


REGULAR ARTICLE

The costs and healing rates of minor injuries in neonatal reef sharks

Shamil F. Debaere^{1,2}  | Ornella C. Weideli^{3,4} | Ryan Daly^{5,6} |
 Elena M. C. Milanese⁷ | José E. Trujillo⁸ | Ian A. Bouyoucos^{3,9} |
 Johann Mourier¹⁰ | Andrew Chin^{11,12} | Serge Planes^{3,13} | Gudrun De Boeck¹ |
 Jodie L. Rummer^{2,9}

¹ECOSPHERE, Department of Biology, University of Antwerp, Antwerp, Belgium

²Marine Biology, College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

³EPHE-UPVD-CNRS, USR 3278 CRILOBE, PSL Research University, Université de Perpignan, Perpignan Cedex, France

⁴SOSF-D'Arros Research Centre (SOSF-DRC), Save Our Seas Foundation (SOSF), Geneva, Switzerland

⁵South African Institute for Aquatic Biodiversity, Grahamstown, South Africa

⁶Oceanographic Research Institute, Durban, South Africa

⁷Department of Earth and Environmental Sciences (DISAT), University of Milano – Bicocca, Milan, Italy

⁸Department of Marine Science, University of Otago, Dunedin, New Zealand

⁹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

¹⁰MARBEC, Univ Montpellier, CNRS Ifremer, IRD, Sète, France

¹¹Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville, Queensland, Australia

¹²Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar, Indonesia

¹³Laboratoire d'Excellence 'CORAIL', EPHE, PSL Research University, UPVD, USR 3278 CRILOBE, Moorea, French Polynesia

Correspondence

Shamil F. Debaere, ECOSPHERE, Department of Biology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium.

Email: shamil.debaere@my.jcu.edu.au

Funding information

Laboratoire d'Excellence 'CORAIL'; Save Our Seas Foundation, Grant/Award Number: KeystoneGrant290

Abstract

Elasmobranch fishes (i.e., sharks, skates, and rays) exhibit remarkable wound-healing capabilities and consistently maintain a high capacity for tissue regeneration throughout their lives. This high capacity for wound healing may be particularly important for neonatal elasmobranchs that are still developing their immune system. However, little is known about the costs associated with wound healing and the potential influence of environmental variables or life history. In this study, we explore (1) the impact of minor, external injuries on the growth and body condition of neonatal blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks using a long-term fisheries-independent dataset from Moorea, French Polynesia, (2) the influence of ambient temperature on healing rates in neonatal blacktip reef sharks at two experimental temperatures (25°C and 29°C), and (3) variations in umbilical wound-healing rates between blacktip reef and sicklefin lemon sharks using an additional long-term dataset from St. Joseph Atoll, Seychelles. We found no impact of minor, external injuries on growth and body condition in neonatal blacktip reef and sicklefin

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of Fisheries Society of the British Isles.

lemon sharks, accelerated umbilical wound healing in neonatal blacktip reef sharks exposed to elevated ambient temperatures, and distinct umbilical wound-healing rates between neonatal blacktip reef and sicklefin lemon sharks. Enhancing our understanding of sharks' healing capabilities and the influence of environmental factors on this process is crucial for informing handling practices aimed at improving post-release survival rates of captured sharks under current and future oceanic conditions.

KEYWORDS

fisheries, predation, recovery, safe-handling practices, wound healing

1 | INTRODUCTION

Neonatal reef sharks face significant survival challenges. After parturition (in viviparous species) or hatching (in oviparous species), these neonatal sharks receive no parental care (Hussey et al., 2010) and must learn how to navigate the shallow tropical waters to meet the demands of survival. Learning how to forage effectively is one of the primary challenges neonatal reef sharks encounter after birth. In their rush to find food, they will spend much time foraging and trying to capture prey, a vital skill acquired through trial and error (Guttridge et al., 2009). While moving throughout the reef system, small-bodied neonates will also likely encounter larger-bodied predators skilled in hunting, exposing them to high predation pressures early in life (Guttridge et al., 2012; Heupel et al., 2007; Hussey et al., 2017; Trujillo et al., n.d. under review). Those unable to evade a predator but fortunate enough to survive the predation attempt may be left with bite wounds.

The close proximity of coastal reefs to human settlements may also expose neonatal reef sharks to high anthropogenic pressures (Knip et al., 2010; Sherman et al., 2023). Coastal ecosystems often harbour a rich diversity and abundance of marine life (Roberts et al., 2002). As such, these highly productive waters can offer considerable economic value to recreational and commercial fisheries (Barbier et al., 2011; Grafeld et al., 2017; Martínez et al., 2007) and provide an important source of income for artisanal fisheries (Kronen et al., 2010). Although neonatal reef sharks are rarely the primary target of these fisheries (but see Barker & Schluessel, 2005; Worm et al., 2013), they can still interact with fishing gear. Sharks that are not taken for consumption or trade on capture but are released back to the reef will often be left with fishing-gear-induced injuries (e.g., hook, spear, or gaff wounds; Bansemer & Bennett, 2010; Danylchuk et al., 2014).

Additionally, in viviparous species (i.e., those that bear live young), which make up 58% of all elasmobranchs (Compagno, 1990; Dulvy & Reynolds, 1997), the most prominent non-inflicted wounds are at the umbilicus of neonates. Umbilical wounds remain open (i.e., underlying muscle tissue remains visible) throughout the first weeks to months post-parturition, depending on the species' life history (Castro, 1993; Chin et al., 2015; Debaere et al., 2023; Ulrich et al., 2007). As such,

these wounds make for a well-suited and non-invasive way of investigating wound-healing dynamics in elasmobranch fishes of conservation concern.

It is evident that neonatal reef sharks can experience myriad external injuries from various sources, including parturition, predation attempts, and human activities (Chin et al., 2015; Hussey et al., 2017), but how the healing process affects these early life stages is not well understood. Sharks consistently show a high susceptibility to structural tissue damage throughout their lives (Chin et al., 2015; Garner, 2013), but they are reported to have a high capacity for wound healing (e.g., Bird, 1978; Black, 2023; Borucinska et al., 2020; Buray et al., 2009; Chin et al., 2015; Marra et al., 2019; Wegner & Cartamil, 2012; Womersley et al., 2021). Rapid wound healing may be particularly important for early life stages where open wounds are potential sources of infection that may cause complications in neonatal sharks that are still actively developing their immune systems (Chin et al., 2015; Rumfelt, 2014). Tissue traumas and subsequent healing may, however, also lead to energy being diverted away from routine metabolic activities, such as somatic growth, and toward recovery processes instead (Romero et al., 2009; Zera & Harshman, 2001). Such negative effects of wound healing on growth have been reported for diverse vertebrate taxa (Rennolds & Bely, 2023). However, the impact of energy allocation to wound healing on the early development and growth of sharks remains unexplored.

The rate of wound healing is likely context- and species-specific. Indeed, in ectotherms, which have limited internal heat production capabilities, physiological processes, such as wound healing, are directly influenced by environmental temperature regimes (e.g., Anderson & Roberts, 1975; Pressinotti et al., 2013; Ream et al., 2003; Smith et al., 1988). Elevated environmental temperatures, up to the point of thermal stress, may accelerate wound-healing rates (Debaere et al., 2023), with particular importance for minimising infection risk, and have been reported across a wide range of teleost fishes (e.g., Anderson & Roberts, 1975; Ang et al., 2021; Bullock et al., 1978; Jensen et al., 2015; Ream et al., 2003). However, in elasmobranch fishes (i.e., sharks and their relatives), the potential effects of temperature on wound healing remain poorly explored, mainly due to logistic challenges (e.g., the migratory behaviour of many species and large body sizes that complicate laboratory-based experiments). In situ

studies on sharks' wound-healing capabilities under different environmental conditions are further complicated by the opportunistic nature of data collection. Long-term, fisheries-independent surveys, such as the ones used in this study, are therefore particularly well-suited to address the broader implications of sharks' wound-healing capabilities.

The aim of this study was to address the knowledge gaps in the wound-healing capabilities of sharks by investigating the costs and healing dynamics of minor, external wounds in neonatal reef sharks. We hypothesised that (1) the energetic cost associated with wound healing after injury will result in reduced growth rates of neonates, (2) umbilical wounds will heal faster at higher temperatures, and (3) umbilical wound-healing rates will vary between species. In this study, we used two long-term fisheries-independent datasets to conduct a series of comparative analyses on injured and uninjured neonatal blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks under a range of field and experimental laboratory scenarios. Improved understanding of wound healing in sharks can directly inform and refine fisheries handling practices, as well as enhancing post-release survival rates under current and future ocean conditions.

2 | METHODS AND MATERIALS

2.1 | Ethical approval

Shark capture and research at the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) on Moorea was approved by the Ministère de la Promotion des Langues, de la Culture, de la Communication et de l'Environnement of French Polynesia (Arrêtés no. 9524, no. 5129, and no. 11,491) and James Cook University's Animal Ethics Committee (protocols A2089, A2394, and A2769). Shark capture, handling, and tagging on St. Joseph Atoll was approved by and conducted with the knowledge of the Ministry of Agriculture, Climate Change and Environment of the Republic of Seychelles. Animal handling and tagging methods were conducted in accordance with the approved guidelines of S. Planes by the Autorisation de pratiquer des expériences sur les animaux no. 006725 (1995) from the Ministry of Agriculture.

2.2 | Study sites, species, and shark capture

The shallow reef flats fringing Moorea, French Polynesia (17°30' S, 149°50' W), and St. Joseph Atoll, Republic of Seychelles (5°26' S, 53°21' E), serve as nursery systems for neonatal and juvenile blacktip reef (*C. melanopterus*) and sicklefin lemon (*N. acutidens*) sharks (Bouyoucos et al., 2022; Weideli, Papastamatiou, & Planes, 2019). Both reef shark species occupy temperature ranges between 25 and 35°C (Bouyoucos, Morrison, et al., 2020) and co-occur in several areas where they exhibit niche segregation, which does not appear to affect early life-history traits (Matich et al., 2017).

On Moorea, neonatal blacktip reef and sicklefin lemon sharks were caught using a 50 × 1.5-m gillnet with 5-cm mesh size set perpendicular to the shore as part of a long-term, fisheries-independent survey carried out as a collaboration between the CRIOBE and the Physioshark Research Programme (e.g., Bouyoucos et al., 2022). Gillnets were set at dusk from ~17 00 h to 20 00 h at 10 sites (Apaura, Haapiti, Maharepa, Paorea, Papetoai, Pihaena, Tiki, Vaiane, Vaiare, and Valorie) between September and February 2017–2022 (peak parturition season; Debaere et al., 2023; Mourier, Mills, & Planes, 2013; Mourier & Planes, 2013). These sites were evenly distributed around the 60-km coastline of Moorea, with each site sampled twice per month (e.g., Bouyoucos et al., 2022; Chin et al., 2015; Mourier, Mills, & Planes, 2013; Mourier & Planes, 2013). On capture, sharks were immediately removed from the net and tagged with internal passive integrated transponder (PIT) tags to allow for unique identification. They also had their umbilicus photographed and morphometrics recorded. A ruler was photographed beside each umbilicus for scale (Debaere et al., 2023).

For sharks that showed signs of external injuries, additional photographs were taken of the injuries (beside a ruler for scale) and a note was made describing the wound type (Table 1). A distinction was made between lateral lacerations (i.e., a collection of superficial cuts and scrapes, in no particular pattern), deep cuts (i.e., a laceration of ca. 1 cm deep), serial tooth marks (i.e., a clean bite mark with clearly distinguishable tooth imprints aligned in sequence), torn fins, and hooks (still present on capture) and hook wounds (i.e., elliptical, often rust-coloured wounds around the jaw) (Figure 1). Lateral lacerations, deep cuts, serial tooth marks, and torn fins are likely associated with predation attempts made by larger-bodied sharks or teleost fishes. None of the wounds showed visual signs of infection.

On St. Joseph Atoll, neonatal blacktip reef and sicklefin lemon sharks were caught using a 20 × 1.5-m gillnet with 5-cm mesh size during the parturition months September to December and March to April 2014–2017 as part of a long-term, fisheries-independent survey carried out by the Save Our Seas Foundation (SOSF) – D'Arros Research Centre (Weideli, Papastamatiou, & Planes, 2019). Similar to the sharks from Moorea, sharks were individually tagged with PIT tags, their umbilicus was photographed, and morphometrics were taken.

2.3 | The cost of wound healing

Between September 2017 and February 2022, morphometric data of individually PIT-tagged neonatal blacktip reef and sicklefin lemon sharks around Moorea were collected to assess potential differences in body condition and growth rates between injured and uninjured sharks to elaborate on the cost of wound healing. Morphometric measurements taken during sampling included total body mass (*M*, in kg) and precaudal length (PCL, distance from the tip of the snout to the origin of the caudal fin, in cm).

TABLE 1 Overview of the injured neonatal blacktip reef and sicklefin lemon sharks used in this study and the various wound types encountered and location of the wounds.

Species	ID	PCL (cm)	M (kg)	TAL (days)	Wound type	Location
Blacktip reef shark (<i>Carcharhinus melanopterus</i>)	Cm1	42.0	1.110	16	Deep cut	Above gills
	Cm2	42.8	1.020	12	Serial tooth marks	Snout
	Cm3	41.6	0.930	8	Deep cut	Second dorsal fin
	Cm4	39.0	0.780	21	Hook wound/serial tooth marks	Jaw/above pelvic fins
	Cm5	43.8	0.990	28	Lateral lacerations	Caudal fin
	Cm6	40.4	0.870	14	Hook wound/serial tooth marks	Jaw/ventral between pectoral fins
	Cm7	42.8	0.950	56	Lateral lacerations and torn fin	Pelvic fins to second dorsal fin
	Cm8	41.2	1.075	84	Hook wound	Jaw
	Cm9	40.4	0.955	56	Serial tooth marks with deep cut	Pelvic fins
	Cm10	41.6	0.840	112	Lateral lacerations	Caudal fin
	Cm11	44.2	1.260	112	Hook	Jaw
Sicklefin lemon shark (<i>Negaprion acutidens</i>)	Na1	49.8	1.230	43	Serial tooth marks	Jaw
	Na2	54.4	1.640	33	Hook	Jaw
	Na3	53.0	1.750	18	Hook wound	Jaw
	Na4	51.0	1.570	37	Lateral lacerations	Under first dorsal fin
	Na5	52.5	1.510	64	Lateral lacerations	Pectoral fins to pelvic fins
	Na6	51.0	1.270	4	Torn fin	First dorsal fin
	Na7	47.0	1.240	23	Lateral lacerations	Above pelvic fins
	Na8	46.4	1.070	77	Two deep cuts	Pectoral and pelvic fins
	Na9	50.0	1.150	7	Hook wound	Jaw
	Na10	50.0	1.230	14	Lateral lacerations	First dorsal fin
	Na11	57.0	2.130	28	Serial tooth marks	Gills

Note: Wound types include deep cuts (i.e., ca. 1-cm deep lacerations), serial tooth marks (i.e., clean bite marks), hooks (still present on capture) and hook wounds (i.e., elliptical, often rust-coloured wounds around the jaw), lateral lacerations (i.e., a collection of superficial cuts and scrapes), and torn fins. Abbreviations: PCL, precaudal length at initial capture (in cm); M, body mass at initial capture (in kg); TAL, time at liberty (in days) between initial capture and recapture.

For each individual, Fulton's body condition factor (K , sensu Ricker, 1975), derived from the length–mass relationship of the sharks, was calculated as follows:

$$K = 10^5 M (\text{PCL})^{-3} \quad (1)$$

Relative change in body condition (ΔK , in %) of recaptured sharks was calculated as:

$$\Delta K = 100 (K_2 - K_1) K_1^{-1} \quad (2)$$

where K_2 is the body condition of the shark at recapture and K_1 is the body condition of the shark at first capture, as calculated from Equation 1.

The specific growth rate (SGR) of recaptured sharks, defined as the percentage increase in body mass per day (% day⁻¹), was calculated as follows:

$$\text{SGR} = (\ln(M_2) - \ln(M_1)) 100 t^{-1}, \quad (3)$$

where M_2 and M_1 are the body mass of the shark at recapture and first capture, respectively, and t is the time (in days) between the two measurements.

2.4 | Temperature dependency of umbilical wound healing

To assess the effect of ambient temperature on the umbilical wound-healing rates in blacktip reef sharks, neonatal sharks with an open umbilical wound ($n = 13$, precaudal length 37.6–47.4 cm) were collected from five sites around Moorea (Haapiti, Maharepa, Papetoi, Tiki, and Vaiare). Sharks were caught between October 2021 and January 2022, uniquely PIT tagged, and isolated in flow-through mesh bags for no longer than 30 min to allow for the capture of additional



FIGURE 1 Representative photographs of the various wound types encountered among the neonatal blacktip reef and sicklefin lemon sharks (indicated by arrows and circles), including (a) a hook wound (individual Cm8), (b) a deep cut (individual Cm9), (c) lateral lacerations (individual Cm11), and (d) serial tooth marks (individual Na1).

sharks. Only sharks in good condition (e.g., no signs of external wounds) were considered for this study. Sharks were subsequently transported to the CRIOBE by car in 200-L insulated coolers with continuously aerated seawater (one or two sharks per cooler) in less than 30 min. At the CRIOBE, sharks were housed in 1250-L circular polyethylene flow-through tanks (three sharks per tank) fitted with aeration and covered with 60% shade cloth in an open-sided holding facility to expose the animals to a natural photoperiod. Clean seawater was continuously supplied from an offshore pump. Sharks were fed approximately 5% of their body mass in tuna (*Thunnus* spp.) every second day to accommodate growth. Water quality (temperature, pH, dissolved oxygen) was monitored daily.

Selected sharks were periodically retrieved from their holding tanks (on days 1, 10, and 14) to track umbilical wound healing. Although the umbilical wound may take up to a month to fully heal in neonatal blacktip reef sharks (Debaere et al., 2023), umbilicus healing was only followed over this 2-week period due to logistical limitations. To assess the size of the umbilicus of the neonatal sharks,

photographs were imported in the open-source image processing package Fiji by ImageJ (version 2.0.0-rc-69/1.53c; Schindelin et al., 2012). The scale was set to 1 cm using the ruler in the photographs, and the circumference of the umbilical wound was carefully traced using the polygon selection tool from ImageJ to calculate umbilicus area and perimeter. For a more thorough description of methodology, refer to Debaere et al. (2023).

After 5 days at ambient temperatures (ca. 27°C at the time of experimentation), temperatures were increased or decreased by 0.5°C per day using commercial bar heaters (Tetra Aquarium High-Performance Heater HT100) and chillers (TK-1000/2000, TECO) (Bouyoucos, Shipley, et al., 2020; Rummer et al., 2014). The two experimental temperature treatments were 25°C (i.e., −2°C, $n = 7$) and 29°C (i.e., +2°C, $n = 6$) (Schoen et al., 2021). Target temperatures were reached after 4 days (day 9) and maintained over the following 48 h. On day 11, temperatures were brought back to ambient conditions by 1°C per day. On day 10, sharks were subjected to a parallel study in which a 560-g iron weight was dropped in close proximity to

the sharks to elicit a quick escape response (Trujillo et al., n.d. under review; see methodology in Trujillo et al., 2022). Neonatal sharks often experience high predation pressures in their natural habitat, and these antipredator behaviours therefore merely simulate those exhibited in the wild. We therefore do not expect this parallel experiment to have influenced our findings.

2.5 | Umbilical wound-healing rates across species

Due to the lack of neonatal sicklefin lemon sharks with remnants of the umbilical cord (i.e., days-old neonates, hereafter time-0 neonates; Debaere et al., 2023) around Moorea, we used the umbilicus size of time-0 sicklefin lemon shark neonates (e.g., Figure S1) caught at St. Joseph Atoll as an intercept for the Moorea population. Umbilicus sizes of time-0 neonatal blacktip reef sharks, for which neonates with remnants of the umbilical cord were caught at both Moorea and St. Joseph Atoll, were first compared between both populations to justify this approach, which did not differ significantly (Figure S2). Considering a linear decline in umbilicus perimeter (Debaere et al., 2023), the slope of the temporal closing of the umbilical wound of sicklefin lemon shark neonates was then estimated based on the umbilicus photographs taken at first capture and recapture. Data were subsequently compared to the slope estimated in Debaere et al. (2023) for neonatal blacktip reef sharks to shed light on potential variations in healing rates between these two species.

2.6 | Statistical analyses

Before statistical analyses, where applicable, data were checked for normality and equal variance using Shapiro–Wilk tests and Levine's tests, respectively. The critical value of statistical significance was set to $\alpha = 0.05$, and all statistical analyses were carried out in RStudio (version 2023.06.0 + 421; RStudio Team, 2020; R Core Team, 2020) using core R packages unless stated otherwise.

Body condition and growth rate were compared between uninjured and injured sharks using two-sample Student's *t*-tests or non-parametric Wilcoxon signed-rank tests. Umbilical wound-healing rates of neonatal blacktip reef sharks exposed to 25 or 29°C temperature treatments were fit using the linear mixed-effects *lmer* function from the *lmerTest* package (Bates et al., 2015), with shark identity as a random factor, and compared between treatments (umbilicus area measurements were first square-root-transformed). Similarly, the umbilical wound-healing rate of sicklefin lemon shark neonates around Moorea was estimated using the *lmer* function with shark identity as a random factor. These estimated slopes were subsequently compared to those reported for blacktip reef shark neonates by Debaere et al. (2023) using a Wilcoxon signed-rank test. Unless stated otherwise, reported values are mean \pm standard deviation.

Note that no discrimination was made between the sexes of the neonates because blacktip reef and sicklefin lemon sharks do not sexually mature until they reach total body lengths of 110 and 220 cm, respectively (Chin et al., 2013; Mourier, Mills, & Planes, 2013; Mourier

et al., 2024; Stevens, 1984). Furthermore, previous studies found no significant difference in PCL 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).

3 | RESULTS

3.1 | The cost of wound healing

From a total of 105 blacktip reef and 84 sicklefin lemon shark neonates caught around Moorea between September 2017 and February 2022 that were subsequently recaptured during the following weeks, 11 blacktip reef and 11 sicklefin lemon sharks had external injuries (e.g., hook wounds, bite marks). On average, SGRs (Figure 2a,c) increased in both species regardless of injury. However, the neonatal blacktip reef sharks consistently experienced a decrease in body condition (mean ΔK ; Figure 2b,d) over time (uninjured $-5.5 \pm 10.7\%$, injured $-11.1 \pm 8.1\%$). Specific growth rates and relative changes in body condition were not significantly different between uninjured and injured neonatal blacktip reef (SGR, $W = 634$, $p = 0.22$; ΔK , $t_{14} = 2.1$, $p = 0.053$) or sicklefin lemon sharks (SGR, $W = 294$, $p = 0.16$; ΔK , $W = 457$, $p = 0.47$).

3.2 | Temperature dependency of umbilical wound healing

Temporal closing of the umbilicus was faster in sharks maintained in the 29°C treatment, relative to those maintained in the 25°C treatment. The slope of the temporal umbilicus perimeter decline was significantly steeper at 29°C, as compared to the 25°C treatment ($t_{44} = -3.28$, $p = 0.002$; Figure 3a), although the slope of the temporal umbilicus area decline (after square root transformation) appeared unaffected by temperature ($t_{45} = -1.30$, $p = 0.20$; Figure 3b).

3.3 | Umbilical wound-healing rates across species

The umbilical wound of time-0 sicklefin lemon shark neonates caught around St. Joseph Atoll ($n = 7$) measured 0.054 ± 0.020 cm² in area and 1.41 ± 0.15 cm in perimeter, which was subsequently used as the intercept for the Moorea population. A total of 12 neonates around Moorea had an open umbilical wound at first capture and recapture, allowing for an estimation of the healing rate of the umbilicus (Figure 4a). The linear mixed-effects model calculated a slope for temporal umbilicus perimeter decline of 0.020 ± 0.004 cm day⁻¹. From the obtained slope and intercept, the final equation for umbilicus perimeter closing rate in sicklefin lemon shark neonates around Moorea was then estimated as $y = 1.41 - 0.020x$, where y is the umbilicus perimeter (in cm) and x is the elapsed time since birth (in days) (Figure 4b). Umbilicus perimeter closing rates (i.e., the estimated slopes) were significantly slower in the neonatal sicklefin lemon sharks relative to those reported for neonatal blacktip reef sharks by Debaere et al. (2023) ($W = 37$, $p = 0.007$).

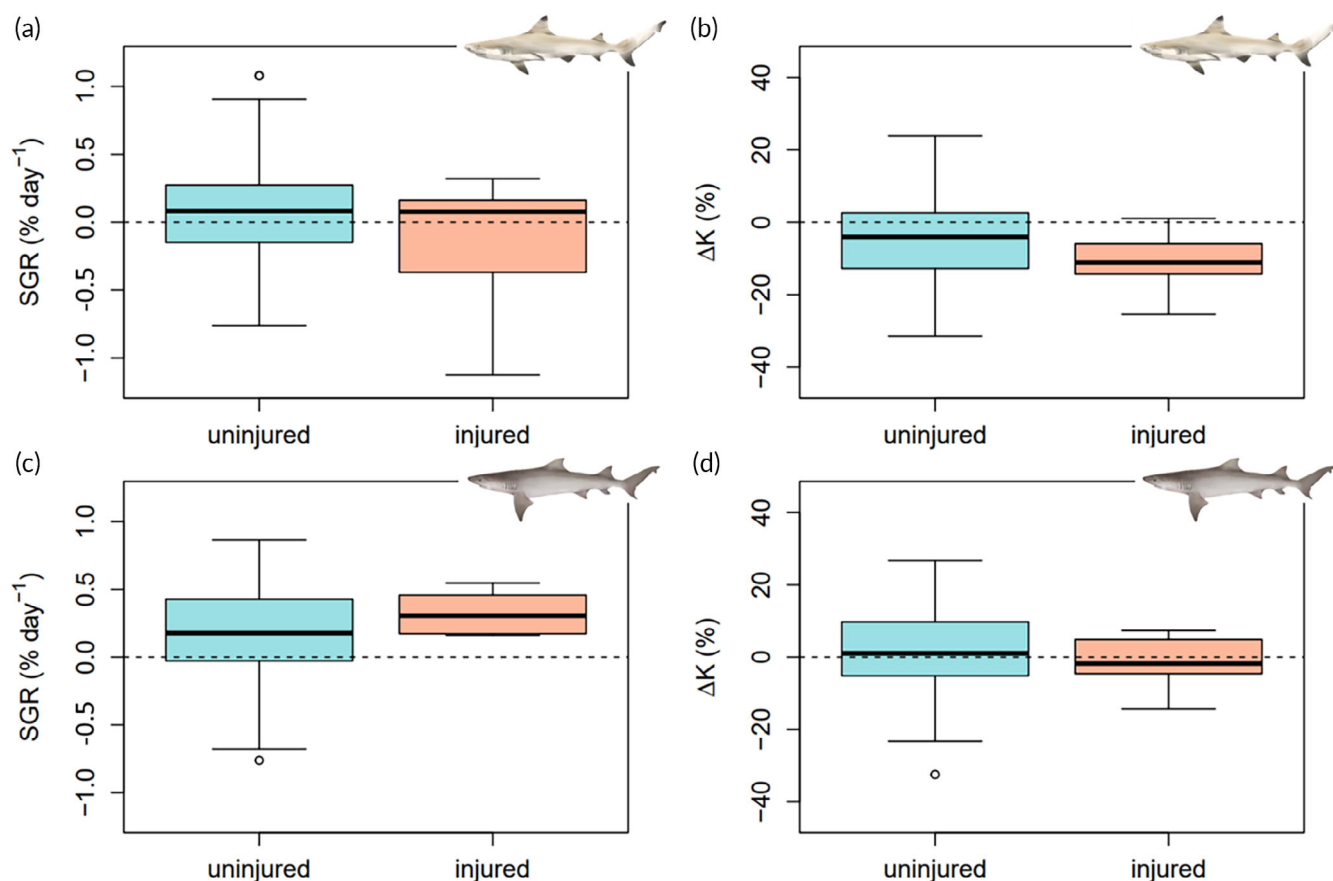


FIGURE 2 Costs associated with the healing of minor external wounds. Specific growth rates (SGR; a, c) and relative changes in body condition (ΔK ; b, d) of uninjured and injured blacktip reef (a, b) and sicklefin lemon shark neonates (c, d). Sample sizes: (a, b) uninjured $n = 94$, injured $n = 11$; (c, d) uninjured $n = 73$, injured $n = 11$.

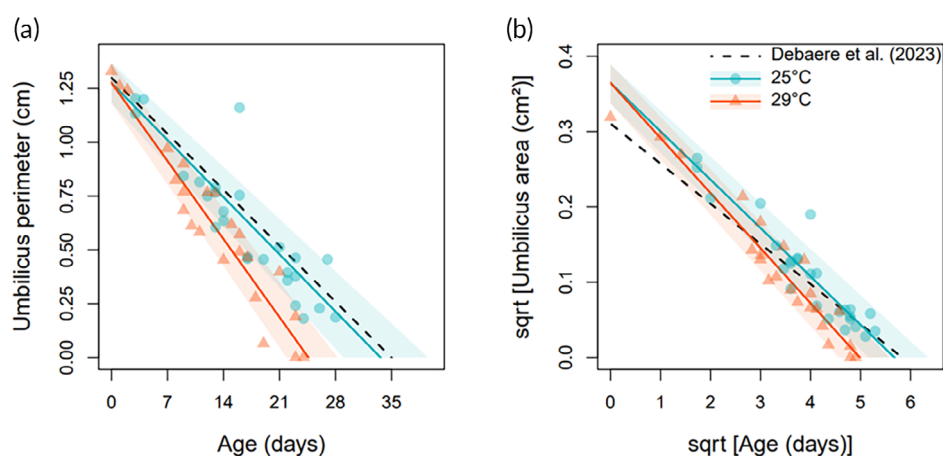


FIGURE 3 Temperature-dependency of umbilical wound-healing rates in neonatal blacktip reef sharks. (a) Temporal change in umbilicus perimeter and (b) temporal change in square root transformed umbilicus area for sharks exposed to 29°C (red, triangles) and 25°C (blue, circles) temperature treatments. The solid line represents the best fit from a linear mixed-effect model with 95% confidence intervals (shaded bands) and the dashed line is modelled from Debaere et al. (2023). Sample sizes: 25°C, $n = 7$ unique individuals; 29°C, $n = 6$ unique individuals.

4 | DISCUSSION

We used two long-term fisheries-independent datasets, one from Moorea, French Polynesia, and one from St. Joseph Atoll, Seychelles,

to conduct a comparative analysis of the healing dynamics of minor wounds in neonatal reef sharks. Using these data, we explored the hypotheses that (1) the energetic cost associated with wound healing after injury will result in reduced growth rates of neonates,

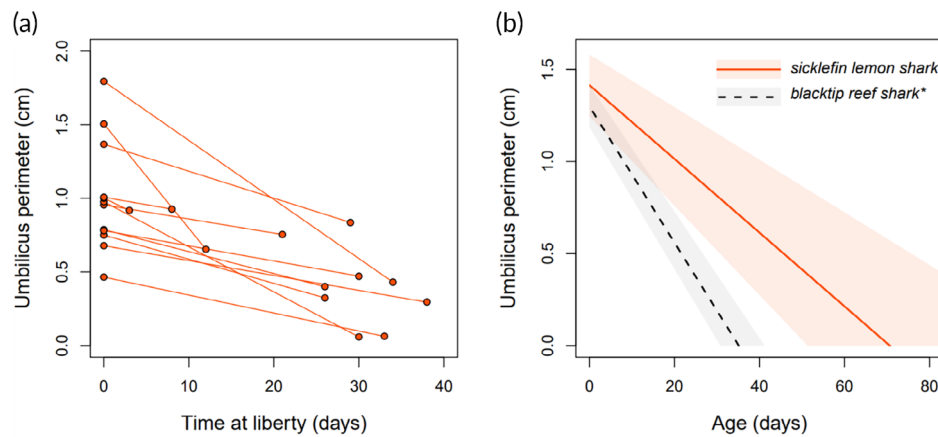


FIGURE 4 Umbilical wound-healing rate of individual neonatal sicklefin lemon sharks. (a) Umbilicus perimeter closing rate of sicklefin lemon shark neonates around Moorea ($n = 12$ unique individuals) with a slope for temporal umbilicus perimeter decline of $0.020 \pm 0.004 \text{ cm day}^{-1}$. (b) The obtained slope and intercept for umbilicus perimeter closing rate of sicklefin lemon shark neonates (solid line, red) ($y = 1.41 - 0.020x$, where y is the umbilicus perimeter [in cm] and x is the elapsed time since birth [in days]). *The umbilicus perimeter closing rate of blacktip reef shark neonates (dashed line, grey; Debaere et al., 2023) is plotted alongside that of the sicklefin lemon sharks.

(2) umbilical wounds will heal faster at higher temperatures, and (3) umbilical wound-healing rates will vary between species. We found no impact of minor, external wounds on growth and body condition in neonatal blacktip reef and sicklefin lemon sharks (refuting hypothesis 1), accelerated umbilical wound healing in neonatal blacktip reef sharks under elevated ambient temperatures (supporting hypothesis 2), and distinct umbilical wound-healing rates between neonatal blacktip reef and sicklefin lemon sharks (supporting hypothesis 3). This study examines how the environment (particularly ambient water temperatures) influences wound-healing rates and the life-history trade-offs associated with injury, and may offer valuable insights into how future ocean conditions (i.e., global ocean warming) could affect the healing capabilities of sharks.

The energy required to recover from skin traumas and repair damaged tissues often leads to a reduced investment in routine metabolic activities (Rennolds & Bely, 2023). As such, the energetic demands of wound healing may impact growth and body condition (e.g., Rennolds & Bely, 2023), which can in turn affect higher levels of biological complexity (e.g., population dynamics). However, although a negative relationship between growth or body condition was expected with injury, specific growth rates and relative changes in body condition did not differ significantly between uninjured and injured neonatal blacktip reef and sicklefin lemon sharks in our study. Note, however, that our study mainly focussed on relatively minor external wounds, whereas larger injuries will likely require a higher energetic cost and may be associated with resource limitations of growth following injury. Additionally, the noteworthy decrease in body condition over time observed here in neonatal blacktip reef sharks (regardless of injury) has been reported previously (Debaere et al., 2023; Weideli, Bouyoucos, et al., 2019) and may be a result of limited prey availability or quality, variable foraging strategies, and/or the negative allometric growth reported for the species (i.e., faster increase in length than in mass).

Given that aquatic ectotherms are governed by environmental water temperatures, the rate of wound healing is expected to be directly influenced by the surrounding water. Our data demonstrated faster healing rates of the umbilical wound of neonatal blacktip reef sharks at ambient temperatures of 29°C , relative to 25°C . Indeed, water temperatures around 29°C have been proposed as the optimal regime to carry out routine metabolic activities for these reef shark neonates (Bouyoucos, Shipley, et al., 2020; Trujillo et al., n.d. under review). In ectothermic animals, metabolic rates increase exponentially with ambient temperature (*C. melanopterus* and *N. acutidens* have a Q_{10} temperature coefficient around 2; Bouyoucos et al., 2022), and higher water temperatures—up to the point of thermal stress—may therefore accelerate wound healing. Similar to our findings, faster healing rates at higher environmental temperatures have been reported across a wide range of fishes (e.g., Anderson & Roberts, 1975; Ang et al., 2021; Bullock et al., 1978; Jensen et al., 2015; Ream et al., 2003). Accelerated wound healing at elevated environmental temperatures across fishes appears to be dictated by increased metabolic rates (Clarke & Johnston, 1999) and may in turn lead to a decreased risk of infection in warmer waters.

It is, however, worthwhile to note that these native umbilical wounds may contain properties that benefit the progression of tissue repair (e.g., Roy et al., 2022) and potentially show different healing dynamics as compared to non-native mechanical wounds (e.g., bite or hook injuries). It is also important to note that the observed accelerated umbilical wound healing at higher ambient temperatures may be specific to our laboratory conditions. In the laboratory, blacktip reef shark neonates were offered 5% of their body mass in food every second day (similar to what the neonates would eat ad libitum), which is likely more food than they would be able to catch and consume in the wild (Bush & Holland, 2002; Duncan & Holland, 2006; Lowe, 2002; Weideli, Bouyoucos, et al., 2019). As metabolic rates increase with ambient temperatures, and the laboratory-maintained sharks can

maintain an adequate consumption rate, the neonates may be able to accelerate metabolic activities, such as wound healing (i.e., metabolic activities become cheaper at higher temperatures). In the wild, however, reef shark neonates may not be able to keep up with the energetic demands required to fuel the higher metabolic rates, making them more prone to starvation (i.e., metabolic activities become more expensive at higher temperatures). A subsequent question arising from this issue is whether sharks can use behaviour to select for favourable environmental temperatures in order to optimise wound healing while also maximising survival (e.g., Warwick, 1991), similar to the reported behavioural thermoregulation linked to foraging and digestion (Speed et al., 2012; Watanabe et al., 2021).

The high capacity for wound healing observed in reef shark neonates may represent a resilient trait that can help them accommodate human-induced elevated environmental temperatures (i.e., ocean warming). Neonatal reef sharks inhabiting thermally dynamic habitats, such as shallow, coastal nursery areas, often exhibit thermally insensitive physiological performance (Bouyoucos et al., 2022). In the context of ocean warming, a high healing capability may therefore be a resilient physiological trait, only minimally affected by minor increases in water temperature. Nevertheless, it is possible that reef sharks occupying such shallow, coastal habitats may already be living close to their thermal tolerance limits (Bouyoucos et al., 2021; Gervais et al., 2018; Rummer et al., 2014). Additionally, whether the response of wound healing remains the same across (interacting) environmental stressors remains uncertain. Although experimental studies on wound healing in sharks are lacking, wound healing in the yellow stingray (*Urolophus hannah*) appears to be unaffected by high CO₂ exposure, associated with ocean acidification (Bouyoucos, Morrison, et al., 2020). Future studies should investigate the resilience of wound healing across environmental conditions, regions, and species.

Indeed, the capacity for and resilience of wound healing may differ considerably across shark species, reflecting their diverse life-history strategies. Our data demonstrate a slower closing rate of the umbilical wound of sicklefin lemon shark neonates as compared to blacktip reef shark neonates (Debaere et al., 2023), albeit with wide confidence intervals calculated for the sicklefin lemon sharks. A more detailed investigation into the closing rate of the umbilical wound for this species, based on time-0 recaptures (i.e., neonates with remnants of the umbilical cord that are subsequently recaptured during the following weeks; similar to Debaere et al., 2023), would likely provide for a more precise estimate and narrower confidence interval. It is likely that the Moorea dataset did not capture the early weeks/months of sicklefin lemon shark parturition due to its earlier season than blacktip reef sharks (Mourier, Buray, et al., 2013), resulting in the absence of time-0 sicklefin lemon sharks. Also note that, although the underlying muscle tissue remains visible throughout the first 2 months, the umbilical vein opening—remnant of the connection to the yolk-sac placenta (see Figure S1)—closes within the first few days post-parturition (personal observation). Rapid closing of the umbilical vein opening is likely an important process in these neonatal carcharhinid sharks as it may be an important source of potential infection.

To conclude, our data revealed minimal consequences of minor wounds on growth and body condition in neonatal reef sharks, accelerated wound healing at higher ambient temperatures in blacktip reef shark neonates, and species-specific differences in wound-healing rates. As such, this study provides key data on the wound-healing dynamics of neonatal reef sharks and the various factors that can impact recovery from external traumas. These data are vital for understanding sharks' wound-healing tolerance and offer essential insights for improving fisheries handling practices, with the goal of enhancing sharks' survival after release. For example, education programmes could inform recreational anglers, who may accidentally capture neonatal reef sharks occupying coastal nursery areas, about the physiological and mechanical recovery potential of sharks, and subsequently encourage minimal-handling practices on capture (e.g., by cutting the fishing line near the hook instead of repetitive attempts at removing hooks and by releasing injured sharks; Chin et al., 2015). Furthermore, although our main study site in French Polynesia lays within the world's largest shark sanctuary, such reserves do not affect the cross-border impacts of global climate change. However, sharks' healing capabilities from minor wounds appear to be a resilient physiological trait to elevated water temperatures. As such, minimal-handling practices will likely remain equally important under future oceanic conditions, although other facets of climate change (e.g., ocean deoxygenation and acidification) remain to be explored. In view of the current threats that coastal shark populations face worldwide under the footprint of human activities, a profound knowledge of their recovery potential from human-inflicted injuries will prove valuable data to inform and refine future management efforts.

AUTHOR CONTRIBUTIONS

Conceptualization: S.F. Debaere, O.C. Weideli, G. De Boeck, J.L. Rummer. Investigation: S.F. Debaere, O.C. Weideli, R. Daly, E.M.C. Milanese, J.E. Trujillo, I.A. Bouyoucos, J.L. Rummer. Data curation & formal analysis: S.F. Debaere. Resources: S. Planes, J.L. Rummer. Writing – original draft: S.F. Debaere. Writing – reviewing & editing: all authors.

ACKNOWLEDGEMENTS

The authors wish to acknowledge that this work was partly conducted on the land of the Mā'ohi people on Mo'orea, French Polynesia. The authors thank the staff, students, and volunteers who were involved in collecting field data at the CRILOBE (Physioshark) and the SOSF-D'Arros Research Centre. We also thank the two anonymous reviewers who provided constructive feedback and suggestions that have greatly improved the quality of this manuscript. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

This project was supported by the Laboratoire d'Excellence "CORAIL", the Station d'Écologie Expérimentale of the CRILOBE, the French Ministère de l'Environnement, and the Save Our Seas Foundation. S.F.D. was supported by a Research Foundation Flanders (FWO) PhD Fellowship (11PMC24N) and received funding from the Company of

Biologists (JEBTF-210547) and Flying Sharks. O.C.W. received funding from the Save Our Seas Foundation (Keystone Grant no. 290; 2014–2017) and was supported by the Basler Stiftung für biologische Forschung. R.D. was supported by the Save Our Seas Foundation D'Arros Research Center in the Republic of Seychelles. E.M.C.M. was supported by the University of Milano-Bicocca (Italy), with the Higher Education Learning Agreement for Exchange mobility (ExtraUE) and by a Flying Sharks Research Grant. J.E.T. was supported by a University of Otago Doctoral Scholarship, a Travelling Fellowship from The Company of Biologists, and received funding from a Flying Sharks Research Grant. I.A.B. was supported by a James Cook University Postgraduate Research Scholarship and received funding from the ARC Centre of Excellence for Coral Reef Studies, Company of Biologists (JEBTF-170510), British Ecological Society, Passions of Paradise/Oceania Chondrichthyan Society, and Europcar Polynésie. J.M. was supported by funding from the Direction à l'Environnement (DIREN) of French Polynesia, Coordination Unit of the Coral Reef Initiatives for the Pacific (CRISP Program) and Ministère de l'Environnement, du Développement Durable et de l'Energie (MEDDE). A.C. received funding from the PADI AWARE Foundation that indirectly facilitated his involvement. G.D.B. was supported by a Research Foundation Flanders (FWO) grant (K802021N) and a University of Antwerp BOF grant (44784) for sabbatical leave. J.L.R. received funding from the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies, a L'Oréal-UNESCO Women in Science Foundation Fellowship (2015–2016) and an ARC Discovery Early Career Researcher Award (PDE150101266).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

ORCID

Shamil F. Debaere  <https://orcid.org/0000-0002-3951-3749>

REFERENCES

- Anderson, C. D., & Roberts, R. J. (1975). A comparison of the effects of temperature on wound healing in a tropical and a temperate teleost. *Journal of Fish Biology*, 7, 173–182. <https://doi.org/10.1111/j.1095-8649.1975.tb04588.x>
- Ang, J., Pierezan, F., Kim, S., Heckman, T. I., Sebastiao, F. A., Yazdi, Z., Abdelrazek, S. M. R., & Soto, E. (2021). Use of topical treatments and effects of water temperature on wound healing in common carp (*Cyprinus carpio*). *Journal of Zoo and Wildlife Medicine*, 52, 103–116. <https://doi.org/10.1638/2020-0072>
- Bansemmer, C. S., & Bennett, M. B. (2010). Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*): Implications for population recovery. *Marine and Freshwater Research*, 61, 97–103. <https://doi.org/10.1071/MF08362>
- Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81, 169–193. <https://doi.org/10.1890/10-1510.1>
- Barker, M. J., & Schluessel, V. (2005). Managing global shark fisheries: Suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15, 325–347. <https://doi.org/10.1002/aqc.660>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bird, P. M. (1978). Tissue regeneration in three carcharhinid sharks encircled by embedded straps. *Copeia*, 1978, 345–349. <https://doi.org/10.2307/1443580>
- Black, C. (2023). Resilience in the depths: First example of fin regeneration in a silky shark (*Carcharhinus falciformis*) following traumatic injury. *Journal of Marine Sciences*, 2023, 6639805. <https://doi.org/10.1155/2023/6639805>
- Borucinska, J., Adams, D. H., & Frazier, B. S. (2020). Histologic observations of dermal wound healing in a free-ranging blacktip shark from the southeastern US Atlantic coast: A case report. *Journal of Aquatic Animal Health*, 32, 141–148. <https://doi.org/10.1002/aah.10113>
- Bouyoucos, I. A., Morrison, P. R., Weideli, O. C., Jacquesson, E., Planes, S., Simpfendorfer, C. A., Brauner, C. J., & Rummer, J. L. (2020). Thermal tolerance and hypoxia tolerance are associated in blacktip reef shark (*Carcharhinus melanopterus*) neonates. *Journal of Experimental Biology*, 223(14), jeb221937. <https://doi.org/10.1242/jeb.221937>
- Bouyoucos, I. A., Shipley, O. N., Jones, E., Brooks, E. J., & Mandelman, J. W. (2020). Wound healing in an elasmobranch fish is not impaired by high-CO₂ exposure. *Journal of Fish Biology*, 96, 1508–1511. <https://doi.org/10.1111/jfb.14320>
- Bouyoucos, I. A., Simpfendorfer, C. A., Planes, S., Schwieterman, G. D., Weideli, O. C., & Rummer, J. L. (2022). Thermally insensitive physiological performance allows neonatal sharks to use coastal habitats as nursery areas. *Marine Ecology Progress Series*, 682, 137–152. <https://doi.org/10.3354/meps13941>
- Bouyoucos, I. A., Trujillo, J. E., Weideli, O. C., Nakamura, N., Mourier, J., Planes, S., Simpfendorfer, C. A., & Rummer, J. L. (2021). Investigating links between thermal tolerance and oxygen supply capacity in shark neonates from a hyperoxic tropical environment. *Science of the Total Environment*, 782, 146854. <https://doi.org/10.1016/j.scitotenv.2021.146854>
- Bullock, A. M., Marks, R., & Roberts, R. J. (1978). The cell kinetics of teleost fish epidermis: Epidermal mitotic activity in relation to wound healing at varying temperatures in plaice (*Pleuronectes platessa*). *Journal of Zoology*, 185, 197–204. <https://doi.org/10.1111/j.1469-7998.1978.tb03321.x>
- Buray, N., Mourier, J., Planes, S., & Clua, E. (2009). Underwater photo-identification of sicklefin lemon sharks, *Negaprion acutidens*, at Moorea (French Polynesia). *Cybius*, 33, 21–27.
- Bush, A., & Holland, K. (2002). Food limitation in a nursery area: Estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kane'ohe bay, O'ahu, Hawai'i. *Journal of Experimental Marine Biology and Ecology*, 278, 157–178. [https://doi.org/10.1016/S0022-0981\(02\)00332-5](https://doi.org/10.1016/S0022-0981(02)00332-5)
- Castro, J. I. (1993). The shark nursery of bulls bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes*, 38, 37–48. <https://doi.org/10.1007/BF00842902>
- Chin, A., Mourier, J., & Rummer, J. L. (2015). Blacktip reef sharks (*Carcharhinus melanopterus*) show high capacity for wound healing and recovery following injury. *Conservation. Physiology*, 3, cov062. <https://doi.org/10.1093/conphys/cov062>
- Chin, A., Simpfendorfer, C., Tobin, A., & Heupel, M. (2013). Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. *Marine and Freshwater Research*, 64(10), 965–975.
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905. <https://doi.org/10.1046/j.1365-2656.1999.00337.x>
- Compagno, L. J. V. (1990). Alternative life-history styles of cartilaginous fishes in time and space. *Environmental Biology of Fishes*, 28, 33–75. <https://doi.org/10.1007/BF00751027>

- Danylchuk, A. J., Suski, C. D., Mandelman, J. W., Murchie, K. J., Haak, C. R., Brooks, A. M., & Cooke, S. J. (2014). Hooking injury, physiological status and short-term mortality of juvenile lemon sharks (*Negaprion brevirostris*) following catch-and-release recreational angling. *Conservation Physiology*, 2, cot036. <https://doi.org/10.1093/conphys/cot036>
- Debaere, S. F., Weideli, O. C., Bouyoucos, I. A., Eustache, K. B., Trujillo, J. E., De Boeck, G., Planes, S., & Rummer, J. L. (2023). Quantifying changes in umbilicus size to estimate the relative age of neonatal blacktip reef sharks (*Carcharhinus melanopterus*). *Conservation Physiology*, 11, coad028. <https://doi.org/10.1093/conphys/coad028>
- Dulvy, N. K., & Reynolds, J. D. (1997). Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proceedings of the Royal Society B*, 264, 1309–1315. <https://doi.org/10.1098/rspb.1997.0181>
- Duncan, K. M., & Holland, K. N. (2006). Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series*, 312, 211–221. <https://doi.org/10.3354/meps312211>
- Garner, M. M. (2013). A retrospective study of disease in elasmobranchs. *Veterinary Pathology*, 50, 377–389. <https://doi.org/10.1177/0300985813482147>
- Gervais, C. R., Nay, T. J., Renshaw, G., Johansen, J. L., Steffensen, J. F., & Rummer, J. L. (2018). Too hot to handle? Using movement to alleviate effects of elevated temperatures in a benthic elasmobranch, *Hemiscyllium ocellatum*. *Marine Biology*, 165, 1–12. <https://doi.org/10.1007/s00227-018-3427-7>
- Grafeld, S., Oleson, K. L., Teneva, L., & Kittinger, J. N. (2017). Follow that fish: Uncovering the hidden blue economy in coral reef fisheries. *PLoS One*, 12, e0182104. <https://doi.org/10.1371/journal.pone.0182104>
- Guttridge, T. L., Gruber, S. H., Franks, B. R., Kessel, S. T., Gledhill, K. S., Uphill, J., Krause, J., & Sims, D. W. (2012). Deep danger: Intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series*, 445, 279–291. <https://doi.org/10.3354/meps09423>
- Guttridge, T. L., Myrberg, A. A., Porcher, I. F., Sims, D. W., & Krause, J. (2009). The role of learning in shark behaviour. *Fish and Fisheries*, 10, 450–469. <https://doi.org/10.1111/j.1467-2979.2009.00339.x>
- Heupel, M. R., Carlson, J. K., & Simpfendorfer, C. A. (2007). Shark nursery areas: Concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, 337, 287–297. <https://doi.org/10.3354/meps337287>
- Hodgkiss, R. D., Grant, A., McClelland, J. H. R., Quatre, R., Rademakers, B., Sanchez, C., & Mason-Parker, C. (2017). Population structure of the sicklefin lemon shark *Negaprion acutidens* within the Curieuse Marine National Park, Seychelles. *African Journal of Marine Science*, 39(2), 225–232. <https://doi.org/10.1007/s00360-021-01347-z>
- Hussey, N. E., DiBattista, J. D., Moore, J. W., Ward, E. J., Fisk, A. T., Kessel, S., Guttridge, T. L., Feldheim, K. A., Franks, B. R., Gruber, S. H., Weideli, O. C., & Chapman, D. D. (2017). Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20170166. <https://doi.org/10.1098/rspb.2017.0166>
- Hussey, N. E., Wintner, S. P., Dudley, S. F., Cliff, G., Cocks, D. T., & Aaron MacNeil, M. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology*, 79, 184–193. <https://doi.org/10.1111/j.1365-2656.2009.01623.x>
- Jensen, L. B., Wahli, T., McGurk, C., Eriksen, T. B., Obach, A., Waagbø, R., Handler, A., & Tafalla, C. (2015). Effect of temperature and diet on wound healing in Atlantic salmon (*Salmo salar* L.). *Fish Physiology and Biochemistry*, 41, 1527–1543. <https://doi.org/10.1007/s10695-015-0105-2>
- Knip, D. M., Heupel, M. R., & Simpfendorfer, C. A. (2010). Sharks in near-shore environments: Models, importance, and consequences. *Marine Ecology Progress Series*, 402, 1–11. <https://doi.org/10.3354/meps08498>
- Kronen, M., Vunisea, A., Magron, F., & McArdle, B. (2010). Socio-economic drivers and indicators for artisanal coastal fisheries in Pacific Island countries and territories and their use for fisheries management strategies. *Marine Policy*, 34, 1135–1143. <https://doi.org/10.1016/j.marpol.2010.03.013>
- Lowe, C. G. (2002). Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kane'ohe bay, O'ahu, HI. *Journal of Experimental Marine Biology and Ecology*, 278, 141–156. [https://doi.org/10.1016/S0022-0981\(02\)00331-3](https://doi.org/10.1016/S0022-0981(02)00331-3)
- Marra, N. J., Stanhope, M. J., Jue, N. K., Wang, M., Sun, Q., Pavinski Bitar, P., Richards, V. P., Komissarov, A., Rayko, M., Kliver, S., Stanhope, B. J., Winkler, C., O'Brien, S. J., Antunes, A., Jorgensen, S., & Shivji, M. S. (2019). White shark genome reveals ancient elasmobranch adaptations associated with wound healing and the maintenance of genome stability. *Proceedings of the National Academy of Sciences*, 116, 4446–4455. <https://doi.org/10.1073/pnas.1819778116>
- Martínez, M. L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P., & Landgrave, R. (2007). The coasts of our world: Ecological, economic and social importance. *Ecological Economics*, 63, 254–272. <https://doi.org/10.1016/j.ecolecon.2006.10.022>
- Matich, P., Kiszka, J. J., Mourier, J., Planes, S., & Heithaus, M. R. (2017). Species co-occurrence affects the trophic interactions of two juvenile reef shark species in tropical lagoon nurseries in Moorea (French Polynesia). *Marine Environmental Research*, 127, 84–91. <https://doi.org/10.1016/j.marenvres.2017.03.010>
- Mourier, J., Buray, N., Schultz, J. K., Clua, E., & Planes, S. (2013). Genetic network and breeding patterns of a sicklefin lemon shark (*Negaprion acutidens*) population in the Society Islands, French Polynesia. *PLoS One*, 8, e73899. <https://doi.org/10.1371/journal.pone.0073899>
- Mourier, J., Mills, S. C., & Planes, S. (2013). Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus*. *Journal of Fish Biology*, 82, 979–993. <https://doi.org/10.1111/jfb.12039>
- Mourier, J., & Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Molecular Ecology*, 22, 201–214. <https://doi.org/10.1111/mec.12103>
- Mourier, J., Planes, S., & Mills, S. C. (2024). Steroid hormones as a non-lethal assessment of the reproductive biology in male and female blacktip reef sharks. *Frontiers in Fish Science*, 1, 1284949. <https://doi.org/10.3389/frish.2023.1284949>
- Papastamatiou, Y. P., Caselle, J. E., Friedlander, A. M., & Lowe, C. G. (2009). Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra atoll: A predator-dominated ecosystem. *Journal of Fish Biology*, 75, 647–654. <https://doi.org/10.1111/j.1095-8649.2009.02329.x>
- Pressinotti, L. N., Borges, R. M., Alves de Lima, A. P., Aleixo, V. M., Iunes, R. S., Borges, J. C. S., Cogliati, B., & Cunha Da Silva, J. R. M. (2013). Low temperatures reduce skin healing in the Jacaré do Pantanal (*Caiman yacare*, Daudin 1802). *Biology Open*, 2, 1171–1178. <https://doi.org/10.1242/bio.20135876>
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ream, R. A., Theriot, J. A., & Somero, G. N. (2003). Influences of thermal acclimation and acute temperature change on the motility of epithelial wound-healing cells (keratocytes) of tropical, temperate and Antarctic fish. *Journal of Experimental Biology*, 206, 4539–4551. <https://doi.org/10.1242/jeb.00706>
- Rennolds, C. W., & Bely, A. E. (2023). Integrative biology of injury in animals. *Biological Reviews*, 98, 34–62. <https://doi.org/10.1111/brv.12894>

- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191, 1–382.
- Roberts, C. M., McClean, C. J., Veron, J. E., Hawkins, J. P., Allen, G. R., McAllister, D. E., Mittermeier, C. G., Schueler, F. W., Spalding, M., Wells, F., Vynne, C., & Werner, T. B. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, 295, 1280–1284. <https://doi.org/10.1126/science.1067728>
- Romero, L. M., Dickens, M. J., & Cyr, N. E. (2009). The reactive scope model – A new model integrating homeostasis, allostatics, and stress. *Hormones and Behavior*, 55, 375–389. <https://doi.org/10.1016/j.yhbeh.2008.12.009>
- Roy, A., Mantay, M., Brannan, C., & Griffiths, S. (2022). Placental tissues as biomaterials in regenerative medicine. *BioMed Research International*, 6751456, 1–26. <https://doi.org/10.1155/2022/6751456>
- RStudio Team. (2020). *RStudio: Integrated development for R*. RStudio, Inc. <http://www.rstudio.com/>.
- Rumfelt, L. L. (2014). Shark reproduction, immune system development and maturation. In S. L. Smith, R. B. Sim, & M. F. Flajnik (Eds.), *Immunobiology of the shark*. CRC Press.
- Rummer, J. L., Couturier, C. S., Stecyk, J. A., Gardiner, N. M., Kinch, J. P., Nilsson, G. E., & Munday, P. L. (2014). Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Global Change Biology*, 20, 1055–1066. <https://doi.org/10.1111/gcb.12455>
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods*, 9, 676–682. <https://doi.org/10.1038/nmeth.2019>
- Schoen, A. N., Bouyoucos, I. A., Anderson, W. G., Wheaton, C. J., Planes, S., Mylniczenko, N. D., & Rummer, J. L. (2021). Simulated heat-wave and fishing stressors alter corticosteroid and energy balance in neonate blacktip reef sharks, *Carcharhinus melanopterus*. *Conservation Physiology*, 9, coab067. <https://doi.org/10.1093/conphys/coab067>
- Sherman, C. S., Simpfendorfer, C. A., Pacoureau, N., Matsushiba, J. H., Yan, H. F., Walls, R. H., & Dulvy, N. K. (2023). Half a century of rising extinction risk of coral reef sharks and rays. *Nature Communications*, 14, 15. <https://doi.org/10.1038/s41467-022-35091-x>
- Smith, D. A., Barker, I. K., & Allen, O. B. (1988). The effect of ambient temperature and type of wound on healing of cutaneous wounds in the common garter snake (*Thamnophis sirtalis*). *Canadian Journal of Veterinary Research*, 52, 120–128.
- Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., & Bradshaw, C. J. (2012). Heat-seeking sharks: Support for behavioural thermoregulation in reef sharks. *Marine Ecology Progress Series*, 463, 231–244. <https://doi.org/10.3354/meps09864>
- Stevens, J. D. (1984). Life-history and ecology of sharks at Aldabra atoll, Indian Ocean. *Proceedings of the Royal Society of London. Series B Biological Sciences*, 222, 79–106. <https://doi.org/10.1098/rspb.1984.0050>
- Trujillo, J. E., Bouyoucos, I., Rayment, W. J., Domenici, P., Planes, S., Rummer, J. L., & Allan, B. J. (2022). Escape response kinematics in two species of tropical shark: Short escape latencies and high turning performance. *Journal of Experimental Biology*, 225, jeb243973. <https://doi.org/10.1242/jeb.243973>
- Trujillo, J. E., Bouyoucos, I. A., Weideli, O. C., Milanese, E. M. C., Debaere, S. F., Rayment, W. J., Planes, S., Domenici, P., Rummer, J. L., & Allan, B. J. M. (n.d.). (under review). Safety in the shallows: nearshore coastal habitats can provide physical and thermal features that optimize escape performance in newborn blacktip reef sharks (*Carcharhinus melanopterus*).
- Ulrich, G. F., Jones, C. M., Driggers, W. B., Drymon, J. M., Oakley, D., & Riley, C. (2007). Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. *American Fisheries Society Symposium*, 50, 125–139.
- Warwick, C. (1991). Observations on disease-associated preferred body temperatures in reptiles. *Applied Animal Behaviour Science*, 28, 375–380. [https://doi.org/10.1016/0168-1591\(91\)90169-X](https://doi.org/10.1016/0168-1591(91)90169-X)
- Watanabe, Y. Y., Nakamura, I., & Chiang, W. C. (2021). Behavioural thermoregulation linked to foraging in blue sharks. *Marine Biology*, 168, 161. <https://doi.org/10.1007/s00227-021-03971-3>
- Wegner, N. C., & Cartamil, D. P. (2012). Effects of prolonged entanglement in discarded fishing gear with substantive biofouling on the health and behavior of an adult shortfin mako shark, *Isurus oxyrinchus*. *Marine Pollution Bulletin*, 64, 391–394. <https://doi.org/10.1016/j.marpolbul.2011.11.017>
- Weideli, O. C., Bouyoucos, I. A., Papastamatiou, Y. P., Mescam, G., Rummer, J. L., & Planes, S. (2019). Same species, different prerequisites: Investigating body condition and foraging success in young reef sharks between an atoll and an island system. *Scientific Reports*, 9, 13447.
- Weideli, O. C., Papastamatiou, Y. P., & Planes, S. (2019). Size frequency, dispersal distances and variable growth rates of young sharks in a multi-species aggregation. *Journal of Fish Biology*, 94, 789–797. <https://doi.org/10.1111/jfb.13968>
- Womersley, F., Hancock, J., Perry, C. T., & Rowat, D. (2021). Wound-healing capabilities of whale sharks (*Rhincodon typus*) and implications for conservation management. *Conservation Physiology*, 9, coaa120. <https://doi.org/10.1093/conphys/coaa120>
- Worm, B., Davis, B., Kettner, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., Kessel, S. T., & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, 40, 194–204. <https://doi.org/10.1016/j.marpol.2012.12.034>
- Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32, 95–126. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114006>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Debaere, S. F., Weideli, O. C., Daly, R., Milanese, E. M. C., Trujillo, J. E., Bouyoucos, I. A., Mourier, J., Chin, A., Planes, S., De Boeck, G., & Rummer, J. L. (2025). The costs and healing rates of minor injuries in neonatal reef sharks. *Journal of Fish Biology*, 106(6), 1777–1788. <https://doi.org/10.1111/jfb.16059>