flats fringing Moorea. The minimal tidal variation at Moorea therefore provides a unique opportunity to isolate the lunar cycle's effects from tidal influences. Moorea's fringe reefs serve as a nursery system for shark neonates (Mourier and Planes 2013; Mourier et al. 2013b; Bouyoucos et al. 2020, 2022), and the two most commonly encountered species are blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks. Once widely distributed throughout the coastal Indo-Pacific, both species have experienced depletion or extirpation due to inshore fisheries and habitat destruction and are considered vulnerable or endangered throughout the remainder of their range (Simpfendorfer et al. 2020, 2023). The increasing impacts of human disturbance—both direct (e.g. coastal development, fisheries) and indirect (e.g. climate change)—therefore highlight a pressing need to address the effects of environmental factors, both natural and anthropogenic, on sharks in an ever-changing climate. Here, we aimed to determine how the lunar cycle affects catch rates and foraging success of neonatal reef sharks within a tide-independent context.

Methods

All shark capture and research protocols were approved under arrêtés n° 9524, n° 5129, and n° 11491 issued by the Ministère de la Promotion des Langues, de la Culture, de la Communication et de l'Environnement of the French Polynesian government and by the James Cook University Animal Ethics Committee (protocols A2089, A2394, and A2769). Data were collected over seven consecutive parturition seasons (from September to February 2016–2023) as part of long-term, fisheries-independent surveys carried out as a collaboration with the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) and the Physioshark Research Programme around Moorea, French Polynesia (17° 30' S, 149° 50' W; Fig. 1).

Catch rates

Neonatal blacktip reef and sicklefin lemon sharks were caught using a 50×1.5 m gillnet with 5 cm mesh size set perpendicular to shore. Gillnets were set at dusk from ~17h00 to 20h00 at ten sites (Apaura, Haapiti, Maharepa, Paorea, Papetoai, Pihaena, Tiki, Vaiane, Vaiare, and Valorie; Fig. 1) five days per week (i.e. Monday through Friday) between September and February (from 2016 to 2023), which represent the peak parturition months (Debaere et al. 2023; Mourier et al. 2013a). These sites, evenly spread out around the 60-km coastline of Moorea, were randomly assigned two fixed sampling slots per month at the start of each season (e.g. Mourier and Planes 2013; Mourier et al. 2013b; Chin et al. 2015; Bouyoucos et al. 2020, 2022).

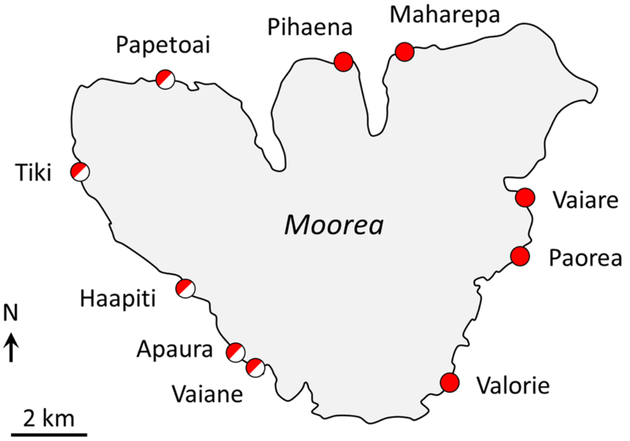

Fig. 1 The island of Moorea in French Polynesia and the ten study sites where neonatal blacktip reef and sicklefin lemon sharks were sampled. Pihaena, Maharepa, Vaiare, Paorea, and Valorie (solid circles) are considered monospecific blacktip reef shark parturition areas (i.e. no neonatal sicklefin lemon sharks occur on the east coast of Moorea). Half circles represent parturition areas where both species co-occur

Foraging success

A subset of blacktip reef sharks was examined to assess foraging success. To do this, gastric lavages were performed on individual sharks by inserting an acrylic tube (2.5–3.8 cm diameter, according to the shark's size) into the shark's stomach via the mouth and through the oesophagus. The tube and stomach were subsequently filled with seawater, and then, the shark was turned upside down—while out of the water—to flush the stomach. Stomach contents were collected in a sieve, and a record was made of the number of empty stomachs and stomachs containing prey for each evening that data were collected during the 2016/2017 and 2020/2021 parturition seasons. Gastric lavages were not carried out on neonatal sicklefin lemon sharks, as this procedure appeared to be too stressful for the species. For a more thorough description of the gastric lavage procedure, refer to Weideli et al. (2019).

Data analyses

Dates of full moons were obtained from the National Oceanic and Atmospheric Administration's Centre for Operational Oceanographic Products and Services website (NOAA CO-OPS; https://tidesandcurrents.noaa.gov/astronomical.html). Obtained Greenwich mean times (GMT) for full moons were converted to local times (GMT-10). Days-since-full-moon (DFM) values (0 to 29, where 0 represents a day with full moon) were assigned to each evening for which data were collected, similar to Grant et al. (2009). DFM values were then converted to angles (in radians) by dividing by 29.5 (the period of a lunar cycle in days) and multiplying by 2π. Due to the small sample sizes of the stomach content data across the lunar cycle, their DFM values were grouped into 8 bins (i.e. each comprising 3.7 days, rather than 1 day).

The periodic nature of circular data separates it from linear data, preventing the use of linear statistics to analyse circular data. We therefore opted for a Bayesian embedding approach to circular regression (i.e. linear predictors with circular outcome). We implemented circular mixed-effects models using the *bpnme* function from the *bpnreg* package (version 1.0.3; Cremers 2020) based on the projected normal (Gaussian) distribution with a circular outcome (i.e. phase difference in DFM). The first model included the categorial variables 'capture success' (i.e. unsuccessful vs. successful sampling event) and 'species' as fixed effects and 'sampling location' as random effect. The second model included the presence of prey items in the stomach (i.e. empty stomach vs. stomach containing prey) as fixed effect and 'sampling location' as random effect. Because the circular mixed-effects models employed in these analyses are based on the projected normal distribution, two model equations were provided for the fixed and random effects (one for the sine [component I] and one for the cosine [component II]; Cremers 2020; Cremers et al. 2021), and the second model equation (i.e. component II) was always set equal to that of component I. Model fit was subsequently evaluated using the built-in model selection criteria of the *bpnme* function. Models were run using the Markov chain Monte Carlo (MCMC) sampler for 10 000 iterations, with the first 300 samples discarded (burn-in = 100, lag = 3). Traceplots were constructed to assess the convergence of the MCMC chains. Additionally, the total number of captured neonatal blacktip reef and sicklefin lemon sharks were compared across the lunar cycle to complement and verify our binary modelling approach. All statistical analyses were carried out in R (version 2023.06.0 + 421; RStudio Team 2020; R Core Team 2020).

Note that no discrimination was made between sex of juveniles because blacktip reef and sicklefin lemon sharks do not sexually mature until they reach a total body length of 105 or 220 cm, respectively (Chin et al. 2013b; Mourier et al. 2013a, b; Stevens 1984). Furthermore, previous studies found no significant differences in body length and first-year growth between male and female neonatal blacktip reef and sicklefin lemon sharks (Hodgkiss et al. 2017; Papastamatiou et al. 2009; Stevens 1984). Additionally, no data were collected on days with extreme weather conditions (i.e. storms, strong winds, heavy rainfall), excluding potential effects caused by such weather events on the catch rates or foraging success of the sharks.

Results

A total of 1269 neonatal blacktip reef sharks were sampled over 804 sampling events, with 60.5% of the sampling events being successful. In parallel, 804 neonatal sicklefin lemon sharks were sampled over 550 sampling events, with 37.5% of the sampling events being successful. Note that sampling events did not target specific species, but sampling events that occurred in monospecific parturition areas (neonatal sicklefin lemon sharks are absent from the east coast of Moorea; i.e. Maharepa, Paorea, Pihaena, Vaiare, Valorie; Fig. 1) were omitted from the total count for the species absent in that area. Of the 1269 neonatal blacktip reef sharks sampled, 191 neonates had their stomachs flushed, of which 115 (60.2%) had empty stomachs and 76 (39.8%) had stomachs containing prey. While none of the prey items were identifiable to the species level, of the stomachs containing prey, 58 (76.3%) contained teleost prey items and 18 (23.7%) contained traces of crustacean prey or unidentifiable prey items.

Catch rates

No effect of lunar phase was observed on the catch rates of the neonatal reef sharks. Highest posterior density (HPD) intervals for the linear regression coefficients for the fixed-effect predictor 'capture success' (i.e. unsuccessful being zero sharks caught, and successful meaning at least one shark caught during a given sampling event) show considerable overlap among categories (81% and 57% overlap of HPD intervals for *C. melanopterus* and *N. acutidens*, respectively), indicating a lack of evidence to reject the null hypothesis that the circular means do not differ significantly (Supplementary Table 1; Cremers et al. 2018, 2021). Note that the posterior modes of the random intercept variance on the circle are rather high, indicating that the sampling locations may differ considerably in their individual intercept estimates (Supplementary Table 1; Cremers & Klugkist 2018). Additionally, the total number of neonates caught appears to be evenly distributed across the lunar cycle. Estimates for the Bayesian 95% HPD intervals for the circular regression coefficients, illustrated in Fig. 2, further corroborate the lack of an effect of the fixed-effect predictor on the average phase difference.

Foraging success

Similarly, as judged by stomach content, no effect of lunar phase was observed on the foraging success of neonatal blacktip reef sharks. HPD intervals for the linear regression coefficients again show considerable overlap between categories (40% overlap of HPD intervals), indicating that there is not enough evidence to reject the null hypothesis

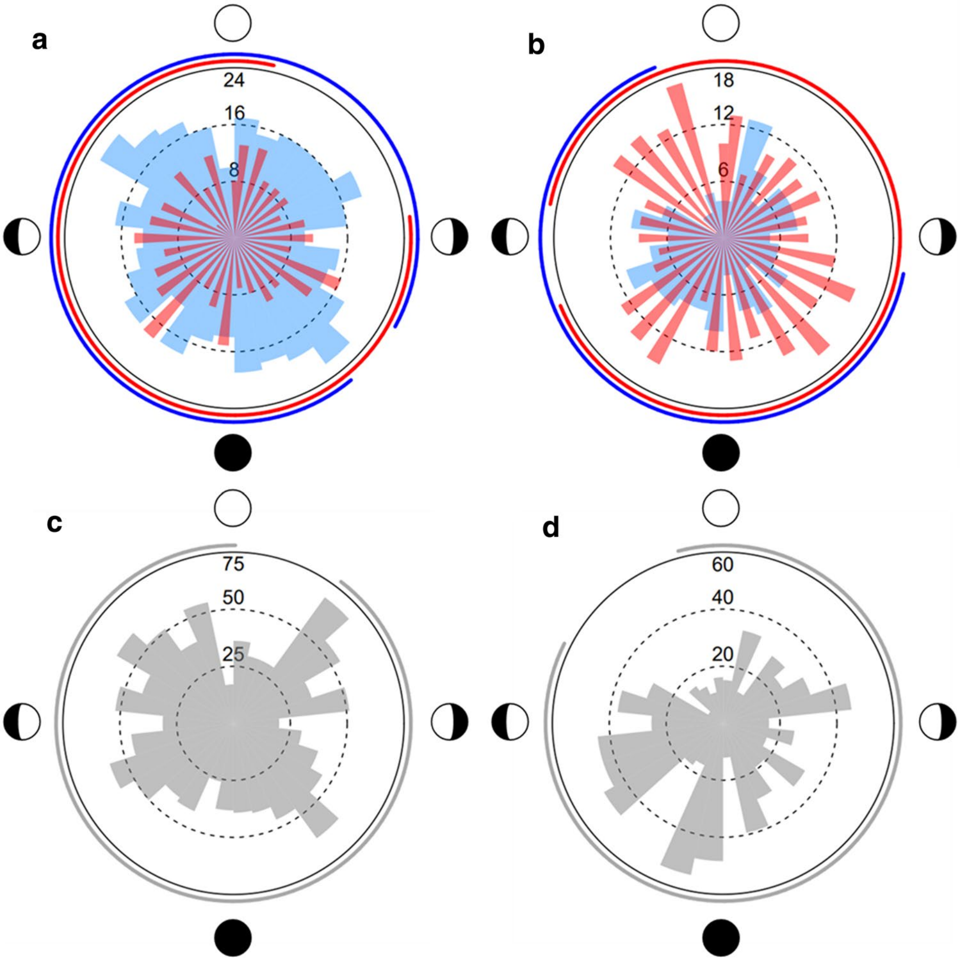

Fig. 2 Rose diagrams with highest posterior density (HPD) intervals (arcs) showing the frequency of sampling events during which no sharks were caught (unseccesful; red, thin bins) and during which at least one shark was caught (successful; blue, wide bins) across the lunar cycle for neonatal (a) blacktip reef and (a) sicklefin lemon sharks, and the total number of neonatal (c) blacktip reef and (d) sicklefin lemon sharks caught across the lunar cycle. Note the broad and overlapping HPD intervals, suggesting no effect of the fixed-effect predictor on the average phase difference. Clockwise from top: full moon, third quarter, new moon, first quarter. Sample sizes: **a** unsuccessful $n = 318$, successful $n = 486$; **b** unsuccessful $n = 344$, successful $n = 206$; **c** $n = 1269$; **d** $n = 804$

(Supplementary Table 2). The posterior modes of the random intercept variance on the circle are low, and the sampling locations therefore do not appear to differ considerably in their individual intercept estimates (Supplementary Table 2). Estimates for the Bayesian 95% HPD intervals for the circular regression coefficients, illustrated in Fig. 3, further corroborate the lack of an effect of the fixed-effect predictor on the average phase difference.

Discussion

We compared catch rates of neonatal blacktip reef and sicklefin lemon sharks in ten distinct parturition sites throughout Moorea's nursery system and stomach content as a proxy for foraging success in the blacktip reef shark neonates across the lunar cycle. Throughout the 7 years of data collection (2016–2023), lunar phase did not influence the catch rates of the neonatal reef shark or foraging success of blacktip reef shark neonates. A lunar influence on behavioural decisions made by mesopredatory reef sharks can be expected when the effects of the moon cycle—primarily tidal variation and moonlight availability—provide periodic advantages (e.g. foraging opportunities) or disadvantages (e.g. predation risk), but we did not find any evidence for lunar-mediated changes in catch rates or foraging success in this study. Note that our analyses were based on a substantial dataset collected over seven consecutive parturition seasons, providing compelling negative results rather than these findings being the consequence of a lack of power. Several reasons can be proposed for the lack of a lunar-induced effect on catch rates and foraging success in neonatal reef sharks reported here: (1) the narrow tidal variation around Moorea, (2) the small home ranges and continuous swimming patterns of these neonatal sharks, and (3) their lack of knowledge and efficiency to exploit periodic foraging opportunities influenced by changes in moonlight availability.

A first explanation may be the location of Moorea within the South Pacific amphidromic system, causing the island to experience a narrow tidal range of about 0.2 m (Hench et al. 2008). Tidal height can be an important factor influencing the behaviour and distribution of coastal shark species (Ackerman et al. 2000; Carlisle & Starr 2010; George et al. 2019; Guttridge et al. 2012; Lea et al. 2020; Medved & Marshall

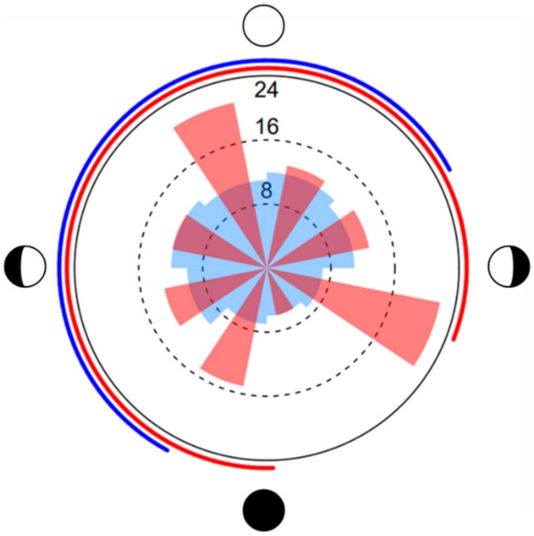

Fig. 3 Rose diagrams with highest posterior density (HPD) intervals (arcs) showing the number of neonatal blacktip reef sharks with an empty stomach (red, thin bins) or stomach containing prey items (blue, wide bins) across the lunar cycle. Note the broad and overlapping HPD intervals, suggesting no effect of the fixed-effect predictor on the average phase difference. Clockwise from top: full moon, third quarter, new moon, first quarter. Sample sizes: empty stomachs $n = 115$, stomachs containing prey $n = 76$

1983; Wetherbee et al. 2007). Indeed, high tides may allow for large-bodied sharks to move from deeper lagoons onto shallower reef flats to exploit the abundant prey resources on the reefs (Lea et al. 2020). To avoid predation, mesopredatory sharks (e.g. neonates) should track the tidal flow to remain in shallow waters that are relatively inaccessible to larger predators or that can provide a propulsive advantage to the smaller neonates, optimising escape performance, as larger predators face increased drag (Trujillo et al., in review). Indeed, juvenile blacktip reef and Atlantic lemon sharks (*N. brevirostris*) at Orpheus Island (along the northeast coast of Australia) and Bimini (in the Bahamas), respectively, exhibit synchronised movements with the tidal cycle, moving into mangrove root habitats at higher tides which also appears to correspond with an increased presence of larger sharks in the surrounding area (George et al. 2019; Guttridge et al. 2012). The absence of substantial variation in tidal height at Moorea suggests that these neonatal reef sharks do not exhibit the movements observed in such areas with a large tidal variation and can explain the lack of a tidal-induced and, hence, lunar-mediated effect on catch rates and foraging behaviour observed in this system.

Reef shark neonates and juveniles inhabit shallow nursery areas that protect them from predation by larger (adult) sharks (Heithaus 2007; Heupel et al. 2007). However, this also means that the neonatal sharks are to some extent confined to these small areas over the reef flats. While larger reef sharks typically live on the outer reef and can move in and out of the reefs via lagoons, neonatal reef sharks stay on the inner reef during their first months to years after birth (Weideli et al. 2019). Furthermore, since blacktip reef and sicklefin lemon sharks are primarily ram ventilators (i.e. they swim to force oxygen-rich water over their gills), they likely exhibit continuous patterns of activity. Thus, considering the small home ranges of these sharks (Bouyoucos et al. 2020), their continuous swimming patterns, and the negligible tidal variation, the probability of capturing neonates at Moorea can be expected to remain somewhat constant, irrespective of lunar phase. In contrast, adult reef sharks can move throughout the deeper parts of the fore reef and lagoons (Compagno 1984; Gruber et al. 1988; Mourier et al. 2013b) or even disperse to other reefs (Chin et al. 2013a; Mourier et al. 2013a) and, hence, are not confined to the small home ranges observed in neonates (Cortes & Gruber, 1990; Morrissey & Gruber 1993). In this case, lunar phase can potentially influence foraging behaviour and decisions of the adult sharks, where the adults move closer to the fringe reefs where prey may be more abundant (Papastamatiou et al. 2009) in anticipation of lunar-mediated foraging opportunities. Indeed, several studies have reported predation by adult reef sharks on repetitive and predictable spawning aggregations that occur annually around full moon (Mourier et al. 2016; Weideli et al. 2015). Additionally, adult blacktip reef and sicklefin lemon sharks often appear to be patrolling reef crests or the edge of the lagoons in anticipation of foraging opportunities (Lea et al. 2020; Papastamatiou et al. 2009).

Several studies have proposed and demonstrated an improvement in foraging abilities with maturation and experience (Ciaccio 2008; Lowe et al. 1996; Newman et al. 2012), providing a third, more general explanation. The absence of lunar-induced effects on the foraging activity of neonatal sharks may be related to the neonates' lack of knowledge and efficiency to exploit such periodic foraging opportunities. In their rush to find food, neonatal sharks can be expected to search for, and try to capture prey at relatively high rates. Due to their naivety, they may not yet know the most efficient ways to forage and will have to learn through trial and error. Weideli et al. (2019) reported that neonatal blacktip reef sharks around Moorea acquire their foraging habits relatively slowly given that less than half of the neonates had prey in their stomachs. Similar results were found for other shark species (Barry et al. 2008; Bush 2003; Duncan et al., 2006; Hussey et al. 2010); although, this may be region-specific. Viviparous shark neonates receive maternal energy reserves in the form of enlarged livers that sustain them during the first weeks to months of their lives (Debaere et al. 2023; Hussey et al. 2010). It is therefore possible that for these neonatal sharks, the lunar cycle is not an important predictor of foraging success because the neonates do not yet need to feed and tend to be predominantly opportunistic foragers (Newman et al. 2012). We therefore encourage future studies to include older juvenile (> 1 y) and (sub-) adult sharks to elaborate on the effects of the lunar cycle on the foraging behaviour of reef sharks.

It is important to note that the state of digestion of the prey items found in the gastric lavage samples was not considered (i.e. assigned DFM values may differ slightly from the precise timing of successful foraging). However, the rate of digestion in juvenile reef sharks is relatively quick (e.g. Cortés & Gruber 1992; Jackson et al. 1987; Medved 1985; Meyer & Holland, 2012) and it therefore seems reasonable to assume that this would result in minimal changes of the circular outcome and subsequent shifts in highest posterior density intervals. Juvenile Atlantic lemon sharks (*N. brevirostris*) evacuate teleost prey within 40 h and juvenile sandbar sharks (*C. plumbeus*) within 90 h, whereas crustacean prey, with evacuation times varying by exoskeleton thickness, are digested more quickly (Cortés & Gruber 1992; Jackson et al. 1987; Medved 1985). Furthermore, mean summer water temperatures at the sampling locations around Moorea range from 25 to 35 °C. These high ambient water temperatures increase routine metabolic rate of elasmobranch fishes and speed up digestion and gastric emptying rates (Brett & Groves. 1979; Bush & Holland 2002; Cortés & Gruber 1992; Nelson & Ross 1995). Therefore, it is reasonable to conclude that gastric evacuation in neonatal blacktip reef and sicklefin lemon sharks around Moorea occurs in under two days, a duration unlikely to substantially affect these results. However, this could also mean that sharks with empty stomachs could have successfully fed several days before being caught. Indeed, active foraging bouts are often followed by periods of fasting, but when the sharks' stomachs are nearly empty, foraging activity again increases (Wetherbee et al. 1990). Sharks with empty stomachs can therefore be expected to be actively searching for prey. Consequently, the swift gastric evacuation observed suggests that the feeding data, despite not accounting for digestion states, reliably reflects the sharks' foraging habits.

In conclusion, no lunar influence was observed on the catch rates and foraging success of neonatal blacktip reef sharks and the catch rates of sicklefin lemon sharks in Moorea's nursery system. The lack of substantial variation in tidal height at Moorea suggests that the neonates do not need to exhibit the synchronised movement patterns with the tidal cycle often observed in other populations to avoid predation in areas with a large tidal variation. Considering the small home ranges of the neonates, their continuous swimming patterns, and the negligible tidal variation, the probability of capturing neonates at Moorea can also be expected to remain somewhat constant, irrespective of lunar phase. Finally, the lack of any effect of moon phase may be due to the neonates' lack of knowledge and efficiency to exploit periodic foraging opportunities. In view of the current threats that neonatal blacktip reef and sicklefin lemon sharks face worldwide and the ever-changing environment they inhabit, unravelling the effects of environmental factors, such as celestial latitude of the moon, on the foraging strategies and decisions of reef sharks will be particularly worthwhile in the face of global change.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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