CHAPTER 11

Improving 'shark park' protections under threat from climate change using the conservation physiology toolbox

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➲ Take-home message

Combining ecophysiology techniques with community outreach and education are valuable steps towards achieving improved protection for shark populations predicted to be vulnerable to climate change.

11.1 Introduction: why protect sharks and rays?

Chondrichthyan fishes (sharks, rays, and chimaeras; hereafter, sharks and rays) are among the most threatened aquatic vertebrate taxa. Many species are thought to be vulnerable to anthropogenic disturbance owing to life-history traits that are characteristic of *K*-selected organisms: slow growth, late maturity, and small litters (Cortés 2000). In general, large-bodied species that occupy shallow habitats with a large geographic range are most at risk of exposure to anthropogenic impacts and categorization under a threatened status (Dulvy et al. 2014; Stein et al. 2018). To date, approximately one quarter of all shark and ray species are threatened with extinction according to the International Union for Conservation of Nature (IUCN) criteria (Dulvy et al. 2014). Targeted fishing—mostly for consumptive purposes—and bycatch (i.e. landings that are unused or without sustainable management) are the predominant threats driving global population declines in sharks and rays (Dulvy et al. 2014; Oliver et al. 2015). Declining shark and ray abundance is well documented, as demonstrated by declining global catch from 2000 to 2011 (Worm et al. 2013; Davidson, Krawchuk and Dulvy 2016). Following exploitation in fisheries, global declines in populations of sharks and rays are driven by habitat loss and degradation (e.g. development, pollution), species control measures (e.g. culling campaigns), and climate change (ocean warming, acidification, and deoxygenation) (Dulvy et al. 2014). Given the sheer number of species and geographic range occupied by sharks and rays across jurisdictional boundaries, their economic value (i.e. fisheries and tourism), and significance as sources of protein, management and conservation strategies for sharks and rays are, at best, complicated (Dulvy et al. 2017; Simpfendorfer and Dulvy 2017).

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Marine protected areas (MPAs) have the potential to halt or reverse declines in shark and ray populations. There is evidence that well-managed and enforced MPAs can contribute to population recovery among reef sharks (Bond et al. 2012; Speed et al. 2018). For some populations of species threatened with extinction, however, MPA coverage can be inadequate such that species' ranges are not well represented in MPAs (Chin et al. 2017; Davidson and Dulvy 2017; White et al. 2017). As conservation tools, MPAs are perceived as moderately effective at achieving shark and ray conservation goals, and MPAs specifically for sharks and rays (e.g. 'shark sanctuaries') are marginally more effective than general MPAs (MacKeracher et al. 2019). MPAs can be effective conservation tools, but not without additional conservation measures (Ward-Paige and Worm 2017; MacKeracher et al. 2019). So-called shark sanctuaries (MPAs specifically for sharks that span a country's entire exclusive economic zone; EEZ) have potential to reduce fishing pressure and population declines for sharks, but a number of unmanaged threats within sanctuaries (e.g. bycatch and ghost fishing, wildlife tourism, climate change) may limit their effectiveness (Ward-Paige 2017; Ward-Paige and Worm 2017). Climate change is a newly recognized threat to sharks and rays globally that will first require evaluation before adequate management and conservation planning can be implemented within MPAs (Chin et al. 2010; Ward-Paige and Worm 2017).

Climate change was only recognized as a threat to sharks and rays in the first decade of the 21st century. Following this, studies started considering the sensitivities of various species to anthropogenic climate change for conservation and management planning (Chin et al. 2010; Fuentes et al. 2016). To this end, research efforts have been dedicated to tracking animals to model future distributions (Hazen et al. 2013; Sequeira et al. 2014; Payne et al. 2018), and experimental studies have been designed to generate a mechanistic understanding of animals' responses to predicted climate change conditions (Rosa et al. 2017; Bouyoucos et al. 2019). Climate change is predicted to alter the physiology and behaviour of sharks and rays through myriad global change phenomena: ocean warming (Rosa et al. 2014; Pistevos et al. 2015; Di Santo 2016; Gervais et al. 2018), increases in storm frequency (Morash et al. 2016; Tunnah et al. 2016), increases in environmental carbon dioxide (i.e. ocean acidification; Rosa et al. 2017), and deoxygenation of ocean habitats (Di Santo et al. 2016; Crear et al. 2019; Schwieterman et al. 2019b). Ocean acidification was first considered a threat in 2014 after targeted studies provided evidence of physiological and behavioural impairments to sharks (Rosa et al. 2017) and skates (Di Santo 2015), despite the previously held notion that this group would be resilient to high environmental carbon dioxide, given their evolutionary history (Rummer and Munday 2017). These global change stressors are predicted to reduce organismal fitness through sublethal impairments to physiological performance, such that adaptive responses include acclimation or redistribution (Sunday et al. 2012; Habary et al. 2017; Donelson et al. 2019). At the time this chapter was written, however, only one species of shark (New Caledonia catshark, *Aulohalaelurus kanakorum*) had been identified as threatened by climate change (Dulvy et al. 2014). Yet, this mostly reflects the scarcity of studies rather than the robustness of these taxa. Species' capacity to acclimate to multiple stressors experienced within an MPA and their potential for redistribution under climate change have clear implications for MPA planning.

Protecting and managing shark and ray populations that are threatened by climate change is a conservation challenge that can be addressed using the conservation physiology toolbox (Madliger et al. 2018). As mentioned above, climate change is predicted to alter the physiology of marine ectotherms (Lefevre 2016). Thus, the conservation physiology toolbox can help improve our understanding of these physiological responses and the mechanisms underpinning changes in performance and fitness (Horodysky et al. 2016; McKenzie et al. 2016). This chapter will discuss how the conservation physiology toolbox has been applied to predict the vulnerability of populations of tropical reef sharks in Australia and French Polynesia to climate change. The overarching goal is to better understand the extent of this threat and suggest conservation strategies. We also discuss the importance of implementing community outreach, education, and social media initiatives, through the collective branding of these projects as the Physioshark project.

11.2 Physioshark: baby sharks and climate change

How can we better protect and manage sharks and rays threatened by climate change if we lack a basic understanding as to the magnitude of the threat to these taxa? To address this key question, the Physioshark project was initiated in 2013 with its purpose being to understand how human-induced stressors, primarily climate change, will affect tropical sharks and rays at all life-history stages, and how that will play into the health and viability of populations. Tropical species represent a major knowledge gap in our understanding of the effects of climate change on sharks and rays (Rosa et al. 2017). Yet, there is an inherent urgency in defining responses of tropical fishes because these species are thought to live close to their upper boundaries for thermal performance and tolerance, such that 1–3°C increases in water temperature may reduce organismal performance with consequences for fitness (Nilsson et al. 2009; Rummer et al. 2014; Comte and Olden 2017). Climate change is not the only threat to sharks being evaluated by Physioshark: bycatch is a considerable problem for sharks and rays within some MPAs and especially within shark sanctuaries (Ward-Paige and Worm 2017). To achieve our goal of generating a mechanistic understanding of the stress tolerance and vulnerability of tropical sharks and rays to anthropogenic stress, Physioshark focuses on species across a range of ecological niches: a small, benthic mesopredator, a medium-sized reef-associated mesopredator, and a large apex predator. In working towards identifying the mechanisms behind tropical species' vulnerabilities to anthropogenic stressors, these data have significance towards managing climate change risk to tropical sharks globally in addition to managing and protecting local populations.

11.3 Case study 1: walking sharks down under

In this first case study we present a series of studies aimed at understanding the climate change vulnerability of a reef-associated shark population, forming the basis of the Physioshark programme. At the time, the work was novel in producing some of the first evidence of physiological and behavioural tolerance of a shark to three major global change stressors (warming, acidification, and deoxygenation), and providing one of the only accounts of the responses of a tropical elasmobranch fish (Rosa et al. 2017; Lopes et al. 2018; Pegado et al. 2018). Here, we describe the comprehensive model approach that initiated this research programme and is now being applied to ongoing projects in French Polynesia.

The Great Barrier Reef (GBR) is home to 133 species of sharks and rays and is part of an MPA that is larger than New Zealand. This World Heritage Area stretches 2300 km along Australia's tropical eastern coastline, includes a series of no-take and no-entry zones, and offers protection to nine species of sharks, five mobulid rays, and all species of sawfishes (GBRMPA 2019). Reef-associated sharks and rays on the GBR are mostly mesopredators with functionally redundant ecosystem roles similar to that of large teleost fishes (Heupel et al. 2014; Roff et al. 2016); regardless, the loss of millions of years of evolutionary history through local extirpations is not an acceptable conservation outcome (Stein et al. 2018). The health of the GBR ecosystem is under considerable threat from climate change, with recent recurrent mass coral bleaching events being responsible for the loss of coral cover and reduced recruitment (Hughes et al. 2017, 2019). Other serious sources of stress include declining water quality and sound pollution (Pratchett et al. 2019), all of which can be investigated with the conservation physiological toolbox (Hess et al. 2017; Jain-Schlaepfer et al. 2018). Sharks on the GBR seem to have benefited from no-entry zones more than no-take areas (Roff et al. 2016; Cinner et al. 2018; Frisch and Rizzari 2019); yet, these protections do not directly buffer against the effects of climate change (Chin et al. 2010). Environmental conditions are important drivers of distribution for some shark species on the GBR, such that some species may move to locate more suitable habitats (Yates et al. 2015; Schlaff et al. 2017). On the other hand, benthic species that are much less capable of redistribution must be able to tolerate local conditions.

The purpose of Physioshark's first investigation into sharks on the GBR was to understand the capacity of a benthic shark with limited dispersal potential to tolerate extreme environmental conditions predicted to occur with climate change. The study species was the epaulette shark (*Hemiscyllium ocellatum*), a species renowned for its remarkable hypoxia and anoxia tolerance (Wise et al. 1998; Routley et al. 2002; Nilsson and Renshaw 2004; Devaux et al. 2019) and ability to 'walk' between tide pools across exposed reef flat using its paired fins (Goto et al. 1999). The epaulette shark is truly a product of its environment. Epaulette sharks on the GBR are found on shallow reef platforms with locally extreme conditions. For instance, diurnal variation in carbon dioxide partial pressures ($p\mathrm{CO}_2$) on a reef flat at Lady Elliot Island on the southern GBR can exceed 1000 µatm (Shaw et al. 2012), the predicted open ocean $p\mathrm{CO}_2$ for the year 2100 under business-as-usual projections (Meinshausen et al. 2011). Reef flats around Heron Island can experience daily summer high temperatures exceeding 35°C (Gervais et al. 2018) and can become hypoxic during low nocturnal tides (Routley et al. 2002). In addition to living a benthic lifestyle, epaulette sharks lay eggs; therefore, developing embryos must also be able to survive such extreme local conditions. Epaulette sharks are listed as a 'least-concern species' by the IUCN Red List, but the report acknowledges a need to research possible threats to epaulette shark populations (Bennet et al. 2015). Therefore, our objectives were to test experimentally, the effects of simulated ocean acidification and warming conditions on physiological performance metrics of epaulette sharks during early ontogeny.

A key tool that is heavily relied upon by Physioshark is respirometry (Madliger et al. 2018). Specifically, intermittent-flow respirometry is a widely used technique to measure oxygen uptake rates ($\dot{M}\mathrm{O}_2$) that serve as proxies of whole-organism metabolic rates (Svendsen et al. 2016). Respirometry systems can be used in the field and laboratory (Farrell et al. 2003; Mochnacz et al. 2017). Moreover, systems come in a variety of designs so that $\dot{M}\mathrm{O}_2$ can be measured at a range of activity levels to elicit an individual's full range of $\dot{M}\mathrm{O}_2$ or aerobic scope, which represents an organism's capacity to take up oxygen to meet metabolic demands (Rummer et al. 2016). Oxygen uptake rates are also widely tested in climate change studies to define thermal performance (via thermal performance of aerobic scope) and hypoxia tolerance (via the critical saturation minimum, P_{crit}), for instance (Bouyoucos et al. 2019). It can be difficult to conduct respirometry on large shark species that must be continuously active (Payne et al. 2015); fortuitously, small, benthic sharks (e.g. epaulette sharks) and juveniles of species that are capable of stationary respiration are well suited to respirometry.

The first series of experiments tested the effects of ocean acidification on sharks developing *in ovo* and juveniles. Across these experiments, sharks were exposed from 1–3 months to a range of static $p\mathrm{CO}_2$ approximating current (~400 µatm), mid-century (~600 µatm), and end-of-century (~900 µatm) values predicted for business-as-usual climate change scenarios (Heinrich et al. 2014, 2016; Johnson et al. 2016). For developing sharks, growth rates, yolk consumption, ventilation rates (i.e. gill movement and tail oscillations), and survival upon hatching were measured. There was no effect of elevated $p\mathrm{CO}_2$ (400 and 900 µatm, ~80 days of exposure) on any trait (Johnson et al. 2016). Next, we tested the effect of elevated $p\mathrm{CO}_2$ (400, 600, and 900 µatm, ~90 days of exposure) on oxygen uptake (resting $\dot{M}\mathrm{O}_2$, as a proxy of basic maintenance costs), hypoxia tolerance (P_{crit}), and a suite of blood- and tissue-based metrics in juvenile epaulette sharks (Heinrich et al. 2014). Sharks had similar P_{crit} and $\dot{M}\mathrm{O}_2$ among $p\mathrm{CO}_2$ treatments that were associated with: (1) elevated plasma bicarbonate ion concentrations to buffer against acidosis; (2) increased whole blood and mean corpuscular haemoglobin concentrations to maintain oxygen uptake; and (3) no change in haematocrit, spleen-somatic index, plasma electrolyte concentrations, and tissue citrate synthase activity (Heinrich et al. 2014). Finally, behavioural endpoints were investigated because of evidence suggesting that behavioural impairments stem from interference with the GABA-A inhibitory neurotransmitter receptor or olfactory epithelium (Heuer et al. 2016; Tresguerres and Hamilton 2017; Porteus et al. 2018). Juveniles exposed to elevated $p\text{CO}_2$ (400, 600, and 900 µatm, ~30 days of exposure) did not exhibit differences in foraging behaviours or shelter-seeking behaviours between treatment groups (Heinrich et al. 2016). Overall, epaulette sharks could tolerate static mid- and end-of-century $p\text{CO}_2$ for months with little to no change across a suite of physiological and behavioural metrics.

A second series of experiments tested the effects of elevated temperature on physiological performance and tolerance of epaulette sharks from embryos to adults. The first study tested for differences in survival of sharks *in ovo* reared at an average summer temperature (28°C) and a predicted end-of-century temperature (32°C) (Gervais et al. 2016). The percentage of embryos that survived to hatch was halved at 32°C, and neonates reared under end-of-century temperatures even lacked pigmentation in their distinctive epaulette patterning (Gervais et al. 2016). Moving forward, juveniles reared at 28°C were tested for differences in growth rates, food consumption rates, temperature preference, and survival following ~140 days of acclimation to either 28 or 32°C (Gervais et al. 2018). Juveniles held at 32°C maintained similar food consumption rates to juveniles held at 28°C but had reduced growth rates and 100 per cent mortality by 80 days into acclimation (Gervais et al. 2018). Sharks maintained at 32°C generally preferred higher temperatures, but a time-of-day effect was also apparent (Gervais et al. 2018). Finally, adult epaulette sharks were collected to characterize seasonal differences in thermal tolerance and ventilation rates (Gervais et al. 2018). Thermal tolerance was quantified using critical thermal maximum (CT_{Max}), which is a measure of the highest temperature an animal can tolerate, beyond which the animal cannot serve a functional ecological role and will eventually die (Dabruzzi et al. 2013). Briefly, sharks are acutely heated until a repeatable, non-lethal behavioural endpoint is achieved, thereby defining an individual's upper thermal tolerance limit. This study found that epaulettes have a thermal safety margin to tolerate some warming; CT_{Max} exceeded maximum winter (~24°C) and summer (~35°C) temperatures (Gervais et al. 2018). Ongoing research by this extended team of researchers into the effects of temperature on physiological performance of epaulette sharks on the GBR aims to investigate development, survival, and acclimatization of embryos, and thermal preference and performance *in situ*.

According to these data, epaulette sharks on the GBR appear well adapted to tolerate two of the three physicochemical challenges of climate change: ocean acidification and deoxygenation. Data suggest that epaulette sharks can tolerate sustained end-of-century $p\text{CO}_2$ conditions without compromising survival (Johnson et al. 2016), predator–prey behaviours (Heinrich et al. 2016), or hypoxia tolerance across this species' early ontogeny (Heinrich et al. 2014). In other words, it's 'business as usual' for epaulette sharks under acidification and hypoxia conditions; although, additional work is needed to characterize sharks' responses to hypoxia and acidification under more natural fluctuating conditions and in combination with other stressors, like warming. Regarding temperature, 4°C of warming drastically reduced embryo, neonate, and juvenile survival (Gervais et al. 2016; Gervais et al. 2018). Furthermore, adult epaulette sharks' upper thermal tolerance limit (~39°C) when held at predicted end-of-century conditions was within several degrees of currently observed summer maximum temperatures (~35°C), although juveniles did exhibit some capacity for using behaviour to select a preferred temperature under summer conditions (Gervais et al. 2018). It remains to be tested whether epaulette sharks are capable of transgenerational acclimation to improve thermal tolerance (Donelson et al. 2018) and whether populations on the GBR are capable of redistribution. Therefore, more work is necessary to determine the extent to which epaulette sharks can maintain their ecological function as mesopredators on the GBR under ocean warming.

In conclusion, the conservation physiology toolbox was employed to identify environmental tolerance limits of epaulette sharks—small-bodied, benthic, tropical mesopredators—under the threat of climate change. The tools used include: bioenergetics and nutritional physiology (growth, body condition, and temperature), cardiorespiratory physiology (oxygen uptake, haematocrit and haemoglobin concentration, muscle enzymes, respiratory rate), and stress physiology (plasma ion concentration, resistance, thermal tolerance) (Madliger et al. 2018). Our data suggest that ocean warming may be a threat to epaulette shark populations on the GBR and can be used in risk assessments to inform species-specific management priorities, especially for this species' northernmost populations (Chin et al. 2010; Gallagher et al. 2012; Fuentes et al. 2016).

11.4 Case study 2: blacktip reef and sicklefin lemon sharks

In this second case study we review an ongoing series of experiments at the core of Physioshark. Here, we discuss the steps taken to establish a research programme focusing on understanding the climate change vulnerability of reef shark populations. In so doing, we describe work done to establish baseline environmental data and quantify performance *in situ* and to experimentally test species' responses to predicted climate change conditions. The research described herein is at the forefront of reef shark science and profits from the success of the epaulette shark case study.

French Polynesia protects all shark species within its 4.7 million km^2 jurisdiction, making it the largest so-called 'shark sanctuary' in the world *c.* 2012 (Andréfouët and Adjeroud 2019). There is apparent high compliance with enforcing regulations and protecting sharks in French Polynesia (Ward-Paige 2017; Ward-Paige and Worm 2017). Among other shark sanctuaries, French Polynesia boasts the largest shark abundance and above-average species richness (Ward-Paige and Worm 2017), including the densest documented aggregation of grey reef sharks (*Carcharhinus amblyrhynchos*) in the world (Mourier et al. 2016). Shark populations are generally considered to be in good health and not in need of further conservation (Ward-Paige and Worm 2017; MacKeracher et al. 2019), yet anthropogenic disturbances related to bycatch (Mourier, Brown and Planes 2017; Bouyoucos et al. 2018b), tourism (Clua et al. 2010; Brena et al. 2015), and marine debris are still considered important threats to sharks in French Polynesia (Ward-Paige and Worm 2017). Climate change is predicted to be a threat to pearl oysters (*Pinctada margaritifera*), giant clams (*Tridacna maxima*), and corals (only under unabated climate change), but ocean warming and acidification are considered threats of least concern to sharks in French Polynesia (Ward-Paige and Worm 2017; Andréfouët and Adjeroud 2019). However, recent evidence documents reductions in performance and survival of tropical sharks, including epaulette sharks, brown-banded bamboo sharks (*Chiloscyllium punctatum*) (Rosa et al. 2014; Rosa et al. 2016a; Rosa et al. 2016b), and white-spotted bamboo sharks (*Chiloscyllium plagiosum*) (Lopes et al. 2018; Pegado et al. 2018). While these species do not occur in French Polynesia, this information was the only baseline for tropical sharks on which to gauge how those of French Polynesia might respond and catalysed much of the research that commenced. The vulnerabilities of shark populations to climate change are slowly becoming apparent, but a considerable knowledge gap remains regarding responses of tropical shark species, and there are no data for high trophic level species (Rosa et al. 2017; Heupel et al. 2019). The best-protected MPAs are not immune to climate change, and French Polynesia's healthy shark populations offer an excellent system for understanding the isolated effects of climate change stressors on reef sharks.

The purpose of our investigation in French Polynesia has been to understand the capacity for high trophic level predators to support fitness-related processes under climate change stress. A secondary goal has been to use this case study as a model for using the conservation physiology toolbox to improve MPA protections for sharks threatened by climate change. Our study species were the 'near threatened' blacktip reef shark (*Carcharhinus melanopterus*), a large-bodied mesopredator, and the 'vulnerable' sicklefin lemon shark (*Negaprion acutidens*), a large-bodied apex predator (Pillans 2003; Heupel 2009). Unlike the small-bodied, benthic species that have previously been investigated (e.g. epaulette and tropical bamboo sharks), large-bodied, high trophic level species can be highly mobile and migratory, have higher energy requirements, and can influence lower trophic level populations through top-down consumptive and fear effects (Heupel et al. 2014; Roff et al. 2016). Climate change-driven impairments to the performance of species like blacktip reef sharks or sicklefin lemon sharks could have population- and ecosystem-level outcomes (Nagelkerken and Munday 2016; Rosa et al. 2017). Similar to previously studied tropical species, however, blacktip reef and sicklefin lemon sharks rely on shallow, nearshore habitats within lagoons as parturition grounds, and neonates appear site-attached to these—potentially shark nursery—habitats (Mourier, Buray et al. 2013; Mourier, Mills et al. 2013). Blacktip reef and sicklefin lemon sharks are also site-attached for reproduction (Mourier and Planes 2013; Mourier, Buray et al. 2013), such that it is unclear whether sharks can select new parturition grounds if conditions reduce survival of neonates and juveniles. Therefore, our objectives were to investigate anthropogenic and ecological sources of stress for neonatal and juvenile blacktip reef and sicklefin lemon sharks and to identify key stressors for targeted management.

Populations of neonatal and juvenile reef sharks have been monitored around Moorea since 2007 by collaborators at the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) (Mourier, Mills et al. 2013). Through research efforts by the CRIOBE and Physioshark, a series of ecological and anthropogenic stressors were identified. The breeding populations of blacktip reef and sicklefin lemon sharks are small enough that inbreeding could affect the survival of offspring (Mourier and Planes 2013; Mourier, Buray et al. 2013). Low interannual recapture rates and low juvenile abundance relative to neonate and adult populations suggest that survival of neonates within their first year of life is intrinsically low (Mourier, Mills et al. 2013). Evidence of infrequent foraging success and scarring/injuries suggest that starvation and predation are common sources of mortality (Chin, Mourier and Rummer, 2015; Weideli et al. 2019). Fishing pressure within the lagoon has affected reef fish communities in the same habitats where neonatal sharks occur; efforts to regulate fishing pressure in these habitats with protected areas have not benefited non-target species, though data for sharks are lacking (Thiault et al. 2017, 2019). Bycatch does occur (Mourier, Brown and Planes, 2017; Bouyoucos et al. 2018b), as indicated by retained fishing hooks, although rates have not been properly quantified and sharks quickly expel hooks (I. Bouyoucos, pers. obs.).

The other issue confounding predictions as to the fate of newborn sharks around Moorea is that these sharks are born during austral summer months (Porcher, 2005; Mourier et al. 2013) when water temperatures average ~30°C (Bouyoucos et al. 2018b). Continuous temperature monitoring and opportunistic dissolved oxygen and pH monitoring at shark capture sites have revealed daily summer trends in the abiotic environment (Figure 11.1a–c). During these monitoring periods, temperatures ranged from 26–35°C with an average daily range of 4°C and extreme range of 8°C in shallow, nearshore water in 2016. Oxygen content was found to decline to ~50% O_2 saturation (3.2 mg O_2/l at ~28°C) during the night and early morning (0100–0500); yet, shallow waters experienced oxygen supersaturation (~120% O_2) during the afternoon and evening owing to high primary productivity. Seawater pH was found to remain relatively high (pH = 7.92–8.47), reflecting oxygen supersaturation and a range of low $p\mathrm{CO}_2$ values (~280–550 μatm) for Moorea's lagoon (Comeau et al. 2014; Edmunds and Burgess, 2016). Given this information, we sought to address the current threat of bycatch, and to quantify physiological performance under warming, low oxygen, and high $p\mathrm{CO}_2$/low pH conditions to understand sharks' climate change vulnerability.

The first series of experiments consulted the conservation physiology toolbox's stress physiology 'kit' to investigate sharks' responses to accidental capture (i.e. bycatch) within the lagoon. As mentioned earlier, it was not uncommon to catch a neonate with fresh or healing bite scars or an embedded fishing hook, suggesting that these animals do have some capacity for surviving and outperforming a predation attempt or fishing encounter (Figure 11.2a–b). We first investigated neonates' capacity for wound healing using the closure of sharks' umbilicus as a proxy for closure of a naturally occurring wound (Chin et al. 2015). These data suggest that blacktip reef sharks have a high capacity for wound healing: umbilicus surface area decreased by ~70 per cent within a week, and these data are corroborated by rapid healing observed in adults with considerable injuries (Chin et al. 2015). Next, sharks faced a fishing stressor *in situ* (gillnet capture with air exposure) to evaluate the

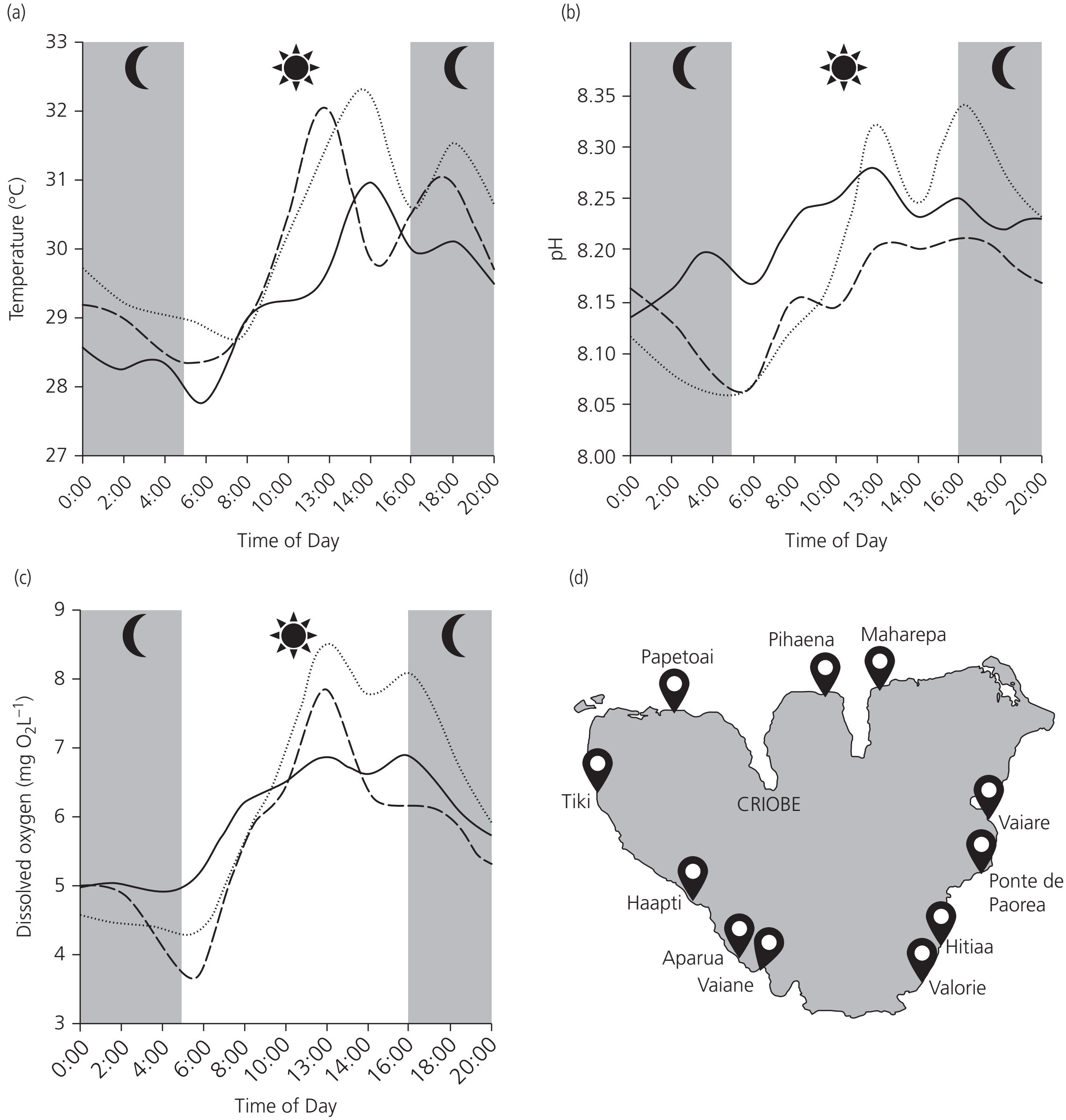

Figure 11.1 Environmental monitoring data from the island of Moorea, French Polynesia. Water temperatures (A), pH (B), and dissolved oxygen concentrations (C) were monitored at 11 locations where newborn reef sharks are found starting in November 2016 through February 2017 (i.e. parturition months). Data were collected at water depths of approximately 50 cm within 10 m of the shoreline, which is where newborn sharks are collected. Values are presented as means in 2-h bins over 24 h for three capture sites (D; Apaura, Pihaena, and Valorie); some of these sites may be defined as shark nursery areas.

physiological status and survival of neonates under stress. Blacktip reef and sicklefin lemon sharks both had increased blood lactate loads and decreased blood pH, relative to minimally stressed reference values, suggesting a reliance on anaerobic metabolism during capture (Bouyoucos et al. 2018b). Other metrics (i.e. blood glucose, haematocrit, and haemoglobin concentration) were unaffected by stress, but glucose and haemoglobin concentrations increased with temperature in blacktip reef and sicklefin lemon

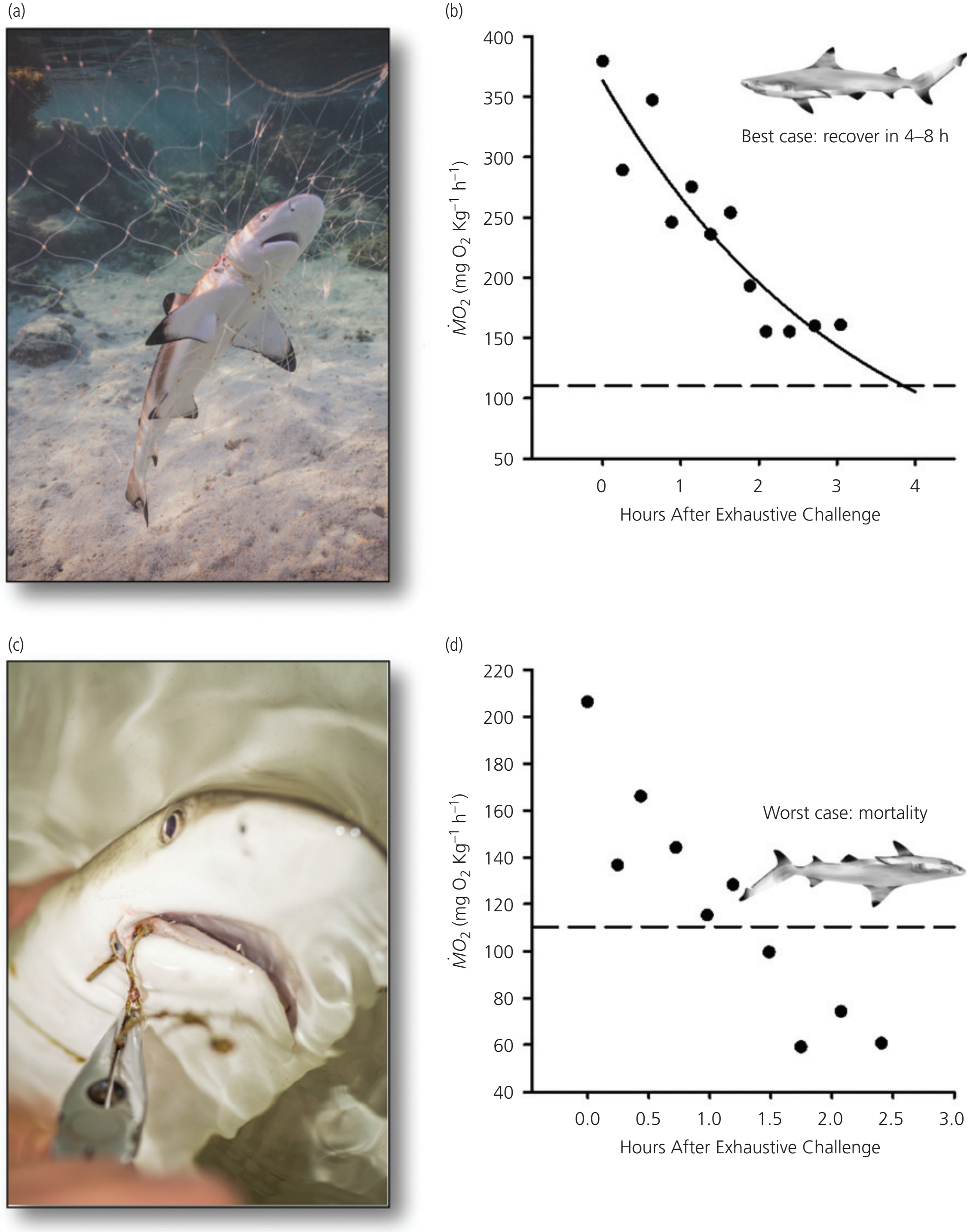

Figure 11.2 Shark bycatch and recovery scenarios for newborn blacktip reef sharks (*Carcharhinus melanopterus*). Around the island of Moorea, French Polynesia, protected reef sharks can be caught accidentally (i.e. bycatch) in nets (A) or on hook-and-line (B). Bycatch interactions initiate a physiological stress response that we assessed using intermittent-flow respirometry *in situ* immediately following capture in a net. We quantified recovery of oxygen uptake rates ($\dot{M}O_2$, a proxy of whole-organism metabolic rate) to a baseline value that was determined in the lab (dashed line in panels C and D). A best-case scenario (C) is full physiological recovery within 4–8 h following net capture. Conversely, a worst-case scenario (D) is delayed mortality. Data are redrawn from Bouyoucos et al. (2018b). Photo credit: Tom Vierus.

sharks, respectively (Bouyoucos et al. 2018b). Both species exhibited delayed mortality; however, blacktip reef sharks had lower (6 per cent) mortality than sicklefin lemon sharks (25 per cent) (Bouyoucos et al. 2018b). Finally, we used respirometry in the field to generate estimates of recovery time for $\dot{M}O_2$ for blacktip reef sharks (Figure 11.2c–d), and estimated that recovery from exhaustive exercise *in situ* could last up to 8.5 h (Bouyoucos et al. 2018b). Taken together, these results suggest that blacktip reef shark neonates are more robust to stress than sicklefin lemon sharks; however, this claim only holds for sharks under stress under the study's 'ideal' temperature conditions (~28–31°C) (Bouyoucos et al. 2018b). Follow-up studies aim to characterize sharks' abilities to cope with stress across a range of environmental conditions.

Examining the overall physiological performance of sharks under variable environmental conditions is an ongoing objective for Physioshark. A similar approach to investigate the effects of ocean acidification in epaulette sharks (Heinrich et al. 2014, 2016) was applied to blacktip reef sharks. Respirometry and blood sampling were used to quantify $\dot{M}O_2$ and underlying physiological status under ambient and end-of-century pCO_2 (~600 and 1000 μatm, respectively) at ambient temperatures (~29°C). Preliminary data suggest that aerobic scope is similar between treatment groups following 30 days of exposure, which is possibly explained by similarities in blood pH, lactate, haematocrit, and haemoglobin concentration between treatment groups (Figure 11.3; Rummer, et al. 2020).

Behavioural responses were also investigated; sharks' behavioural response when exposed to an odour cue (i.e. increased time spent near the odour source and activity level) was the same between treatment groups after 20 days of exposure (Figure 11.4; J. Rummer, unpublished data). Finally, preliminary P_{crit} data suggest that blacktip reef sharks have a higher P_{crit} (~2.6 mg O_2L^{-1} at ~29°C) and are, therefore, less hypoxia-tolerant than epaulette sharks (Heinrich et al. 2014). At a glance, there are similarities among responses of tropical sharks to ocean acidification. Limited physiological responses and no behavioural changes have been documented; although, it remains to be seen how temperature affects reef sharks and how it interacts with ocean acidification conditions (Rosa et al. 2017).

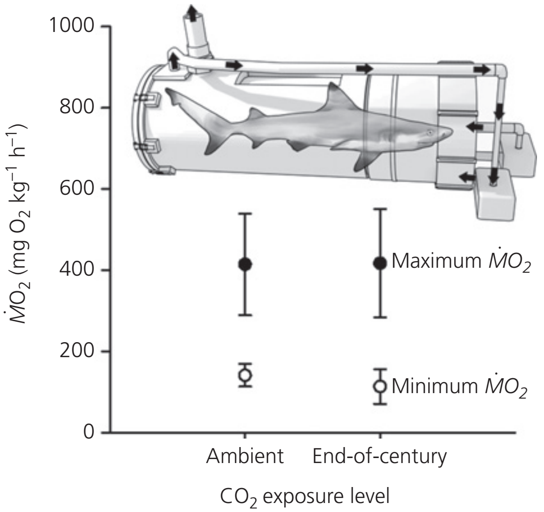

Figure 11.3 Effects of elevated CO_2 exposure level on oxygen uptake rates ($\dot{M}O_2$) of newborn blacktip reef sharks (*Carcharhinus melanopterus*) quantified via intermittent-flow respirometry. Sharks were exposed to ambient (~600 μatm) or end-of-century (~1000 μatm) CO_2 partial pressures (pCO_2) for 30 days. Intermittent-flow respirometry—the respirometry chamber is embedded in the top of the graph—was used to measure sharks' maximum (i.e. upper limit to oxygen uptake) and minimum (i.e. oxygen demand to sustain life) $\dot{M}O_2$. There was no effect of CO_2 exposure. Preliminary data are presented from sharks (ambient $n = 8$, end-of-century $n = 4$) tested at 29°C during 2014 (Rummer et al. 2020).

In conclusion, the conservation physiology toolbox was used to characterize sharks' stress tolerance *in situ* and test sharks' responses to climate change stressors. The tools used include: bioenergetics and nutritional physiology (energy expenditure, metabolic rate, plasma glucose, plasma lactate), cardiorespiratory physiology (aerobic scope, haematocrit and haemoglobin concentration, respiratory rate), and stress physiology (blood pH, resistance) (Madliger et al. 2018). These data suggest that exercise stress (e.g. bycatch, during and following predator evasion) is a considerable stressor for blacktip reef and sicklefin lemon sharks, although blacktip reef sharks at least appear to have a

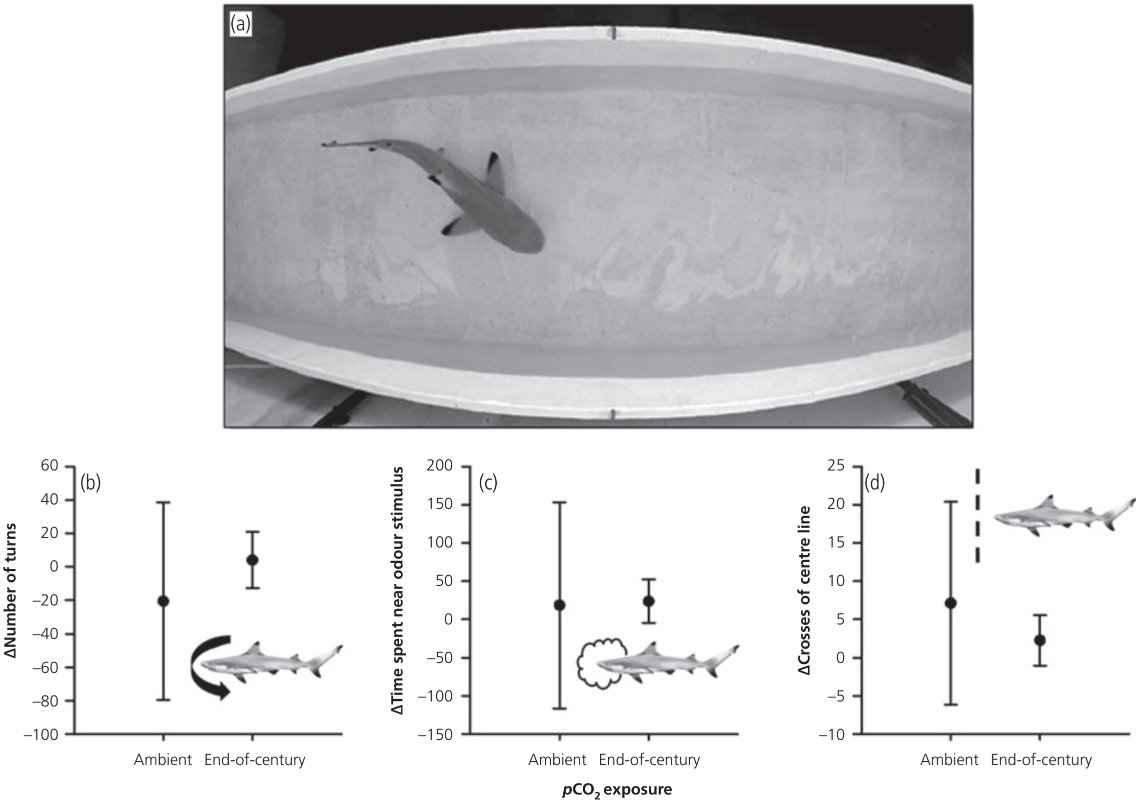

Figure 11.4 Effects of exposure to elevated CO$_2$ partial pressures (pCO$_2$) on the foraging behaviour of newborn blacktip reef sharks (*Carcharhinus melanopterus*). Sharks were exposed to ambient (~600 μatm) or end-of-century (~1000 μatm) pCO$_2$ for 20 days. A raceway tank was used to quantify sharks' behavioural responses to exposure to a prey odour cue (A). The number of times sharks turned (B), the time spent near the odour cue (C), and the number of times sharks crossed the centre line (D) were scored. The differences between behaviours scored during 10 min before and after introducing the odour cue were compared within treatments. There was no effect of CO$_2$ exposure. Preliminary data are presented from sharks (ambient $n = 8$, end-of-century $n = 4$) tested at 29°C during 2014 (J. Rummer, unpublished data).

remarkable capacity for recovery (Chin et al. 2015; Bouyoucos et al. 2018b). Preliminary data suggest that sharks' stress response was temperature-sensitive and that ocean acidification conditions had little effect on physiological and behavioural traits of blacktip reef sharks. Furthermore, nearshore habitats currently do not become too hypoxic for blacktip reef sharks. Ongoing research by Physioshark into compounding stressors will draw conclusions on these populations' vulnerability to climate change to better prepare French Polynesia to protect biodiversity and its natural resources. These data will be the first of their kind for these Indo-Pacific species that occur in many MPAs across their range. Furthermore, these data are directly relevant to addressing the most recent evaluation of French Polynesia's shark sanctuary that claims ocean warming and acidification are considered relatively non-important threats (Ward-Paige and Worm 2017).

11.5 Collaboration towards a global approach

Physioshark is only one of a series of research programmes dedicated to generating conservation outcomes for elasmobranch fishes by applying the conservation physiology toolbox. Other research teams around the world have taken a physiological approach to understanding conservation problems for sharks, including understanding shark declines owing to bycatch and the impact of climate change. For instance, a team based in Australia has done tremendous work characterizing physiological responses in a diversity of shark, ray, and chimaera species to a diversity of gear types (Frick et al. 2010; Heard et al. 2014; Dapp et al. 2017; Martins et al. 2018), validating new physiological and behavioural metrics to measure stress (Van Rijn and Reina 2010; Guida et al. 2016; Guida et al. 2017a), and predicting mortality (Dapp et al. 2016a; Dapp et al. 2016b; Dapp et al. 2016c), and were the first to document sublethal reproductive consequences of capture for sharks and rays (Guida et al. 2017b). In addition, collaboration between groups based in the United States, UK, and The Bahamas has contributed to an understanding of sharks' vulnerabilities to longline (Brooks et al. 2012; Bouyoucos et al. 2017; Bouyoucos et al. 2018a) and drumline capture (Gallagher et al. 2014, 2017; Jerome et al. 2018), suggested alternative methods and techniques to reduce stress on sharks used in research (Brooks et al. 2011a; Brooks et al. 2011b; Sloman et al. 2019), and provided some of the first data on the physiological responses of deep-sea sharks—a group that has recently been exploited by fisheries—to capture (Brooks et al. 2015; Talwar et al. 2017b). Researchers have even contributed to validating veterinary and food industry pH meters and a haemoglobin point-of-care device for use in elasmobranch stress physiology (Harter et al. 2015; Talwar et al. 2017a; Schwieterman et al. 2019a).

The way in which shark stress physiology research has contributed to conservation physiology is well established, yet climate change-driven research has recently begun to emerge *c.* 2014. Much of this work has been predominantly driven by a research group from Portugal (Rosa et al. 2017). This group has contributed to an understanding of the effects of ocean warming and acidification on the embryonic development and performance in juveniles for two tropical benthic sharks (Rosa et al. 2017). Specifically, this group has identified responses to climate change in the form of oxidative damage (Rosa et al. 2016a; Lopes et al. 2018), digestive impairment (Rosa et al. 2016b), and overall reductions in fitness and survival (Rosa et al. 2014; Pegado et al. 2018). Other significant contributions to the growing field come from a team based in the United States that took the first steps towards characterizing physiological responses of embryonic and juvenile rays to ocean acidification (Lauder and Di Santo 2015; Di Santo 2019), warming (Di Santo 2015, 2016), and deoxygenation (Di Santo et al. 2016). Physioshark's focus on bycatch and climate change as conservation issues is not meant to undervalue the considerable research effort of others who have applied the conservation physiology toolbox to sharks and rays (Madliger et al. 2016, 2018; Illing and Rummer 2017). Indeed, Physioshark would not have been possible without collaboration with research teams in the United States, Australia, and France. Thus, it is our hope that continued collaborative efforts of projects like Physioshark ultimately contribute significantly to shark and ray conservation.

11.6 Education and outreach

Public outreach and education about the conservation issues facing sharks is an important component of Physioshark. On the ground in French Polynesia, our team visits primary and secondary schools and receives school groups at the CRIOBE laboratory on Moorea to give presentations on the value of sharks in French Polynesia, the threat of climate change, and the significance of our work to achieving conservation outcomes. Physioshark has also prioritized opportunities to present research at seminar series hosted by the CRIOBE that are open to the public, including France's *Fête de la Science* (Science Celebration) and the International Year of the Reef. Cooperation with respectful media outlets has resulted in numerous print publications and several televised specials broadcast on local and international television networks (e.g. ABC, Polynésie Première), and the ability to interact with media companies (e.g. Disney Nature, Discovery Channel, and National Geographic) for consultation on sharks in French Polynesia. We employ a similar approach in Australia, prioritizing press releases for key papers, appearing on local and national radio, and presenting to diverse audiences at public events.

Physioshark's reach has dramatically expanded, however, largely through use of social media to disseminate information on the programme's key concepts, publications, presentations, media, and successes. Physioshark began on social media using Facebook and Instagram and via the search term #physioshark. During the first two seasons operating on social media, Physioshark's following (56 per cent female, 42 per cent male, 2 per cent other, predominantly ages 25–34, English-speaking, with a bit of French) on Facebook and Instagram steadily increased (Figure 11.5). During our first year using social media, total Facebook impressions exceeded 53 000, with an average of nearly 400 impressions per day (Figure 11.5). This metric represents the number of times our page entered a person's screen. On Instagram, we uploaded 95 posts during this time period, which attracted nearly 12 000 clicks, averaging 125 clicks per post (Figure 11.5). Our top video during our first year using social media, with over 1600 views on Facebook and nearly 500 views on Instagram, was regarding laboratory temperature tolerance tests with juvenile blacktip reef sharks. Our top photo on Instagram was regarding sharks' umbilical scars (i.e. their belly buttons). During our second season employing social media (October 2018 through March 2019), our top video on Facebook reached nearly 19 000 people, resulted in nearly 27 000 impressions, and was regarding our 8-min baby shark documentary that debuted in New York City at the Wildlife Conservation Film Festival and then again at several other international film festivals (Figure 11.5). Clearly, presence on social media has extended the reach of our research and made the questions and answers—our findings—more accessible to the general public. We have continued to upload content to social media while research is ongoing; the 'reach' of social media posts is dramatically higher when content (photographs or videos) is current and of high quality, but also during the off season to keep our following engaged.

Indeed, storytelling through digital media is an important means for attracting attention to research, and an attempt at exposing the viewer to content that can achieve an emotional connection and, in many instances, can result in support and even action. For Physioshark, posting photos and videos

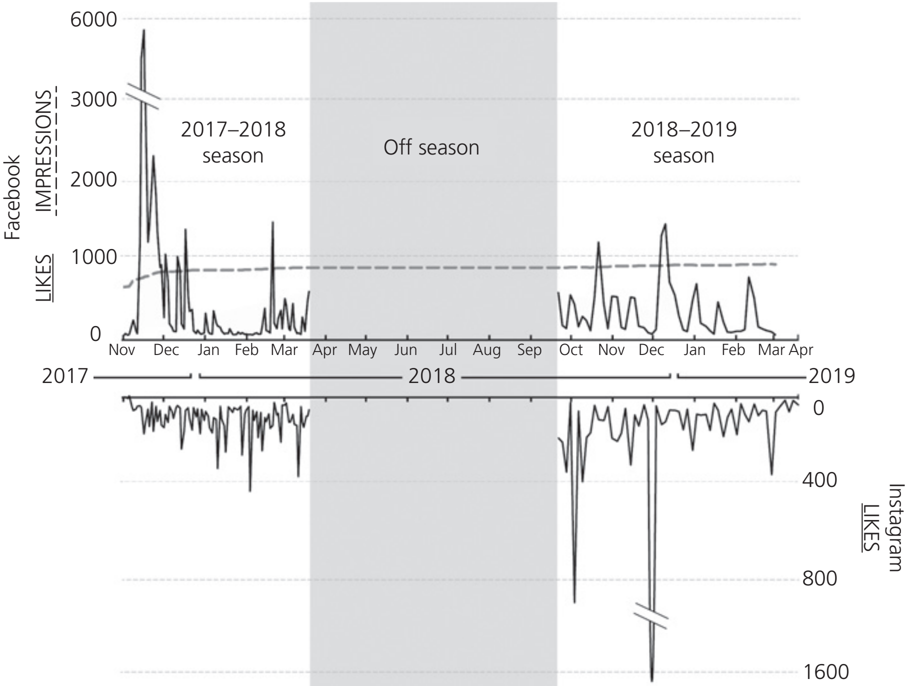

Figure 11.5 Graphical depiction of social media engagement via Facebook (left *y*-axis) and Instagram (right *y*-axis) over two field seasons (2017–2018 and 2018–2019), including an intermediate off-season (April–September 2018) on the *x*-axis. For Facebook, page likes (solid line) and post impressions (the number of times a post appeared on someone's screen; hashed line) are displayed. For Instagram, individual post likes/clicks (solid line) are displayed.

on social media, and engaging in conversations around the topics that are being highlighted as well as the creation of several short documentaries, have also attracted the attention of larger video projects, including a feature-length documentary and television special. Finally, we would be remiss if we did not mention the importance of influential members of the local community, both in French Polynesia and Australia, and their support in promoting Physioshark's research through their channels.

11.7 Conclusions and future directions

In this chapter, we discussed two case studies investigating tropical reef sharks' physiological tolerances to stress and climate change with the conservation physiology toolbox. Two of the study species, the epaulette shark and blacktip reef shark, appear to possess physiological mechanisms to tolerate local hypercapnia and hypoxia without experiencing reductions in physiological performance (Heinrich et al. 2014, 2016; Johnson et al. 2016). Extreme high temperatures appear to reduce survival of epaulette sharks, and ocean warming is predicted to be a threat, at least for this species. Our investigation has also revealed that bycatch interactions can affect the survival of neonatal blacktip reef and sicklefin lemon sharks under current environmental conditions (Chin et al. 2015; Bouyoucos et al. 2018b). Identifying these stressors in our study species and systems has been essential to addressing a knowledge gap for many shark and ray species: is climate change a conservation problem for sharks and rays (Rosa et al. 2017)? Physioshark's research in French Polynesia is in its sixth year at the time that this work is being written (*c.* 2019), and research on epaulette sharks in Australia and with collaborators in the United States are ongoing to achieve conservation outcomes for reef sharks.

The conservation physiology toolbox has much to offer in the way of helping Physioshark achieve its desired conservation outcomes (Madliger et al. 2018). Overall, Physioshark relies on the conservation physiology toolbox primarily for bioenergetics and nutritional physiology, cardiorespiratory physiology, and stress physiology. However, a clear extension of this work is incorporating physiological genomics for a deeper mechanistic understanding of sharks' responses to climate change. Neurophysiology and sensory biology tools are relevant to identifying mechanisms underlying susceptibility to behavioural change in response to ocean acidification. In general, relating ecophysiology to behaviour would be relevant to predicting habitat suitability, an important consideration when studying species with documented site fidelity that may exhibit natal philopatry (Mourier and Planes 2013; Mourier et al. 2013). For our work in Moorea, utilizing tools to characterize reproductive physiology would be particularly relevant for identifying environmental drivers of population abundance and successful lineages with 'climate change-resistant' phenotypes. Immunology has been used for characterizing fisheries stress in elasmobranch fishes but, to our knowledge, has not yet been applied to sharks and rays in an environmental change context. Finally, toxicology tools can help identify cryptic stressors that shark and ray MPAs may not manage. In addition to the conservation physiology toolbox, Physioshark aims to support research through education and outreach. Indeed, we aim to conduct research with deliverables in mind that are palatable to conservation practitioners (Cooke and O'Connor 2010). It is paramount to the success of Physioshark that the conservation problems we address are understood by the general public.

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