Rev Fish Biol Fisheries (2019) 29:297–311
https://doi.org/10.1007/s11160-019-09553-3

REVIEWS

Estimating oxygen uptake rates to understand stress in sharks and rays

Ian A. Bouyoucos · **Colin A. Simpfendorfer** · **Jodie L. Rummer**

Received: 7 August 2018 / Accepted: 6 February 2019 / Published online: 10 April 2019

Abstract Elasmobranch populations face worldwide declines owing to anthropogenic stressors, with lethal and sub-lethal consequences. Oxygen uptake rates ($\dot{M}O_2$, typically measured in mg O_2 kg^{-1} h^{-1}) can be quantified as proxies of whole-organism aerobic metabolic rates and are relevant to fisheries management and conservation through aerobic performance's relationship with fitness and spatial ecology. The purpose of this review was to better understand how $\dot{M}O_2$ has been and can be applied to predict how elasmobranch populations will respond to current and future anthropogenic stressors. We identified 10 studies spanning 9 elasmobranch species that quantified $\dot{M}O_2$ to understand elasmobranch populations' responses to exposure to anthropogenic stressors. Studies measuring responses to climate change stressors (ocean warming and acidification, declining oxygen content, increasing storm frequency) were most common. Studies with relevance to fisheries stressors used $\dot{M}O_2$ to approximate energetic costs of capture and estimate recovery times in bycatch scenarios. Ecotourism encounters were investigated in the context of increases in energetic requirements owing to anthropogenic disruption of diel activity cycles. Furthermore, we discuss how an understanding of $\dot{M}O_2$ in elasmobranchs has been and can be applied to predict populations' responses to anthropogenic stressors with deliverables for improving species management and conservation. Specifically, $\dot{M}O_2$ can be applied to predict population-level responses to stressors by quantifying associations between $\dot{M}O_2$ and fitness-related processes, spatial ecology, and impact on ecosystem function (via bioenergetics modelling). This review is meant to serve as a call-to-action to further bridge the gap between experimental biology and elasmobranch conservation in the "good Anthropocene".

Keywords Aerobic scope · Anthropogenic stress · Climate change · Conservation physiology · Elasmobranchs · Fisheries

I. A. Bouyoucos (✉) · J. L. Rummer
Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
e-mail: ian.bouyoucos@my.jcu.edu.au

I. A. Bouyoucos
PSL Research University, EPHE-UPVD-CNRS, USR 3278 CRIOBE, Université de Perpignan, 58 Avenue Paul Alduy, 66860 Perpignan Cedex, France

C. A. Simpfendorfer
Centre for Sustainable Tropical Fisheries and Aquaculture, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

Introduction

Elasmobranch populations (sharks and rays) have seen worldwide declines that necessitate better protection for threatened populations and improved management for sustainable populations (Simpfendorfer and Dulvy 2017; Dulvy et al. 2017). Overall, elasmobranchs are one of the most threatened vertebrate taxa, partly owing to their life history characteristics that limit species' abilities to rapidly respond to anthropogenic threats (Dulvy et al. 2014; Stein et al. 2018). Overexploitation and bycatch, habitat loss, and climate change have been identified as predominant threats driving declines in many species (Chin et al. 2010; Dulvy et al. 2014). Population declines can occur as a result of direct mortality (e.g., harvest), but also via sub-lethal effects (Wilson et al. 2014). Considering sub-lethal effects is important for understanding outcomes following an animal's exposure to a stressor because sub-lethal effects can have cryptic fitness consequences (Romero et al. 2009). The efficacy of management tools (i.e., ecological risk assessments, stock assessments, etc.) could be improved with physiological data that quantifies sub-lethal responses, thereby allowing for a better understanding of animals' responses to current threats, and the ability to predict responses to anticipated threats (Horodysky et al. 2016; McKenzie et al. 2016). Effectively addressing threats that elasmobranchs are currently facing and predicted to face in the future will require examining species' susceptibility to both lethal and sub-lethal outcomes.

Physiological studies have much to offer elasmobranch conservation. Defining physiological mechanisms underlying conservation problems can provide important information to support management decisions (Cooke et al. 2013), including fisheries management (Horodysky et al. 2016; Illing and Rummer 2017). Numerous studies on elasmobranch species have taken physiological approaches to address prominent conservation issues, such as characterizing injury and stress from commercial and recreational fisheries capture (Skomal and Mandelman 2012) to measuring whole-organism responses to climate change (Rosa et al. 2017). Notably, physiologically-informed models of the condition of southern stingrays (*Hypanus americanus*) at an ecotourism site provided managers with evidence suggesting a need to regulate anthropogenic influences on these animals (Semeniuk et al. 2010; Madliger et al. 2016). As such, there is a utility in implementing and refining physiological tools that are both informative and palatable to conservation practitioners and stakeholders (Cooke and O'Connor 2010; Madliger et al. 2018). In particular, there has been a general call to investigate physiological markers used elsewhere for their applicability as "new" tools to measure stress or predict mortality for elasmobranchs following exposure to anthropogenic stressors (Van Rijn and Reina 2010; Awruch et al. 2011; Guida et al. 2016). Such approaches can help to realise the benefits that physiological research can provide toward elasmobranch conservation.

Changes in oxygen uptake rates ($\dot{M}O_2$, typically in mg O_2 kg^{-1} h^{-1}) can be informative of whole-organism responses to stressors. The $\dot{M}O_2$ of fishes have been quantified since the nineteenth century as a proxy for metabolic rates and therefore a fundamentally important metric for understanding the behavioural and physiological ecology of an organism (Brown et al. 2004; Nelson 2016). Conservation-focused studies on fishes have quantified $\dot{M}O_2$ to address conservation problems, such as those relating to species' or populations' vulnerabilities to environmental change and anthropogenic stressors (Horodysky et al. 2016; McKenzie et al. 2016; Illing and Rummer 2017). For instance, $\dot{M}O_2$ has been used as proxy for various fitness-related metrics to understand vulnerability of many marine ectotherms to climate change (Pörtner et al. 2017; Jutfelt et al. 2018). For elasmobranchs, studies quantifying $\dot{M}O_2$ focus largely on quantifying metabolic costs in a behavioural and physiological ecology context, with relatively few measuring responses to stressors. Indeed, while various studies of stress in elasmobranchs claim that metabolic rates (i.e., $\dot{M}O_2$) should explain species- and population-level variation in elasmobranchs' vulnerability to stressors, a general lack of empirical evidence highlights a mismatch between what conservation-minded studies claim and can support (Skomal and Mandelman 2012).

The purpose of this review was to better understand the utility of quantifying whole-organism performance (i.e., $\dot{M}O_2$) to predict how elasmobranch populations will respond to current and future anthropogenic stressors. We accomplish this goal in two steps. We first describe studies that quantify $\dot{M}O_2$ with the specific objective of predicting elasmobranch populations' responses to various anthropogenic stressors; in so doing, we briefly discuss the specific $\dot{M}O_2$ traits that were measured. Second, we discuss how $\dot{M}O_2$ data have, and can, be applied to predict elasmobranch populations' responses to various anthropogenic stressors. In so doing, this review is intended to serve as a call to action in further bridging the gap between elasmobranch conservation and experimental biology (Cooke et al. 2017).

Methods

To achieve our first objective of reviewing how $\dot{M}O_2$ has been quantified to predict elasmobranch populations' responses to stress, we first targeted all studies that directly measured $\dot{M}O_2$. We included the following caveats in our literature search: (1) only whole-organism—including embryos—$\dot{M}O_2$ was considered and not that of perfused tissues; (2) studies measuring $\dot{M}O_2$ of catheterized or perfused animals were also considered. A systematic literature search of all published research since 1965 (i.e., no theses) was conducted on 1 June 2018 using the Thomas Reuter's Web of Science database with the following search terms: (elasmobranch* OR shark* OR chondrichth* OR dogfish*) AND (oxygen* OR metabol* OR transport* OR binding OR capacity OR respir* OR aerobic* OR ventilat* OR o2 OR gas* OR blood OR h*emato* OR h*emoglobin* OR consum* OR scope). The authors acknowledge that although $\dot{M}O_2$ denotes oxygen uptake strictly in milligrams of O_2 per unit mass per unit time (oxygen uptake was classically measured in millilitres of O_2; $\dot{V}O_2$), $\dot{M}O_2$ will be used throughout to generically refer to oxygen uptake rates (Rummer et al. 2016). Because targeted studies approximated whole-organism metabolic rate via rates of oxygen uptake, this study preferentially refers to $\dot{M}O_2$ rather than "metabolic rates" (Nelson 2016). Indeed, we acknowledge that there are several thorough reviews of $\dot{M}O_2$ in elasmobranchs (Carlson et al. 2004; Bernal et al. 2012). Herein, we briefly describe the few studies that have quantified $\dot{M}O_2$ in response to targeted stressors, and then describe how these data have been, and can be, applied to predict current and future elasmobranch populations' physiological and behavioural responses.

Results and discussion

Estimating $\dot{M}O_2$ to understand stress in elasmobranchs

Commonly measured $\dot{M}O_2$ traits to quantify stress

This review identified 81 studies of $\dot{M}O_2$ spanning 35 shark and ray species (of nearly 1200 total species), of which only 10 studies spanning 9 species were relevant to directly quantifying elasmobranch populations' responses to anthropogenic stressors (Table 1). Five $\dot{M}O_2$ traits were commonly measured in studies measuring stress responses and are discussed below.

The minimum $\dot{M}O_2$ of a quiescent, fasted fish at rest and at stable temperatures represents its $\dot{M}O_{2\mathrm{Min}}$ (Chabot et al. 2016b) and can be a proxy for estimating routine/resting or standard metabolic rates. $\dot{M}O_{2\mathrm{Min}}$ is the most commonly measured component of elasmobranchs' metabolic phenotype, and is often the only metric measured (Carlson et al. 2004; Bernal et al. 2012). Changes in $\dot{M}O_{2\mathrm{Min}}$ in response to stressors can be interpreted as changes in the minimum energetic investment in maintenance, although interpretation is less meaningful without reference to other components of the metabolic phenotype (Hannan and Rummer 2018). The effects of environmental change on $\dot{M}O_{2\mathrm{Min}}$ are well-described elsewhere; briefly, elasmobranchs generally exhibit transient changes in $\dot{M}O_{2\mathrm{Min}}$ in response to osmoregulatory and/or acid–base challenges (e.g., hyposalinity or hypercapnia), $\dot{M}O_{2\mathrm{Min}}$ is highly sensitive to environmental oxygen saturation, and elasmobranchs are not known to thermally compensate (i.e., restoration of $\dot{M}O_{2\mathrm{Min}}$ following temperature change) (Carlson et al. 2004; Tullis and Baillie 2005; Bernal et al. 2012; Hannan and Rummer 2018). While $\dot{M}O_{2\mathrm{Min}}$ is a desirable metric to measure, it has been argued that, for sharks, the lowest swimming $\dot{M}O_2$ is a more ecologically relevant metric than $\dot{M}O_{2\mathrm{Min}}$ because obligate ram-ventilating species cannot achieve $\dot{M}O_{2\mathrm{Min}}$ in the wild anyway (Lowe 2001). Indeed, $\dot{M}O_{2\mathrm{Min}}$ can be approximated for obligate-ram ventilating species by

Table 1 Studies that use oxygen uptake to understand responses of elasmobranch populations to anthropogenic stress

Stressor	Treatments	Metrics	Species (n = 9 of ~ 1200)	References (n = 10 of 81)
Climate change	$p\mathrm{CO}_2^a$, $p\mathrm{O}_2^b$, salinity^c, temperature^d	AS^1, EPOC^2, $\dot{M}\mathrm{O}_{2\mathrm{Min}}^3$, $\dot{M}\mathrm{O}_{2\mathrm{Max}}^4$, $\dot{M}\mathrm{O}_{2\mathrm{Swim}}^5$	*Chiloscyllium punctatum*^{a,d,3}, *Galeorhinus galeus*^{c,3}, *Hemiscyllium ocellatum*^{a,3}, *Leucoraja erinacea*$^{a,b,d,1-5*}$, *Mustelus antarcticus*^{c,3}, *Scyliorhinus canicula*^{a,1,3,4}	Heinrich et al. (2014), Rosa et al. (2014), Green and Jutfelt (2014), Di Santo (2015), Morash et al. (2016), Di Santo et al. (2016) and Di Santo (2016)
Fisheries stressors	Exhaustive exercise	AS^1, EPOC^2, $\dot{M}\mathrm{O}_{2\mathrm{Min}}^3$, $\dot{M}\mathrm{O}_{2\mathrm{Max}}^4$, $\dot{M}\mathrm{O}_{2\mathrm{Swim}}^5$	*Carcharhinus melanopterus*$^{1–4}$, *Negaprion brevirostris*$^{1–5}$	Bouyoucos et al. (2017b, 2018)
Ecotourism encounters	Diel activity	$\dot{M}\mathrm{O}_{2\mathrm{Min}}$, $\dot{M}\mathrm{O}_{2\mathrm{Swim}}$	*Triaenodon obesus*	Barnett et al. (2016)

Lettered superscripts indicate the conditions species were tested under, and numbered superscripts indicate the metrics that were measured. For instance, the notation *Chiloscyllium punctatum*^{a,d,3} indicates that $\dot{M}\mathrm{O}_{2\mathrm{Min}}$ (^{3}) was measured in response to $p\mathrm{CO}_2$ (^{a}) and temperature (^{d})

AS aerobic scope, *EPOC* excess post-exercise oxygen consumption, $\dot{M}O_{2Max}$ maximum oxygen uptake rate, $\dot{M}O_{2Min}$ minimum oxygen uptake rate, pCO_2 partial pressure of carbon dioxide, pO_2 partial pressure of oxygen, $\dot{M}O_{2Swim}$ swimming oxygen uptake rate

*$\dot{M}\mathrm{O}_{2\mathrm{Swim}}$ quantified as tail-beats in *L. erinacea* embryos

extrapolating $\dot{M}\mathrm{O}_2$-activity level relationships to zero activity, although this approach may overestimate $\dot{M}\mathrm{O}_{2\mathrm{Min}}$ (Roche et al. 2013; Di Santo et al. 2017). Alternatively, $\dot{M}\mathrm{O}_{2\mathrm{Min}}$ can be measured for obligate ram-ventilating animals that have been chemically immobilized, but this is a lethal endpoint (Carlson and Parsons 2003; Dowd et al. 2006b).

The highest $\dot{M}\mathrm{O}_2$ value achievable under sustained maximal activity or following fully exhaustive exercise represents maximum $\dot{M}\mathrm{O}_2$ ($\dot{M}\mathrm{O}_{2\mathrm{Max}}$), which serves as a proxy for maximum metabolic rate (Norin and Clark 2016). In elasmobranchs, $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ is limited by the capacity of the cardiorespiratory system for oxygen transport (Hillman et al. 2013), and changes in response to stressors represent changes in the upper limit for oxygen uptake. Relatively few studies have quantified $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ for any elasmobranch in the context of characterising metabolic costs, and fewer have quantified changes in $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ in response to stressors. To date, the available literature suggests equivocal effects of aquatic acidification (via carbon dioxide) on $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ and no temperature effect; no other stressors, like reduced oxygen availability, have been tested (Green and Jutfelt 2014; Di Santo 2016). Research on *Carcharhinus melanopterus* corroborates an absent temperature effect on $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ (IA Bouyoucos, unpublished data); although, challenges associated with measuring $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ for fishes, such as behavioural *versus* physiological fatigue in swimming respirometry chambers or compounding behavioural effects of aquatic acidification should invoke a healthy scepticism of the precision of $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ estimates, especially for elasmobranchs (Peake and Farrell 2006; Lefevre 2016). Clearly, it is difficult to quantify $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ for many elasmobranchs; $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ is typically estimated via swimming in a swimming respirometry chamber or upon chasing to exhaustion (Norin and Clark 2016; Rummer et al. 2016). The former swims fish in a flume or swim tunnel over a range of increasing flow velocities for a fixed period of time and constant velocity increment and estimates $\dot{M}\mathrm{O}_2$ at each flow velocity; $\dot{M}\mathrm{O}_{2\mathrm{Max}}$ is typically estimated as the $\dot{M}\mathrm{O}_2$ value at the flow velocity when fish recruit anaerobic metabolism to support swimming and fatigue. The latter method encourages fish to burst swim in a small pool for a fixed period of time (usually minutes) or until the fish no longer responds to chasing stimuli, after which animals can be air exposed before being placed in a resting respirometry chamber to measure $\dot{M}\mathrm{O}_2$. Some species are too large, even as juveniles, to swim in flume respirometry chambers, or are simply not amenable to forced swimming (Brett and Blackburn 1978; Lowe 2001; Sepulveda et al. 2007). Chasing to exhaustion can produce similar $\dot{M}O_{2Max}$ estimates to swimming in a flume for some teleosts (Killen et al. 2017), but it remains to be determined whether chasing is a viable alternative to swimming elasmobranchs in a flume to generate accurate $\dot{M}O_{2Max}$ estimates. Anecdotally, $\dot{M}O_{2Max}$ measured after exhaustion in a flume was higher than measured after chasing for juvenile *Negaprion brevirostris* (Bouyoucos et al. 2017a, b).

Aerobic scope (AS) represents the oxygen available to support multiple oxygen-demanding processes above $\dot{M}O_{2Min}$ and can be calculated as the difference between (or ratio of) $\dot{M}O_{2Max}$ and $\dot{M}O_{2Min}$ (Clark et al. 2013). Changes in AS are often interpreted as changes in an organism's capacity to use oxygen for fitness-related processes (e.g., growth, reproduction, etc.) (Fry 1947; Claireaux and Lefrançois 2007; Farrell 2016). Among teleost fishes, studies have documented associations between AS and species' ecology (e.g., life-history traits), and can even explain variation among physiological and behavioural traits (Clark et al. 2013; Metcalfe et al. 2016; Killen et al. 2016). Aerobic scope was first referenced in the elasmobranch literature in 1988, or 41 years after its inception (Fry 1947; Du Preez et al. 1988). Several studies provide enough information to calculate AS post hoc (Brett and Blackburn 1978; Graham et al. 1990; Lowe 2001; Bouyoucos et al. 2017a, 2018), but only two have directly tested factors that affect AS in the context of climate change (Green and Jutfelt 2014; Di Santo 2016). Stress physiology studies have suggested that the intensity and magnitude of the elasmobranch stress response during fishing capture is associated with AS, yet none have directly tested this hypothesis (Skomal and Mandelman 2012). The $\dot{M}O_{2Min}$ data appear to support this idea indirectly, where sluggish, benthic species with low $\dot{M}O_{2Min}$ experience lower mortality than active or ram-ventilating species (Skomal and Bernal 2010; Dapp et al. 2016). Furthermore, lamnid and sphyrnid sharks are predicted to have the highest AS among elasmobranchs (Lowe 2001; Sepulveda et al. 2007); yet, lamnid sharks generally exhibit high resilience to stress and high post-release survivorship, whereas sphyrnid sharks experience tremendously high at-vessel and post-release mortality (Marshall et al. 2012; Gallagher et al. 2014; Butcher et al. 2015; French et al. 2015). Thus, studies that directly quantify AS are necessary to fully support or refute this hypothesis.

Excess post-exercise oxygen consumption (EPOC) represents an increase in $\dot{M}O_2$ to resolve a physiological stress response following exhaustive exercise (Gaesser and Brooks 1984; Wood 1991; Milligan 1996). Studies of sharks and rays have measured EPOC as a proxy of anaerobic exercise capacity, to quantify the energetic cost of an activity, and as a means for estimating time to recover following exhaustive exercise (Brett and Blackburn 1978; Bouyoucos et al. 2017a; Di Santo et al. 2017). The presence of EPOC alone can be indicative of a stress response, and changes in the magnitude of EPOC and recovery time can reflect differences in the intensity of stressors (e.g., exhaustive exercise vs fishing capture) and/or changes in an organism's capacity to respond to stress. However, sharks and rays can incur EPOC simply by swimming at routine activity levels; indeed, some elasmobranchs recruit anaerobic metabolism to support sub-maximal swimming (Piiper et al. 1977; Di Santo and Kenaley 2016; Di Santo et al. 2017). The duration and magnitude of EPOC measured for sharks and rays is variable and appears to be related to the duration and intensity of activity. For instance, exhaustion following maximal aerobic swimming resulted in a shorter recovery period and smaller EPOC than exhaustive chasing for juvenile *N. brevirostris* (Bouyoucos et al. 2017a, b). In addition, EPOC and recovery time exhibit sensitivity to environmental stressors; juvenile *Leucoraja erinacea* take longer to recover following exhaustive exercise under aquatic acidification conditions (Di Santo 2016). Previously, studies have referred to animals experiencing—or paying back—an "oxygen debt" from relying on anaerobic metabolic pathways during exercise (Piiper et al. 1977; Brett and Blackburn 1978). It should be noted that the term "oxygen debt" implies a causal mechanism underlying the increase in metabolic rate post-exercise; "EPOC" avoids such confusion (Gaesser and Brooks 1984).

The range of submaximal $\dot{M}O_2$ values of swimming sharks and rays (i.e., swimming $\dot{M}O_2$) can be the most energetically costly and variable component of an elasmobranch's energy budget (Lowe 2001). As such, changes in swimming $\dot{M}O_2$ can represent changes in energy allocation within the available AS, where more time and energy invested in activity over possible fitness-related processes can increase an individual's susceptibility to mortality (Priede 1977). At routine activity levels, available data suggest that sharks' swimming $\dot{M}O_2$ accounts for 25–46% of their AS (Brett and Blackburn 1978; Lowe 2001; Dowd et al. 2006a, b; Bouyoucos et al. 2017b); similar data do not exist for rays. Increases in swimming $\dot{M}O_2$ with activity become proportionally less at higher temperatures; although, swimming $\dot{M}O_2$ at a given velocity increases with temperature (Du Preez et al. 1988; Whitney et al. 2016; Lear et al. 2017). Furthermore, the swimming speed with the lowest cost of transport increases with temperature, making life at higher temperatures inherently more costly (Whitney et al. 2016). Swimming $\dot{M}O_2$ also changes in sharks exposed to hypoxia, but responses likely reflect changes in activity levels rather than changes in the cost of activity; obligate ram-ventilating species generally increase activity levels to minimize time in the hypoxic zone, and buccal-pumping species appear to decrease activity (Parsons and Carlson 1998; Carlson and Parsons 2001). Finally, bio-logging and biotelemetry technologies have made it possible to estimate swimming $\dot{M}O_2$ in situ by calibrating $\dot{M}O_2$ across an ecologically relevant range of activity levels (and temperatures) with electronic tag outputs (e.g., acceleration) (Barnett et al. 2016; Bouyoucos et al. 2017a; Lear et al. 2017).

Climate change

Climate change is a threat to elasmobranch populations, and studies have quantified $\dot{M}O_2$ to better understand the extent of physiological impairment elasmobranchs may experience (Rosa et al. 2017). Ocean acidification is the most-investigated stressor (Heinrich et al. 2014; Rosa et al. 2014; Green and Jutfelt 2014; Di Santo 2015, 2016), despite only recently being considered a threat to elasmobranchs (Chin et al. 2010; Rummer and Munday 2017; Rosa et al. 2017). Thus far, ocean warming has only been investigated alongside acidification (Rosa et al. 2014; Di Santo 2015, 2016). The effects of declining oxygen levels on $\dot{M}O_2$ have been investigated to understand species' hypoxia tolerance in the context of climate change (Heinrich et al. 2014; Di Santo et al. 2016). Similarly, the effects of salinity on $\dot{M}O_2$ have received attention, but only one study to date has investigated the effects of changing salinity in the context of increasing storm frequency with climate change (Carlson et al. 2004; Morash et al. 2016). The paucity of available literature highlights knowledge gaps regarding changes in aerobic (i.e., $\dot{M}O_{2\mathrm{Max}}$ and AS) and anaerobic (e.g., EPOC) capacity in response to key climate change stressors (i.e., ocean acidification and warming, declining oxygen content). In addition, there are a lack of studies investigating species in high trophic positions (e.g., large mesopredators or apex predators), including tropical or deep-sea species (Rosa et al. 2017). Finally, studies have investigated elasmobranch's capacity for developmental and reversible acclimation, but no study to date has investigated sharks' or rays' capacity for transgenerational acclimation (Donelson et al. 2018).

Ocean acidification and warming are predicted to have negative consequences for oxygen uptake rates ($\dot{M}O_{2\mathrm{Min}}$, $\dot{M}O_{2\mathrm{Max}}$, and AS) in embryonic, juvenile, and adult sharks and rays. Both temperate and tropical species are expected to have higher $\dot{M}O_{2\mathrm{Min}}$ and are predicted to develop—from the early embryonic stages—faster under warming and acidification conditions, but neonates may exhibit reduced body condition and lower survival than conspecifics reared under current-day conditions (Rosa et al. 2014; Di Santo 2015; Gervais et al. 2016). The effects of acidification alone on $\dot{M}O_{2\mathrm{Min}}$, $\dot{M}O_{2\mathrm{Max}}$, and AS are equivocal (Heinrich et al. 2014; Green and Jutfelt 2014; Hannan and Rummer 2018). However, acidification appears to lengthen recovery from exhaustive exercise, and exacerbates the effects of warming on $\dot{M}O_{2\mathrm{Min}}$, $\dot{M}O_{2\mathrm{Max}}$, and AS (Rosa et al. 2014; Di Santo 2015; Lefevre 2016; Di Santo 2016). There is also evidence of population-level differences in $\dot{M}O_2$ and responses to warming and acidification (Di Santo 2015, 2016). Temperature sensitivity of $\dot{M}O_2$ in elasmobranchs should be expected; mitochondrial ATP production becomes increasingly inefficient at high temperatures (i.e., increased proton leak across mitochondrial membranes), ectothermic species have relatively temperature-sensitive haemoglobins, and no species has been documented to exhibit thermal compensation of $\dot{M}O_{2\mathrm{Min}}$ (Tullis and Baillie 2005; Schulte 2015; Bernal et al. 2018). Furthermore, elasmobranchs' apparent resilience to some of the effects of ocean acidification may be a result of elasmobranchs' high plasma buffering capacities and ability to maintain haemoglobin-oxygen affinity (i.e., weak or absent Bohr-shifts) under acidotic conditions, relative to teleosts (Berenbrink 2005; Morrison et al. 2015). Indeed, elasmobranchs appear to possess physiological mechanisms to maintain $\dot{M}O_2$ under acidotic conditions; although, the mechanism is different to that in teleosts and has not yet been identified (Hannan and Rummer 2018).

The effects of hypoxia on $\dot{M}O_2$ in the context of climate change have been investigated for elasmobranchs with confined distributions (i.e., benthic species and embryos in egg cases). Briefly, a common hypoxia tolerance metric is the oxygen level at which $\dot{M}O_{2\mathrm{Min}}$ can no longer be regulated, and decreases with declining oxygen content (Wood 2018). The epaulette shark, *Hemiscyllium ocellatum*, a species renowned among elasmobranchs for its hypoxia tolerance, did not experience changes in $\dot{M}O_2$ or hypoxia tolerance under elevated $p\mathrm{CO}_2$ (Heinrich et al. 2014). Egg-bound embryonic *L. erinacea* reared at 15 °C were found to reduce $\dot{M}O_2$ but increase tail-beating activity (i.e., for ventilation) at moderately low oxygen saturations, possibly supporting their activity anaerobically (Di Santo et al. 2016). Indeed, metabolic scope (tail-beating $\dot{M}O_2$–$\dot{M}O_{2\mathrm{Min}}$) for embryonic *L. erinacea* was higher at 18 °C and 20 °C relative to 15 °C, which suggests embryonic *L. erinacea* could have a greater capacity for tail-beating and tolerating hypoxia under warming (Di Santo 2015; Di Santo et al. 2016). Elasmobranchs are generally considered to have poor hypoxia tolerance (Routley et al. 2002); elasmobranch haemoglobins generally have higher oxygen affinities than teleost haemoglobins, but lack comparable mechanisms to improve oxygen delivery, such as increases in haematocrit, strong pH-sensitivity of haemoglobins, or a β-adrenergic stress response at the red blood cells (Brill and Lai 2015; Morrison et al. 2015). Clearly, more research is needed to characterize the responses of elasmobranchs to hypoxia in the context of climate change.

The effects of changing salinity on elasmobranchs are variable and dependent on the duration of exposure. The frequency of storm and drought events are predicted to increase as climate change progresses, and these environmental challenges could have consequences for salinity exposure (e.g., acute changes in $\dot{M}O_{2\mathrm{Min}}$), particularly in coastal and estuarine environments (Morash et al. 2016; Tunnah et al. 2016). Sharks (*Galeorhinus galeus* and *Mustelus antarcticus*) that were acutely exposed to changes in salinity over a 48-h period exhibited changes in $\dot{M}O_{2\mathrm{Min}}$ (Morash et al. 2016; Tunnah et al. 2016). Increases in $\dot{M}O_{2\mathrm{Min}}$ can represent increased osmoregulatory maintenance costs, while reduced $\dot{M}O_{2\mathrm{Min}}$ may relate to reductions in Hb–O_2 affinity. Notably, the potential mechanism underlying changes in $\dot{M}O_{2\mathrm{Min}}$ in response to osmotic challenges, the osmorespiratory compromise, has not been identified in elasmobranchs (Tunnah et al. 2016). Given the relevance of increased frequency and severity of storm events with climate change, further investigation into the effects of osmotic challenges on elasmobranchs is warranted.

Fisheries stressors

The energetic costs and recovery times associated with fisheries capture have been estimated by quantifying EPOC. Chasing protocols supplemented with air exposure are often employed in teleost stress studies because these techniques induce a similar physiological disturbance as fishing capture and handling (Clark et al. 2012; Currey et al. 2013). For example, EPOC estimated by chasing juvenile *N. brevirostris* to exhaustion was paired with swimming $\dot{M}O_2$ estimated from acceleration data from juveniles hooked on experimental longlines to produce an estimate of the total energetic cost of a longline capture event (Bouyoucos et al. 2017b). In this case, capture resulted in a 58% increase in energy expenditure during a 1-h capture event; although, the estimated 5-h recovery costs only represented a 2% increase in daily activity energy expenditure (Bouyoucos et al. 2017b). Alternatively, the cost of the initial struggling period during capture can be estimated by immediately transferring animals to respirometry chambers in situ; using this approach, gill-net capture was estimated to increase the daily activity energy expenditure of juvenile *C. melanopterus* by 15% and required almost 9 h of recovery (Bouyoucos et al. 2018). Estimates of $\dot{M}O_2$ may also partially explain inter-specific variation in stress responses following capture. When compared to *N. acutidens*, the reduction in blood pH following gill-net capture and delayed mortality rates were both less pronounced (Bouyoucos et al. 2018).

Ecotourism encounters

Finally, $\dot{M}O_2$ has been applied to understand the energetic costs of human-wildlife encounters. Human-wildlife encounters, such as those mediated through ecotourism, can be a source of stress for elasmobranchs (Brena et al. 2015; Gallagher et al. 2015). Interacting with wildlife tourism operations has been demonstrated to affect $\dot{M}O_2$ in elasmobranchs through changes in diel activity levels (Barnett et al. 2016). Specifically, changes in activity levels have been related to swimming $\dot{M}O_2$ and $\dot{M}O_{2\mathrm{Min}}$ through calibrated relationships between $\dot{M}O_2$ and telemetry device output (i.e., overall dynamic body acceleration as a proxy of $\dot{M}O_2$ and metabolic rate). For instance, provisioning was documented to increase oxygen uptake rates of whitetip reef sharks (*Triaenodon obesus*) by increasing activity levels during the day when sharks would normally rest (Barnett et al. 2016). Although this is the only instance where $\dot{M}O_2$ has been applied to understand elasmobranchs' responses to stress associated with human-wildlife encounters, it is also possible to quantify $\dot{M}O_2$ as it applies to provisioning via specific dynamic action (SDA; the increase in $\dot{M}O_2$ during digestion and assimilation of food). Large meals, such as those that might occur for bold sharks that consistently feed or sharks that gorge during competitive interactions, may reduce aerobic capacity by reducing the available AS for other oxygen-demanding processes (Norin and Clark 2017). Indeed, single provisioning events can satiate sharks for days (Brunnschweiler et al. 2018). Given concerns that human-wildlife encounters can have consequences for the health of sharks and rays (Semeniuk et al. 2010), $\dot{M}O_2$ can be applied to quantify stress, especially in the context of bioenergetics, that is associated with ecotourism.

Predicting population-level responses from $\dot{M}O_2$ data

To date, laboratory studies of $\dot{M}O_2$ in elasmobranchs have largely taken a basic approach to characterising metabolic costs. While the studies presented in this review take an applied approach in estimating $\dot{M}O_2$ to achieve conservation-minded objectives, these studies' application toward predicting species- or population-level responses to the investigated anthropogenic stressors can be vague. Herein, we attempt to demonstrate how estimates of $\dot{M}O_2$ for elasmobranch populations can be of relevance to elasmobranch fisheries management and conservation. Specifically, we discuss how $\dot{M}O_2$ estimates (with an emphasis on AS) can be applied to predict changes in fitness, spatial ecology, and bioenergetics for elasmobranch populations (Claireaux and Lefrançois 2007; Horodysky et al. 2016).

Fitness

Aerobic scope has well-documented associations with fitness-related processes (i.e., growth and reproduction) among teleost fishes, such that AS can be applied to understanding and predicting population-level responses to stressors (Claireaux and Lefrançois 2007; Farrell 2016). For some species and populations, AS is optimized under specific environmental conditions; deviation from optimal conditions can result in a decrease in AS that may translate to a decrease in organismal fitness (Fry 1947). Given that the abiotic conditions of the ocean are predictably changing owing to global climate change, AS has emerged as an attractive metric for predicting changes in fitness as climate change progresses (Farrell 2016; Pörtner et al. 2017). Indeed, the concept of an optimum temperature for AS (i.e., a "bell-shaped" thermal performance curve), is central to the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis, that has been applied to predict species' responses to ocean warming and acidification, and has been consulted by managing bodies like the Intergovernmental Panel on Climate Change (IPCC; Pörtner et al. 2017). Therefore, elasmobranch species' or populations' vulnerability to climate change stressors can (potentially) be assessed by constructing thermal performance curves for AS and related fitness metrics (e.g., growth rates, reproductive investment, etc.) under the OCLTT framework. Such an approach has, thus far, only been applied to two populations of *L. erinacea*, with a focus on embryos and juveniles (Di Santo 2015; Lefevre 2016; Di Santo 2016). Applying $\dot{M}O_2$ for these two populations of *L. erinacea* to the OCLTT framework suggested that temperatures exceeding the thermal optimum for aerobic performance in embryos was associated with increased mortality, while juveniles experienced sub-lethal reductions in aerobic (i.e., AS) and anaerobic (i.e., escape endurance) performance (Di Santo 2015, 2016). It should be noted, however, that AS is a controversial metric for predicting the vulnerability of ectotherms to climate change, and indeed, the ubiquity of the OCLTT hypothesis is highly controversial (Jutfelt et al. 2018). It has also been suggested that multiple performance metrics ought to be considered, given that different metrics may be optimized under different conditions (Clark et al. 2013). However, given the general lack of measurement of AS in elasmobranchs, further studies to improve our understanding of frameworks like the OCLTT for predicting elasmobranch populations' responses to climate change are warranted (Lefevre 2016).

As a consequence of ocean warming, fishes are predicted to achieve smaller maximum body sizes according to the temperature-size rule, and measuring $\dot{M}O_2$ can help elucidate the extent of the "shrinkage" threat to elasmobranchs. The temperature-size rule highlights a well-documented negative correlation between body size and temperature, and although the specific underlying mechanism is unclear, it may be related to oxygen supply and, therefore, $\dot{M}O_2$ (Forster et al. 2012; Audzijonyte et al. 2018). A highly controversial hypothesis (gill-oxygen limitation, or GOL) posits that a mismatch between oxygen demand at elevated temperatures and capacity for supply across the gills owing to geometric constraints limits fishes' maximum body size (Pauly and Cheung 2017). In other words, for a sufficiently large fish, AS is entirely devoted to $\dot{M}O_{2\mathrm{Min}}$, and increases in temperature increase $\dot{M}O_{2\mathrm{Min}}$, thereby reducing the size when AS is zero. Empirical evidence from elasmobranch studies suggests that $\dot{M}O_{2\mathrm{Min}}$ is proportionally less in larger fishes, and that gill surface area scales with a similar exponent (Wegner 2015; Bigman et al. 2018). Substantial evidence from teleost literature suggests that $\dot{M}O_{2\mathrm{Max}}$ scales with body mass with a similar exponent as $\dot{M}O_{2\mathrm{Min}}$, such that AS could not be reduced to zero (i.e., to only support $\dot{M}O_{2\mathrm{Min}}$) as fish grow (Killen et al. 2016; Lefevre et al. 2017, 2018). Mass- and temperature-scaling (i.e., Q_{10}, the exponential increase in $\dot{M}O_2$ over a 10 °C increment) data for $\dot{M}O_{2\mathrm{Max}}$ do not exist for elasmobranchs. Indeed, there is a dearth of information on mass- and temperature-scaling data for $\dot{M}O_2$ in elasmobranchs, and these data would be of great importance for understanding the mechanism by which elasmobranchs may be expected to shrink as climate change progresses and for modelling the potential apparent shrinkage. Given that hypotheses like GOL have received support from management bodies like the International Union for Conservation of Nature (IUCN), there is certainly interest in applying $\dot{M}O_2$ data to understand how climate change will affect elasmobranch populations.

Spatial ecology

Temperature's profound effect on $\dot{M}O_2$ of ectotherms has been used to link aerobic performance with habitat use and species redistributions, partially in the context of climate change (Portner and Farrell 2008; Sunday et al. 2012). Indeed, various performance metrics, including AS, are thought to be linked with populations' thermal niche, such that populations may occur at temperatures near their optimal temperature for performance (Speers-Roesch and Norin 2016; Payne et al. 2016). Latitudinal shifts in boundary temperatures (i.e., where performance is reduced) may, therefore, coincide with shifts in species' distributions. Studies of elasmobranchs have provided indirect evidence of relationships between performance metrics related to $\dot{M}O_2$ (i.e., activity) and distribution, with one suggesting distribution shifts for *Galeocerdo cuvier* with ocean warming as sharks "follow" water temperatures that optimize activity performance (Payne et al. 2016, 2018). Studies have also provided evidence of shifts in the distribution of pelagic and coastal sharks with warming, although without offering evidence of links to aerobic performance (Hazen et al. 2013; Bangley et al. 2018). Overall, there is much interest for management and conservation in characterising species redistributions for managing changes in ecosystem function and even human wellbeing (Pecl et al. 2017). Indeed, species redistributions can be explained or even predicted by the influence of factors like temperature on $\dot{M}O_2$. Most notably, a physiologically-informed habitat suitability model, centred around estimates of AS, predicted vertical habitat compression for commercially important *Thunnus albacares* in response to climate change driven warming, acidification, and deoxygenation of the pelagic environment (Del Raye and Weng 2015). Ultimately, field and laboratory studies that take an ecophysiological approach to measuring whole-animal performance in elasmobranchs (i.e., $\dot{M}O_2$) can generate meaningful model inputs for predicting changes in species' and populations' habitat use in response to anthropogenic stressors like climate change.

Bioenergetics

Finally, $\dot{M}O_2$ has direct application to elasmobranch fisheries management and application, through its input value in bioenergetics models. For most simplified bioenergetics models, consumption requirements are modelled as the sum of energy invested in metabolism (i.e., $\dot{M}O_2$), generation of waste products, and somatic investment (i.e., growth and reproduction) (Sundström and Gruber 1998; Lowe 2002). Specifically, $\dot{M}O_{2\mathrm{Min}}$ and swimming $\dot{M}O_2$ are valuable model inputs; swimming $\dot{M}O_2$ can be the most variable and energetically costly activity in a fish's daily regime (Lowe and Goldman 2001; Bernal and Lowe 2015). Data on at least mass- and temperature-scaling of $\dot{M}O_2$ should be available to generate precise model estimates that are sensitive to environmental change (Dowd et al. 2006a; Chen et al. 2008; Dale et al. 2013). Bioenergetics models can then be applied to predict consumption requirements of current populations with the goal of quantifying a population's influence on ecosystem function; for high trophic-level species, models can suggest the extent to which populations exert top-down control and contribute to mortality of other commercially important species (Dowd et al. 2006a; Barnett et al. 2017). Furthermore, models can be applied to predict changes in consumption requirements for populations in response to threats like climate change, so that inference can be drawn about future ecosystem function (Luongo and Lowe 2018). Therefore, there is clear support from the literature for applying $\dot{M}O_2$ to create bioenergetics models for elasmobranch populations to support management and conservation goals.

Conclusions and future directions

As this review highlights, there is potential for measuring $\dot{M}O_2$ to predict responses of elasmobranch species and populations to anthropogenic stressors. Indeed, aquatic respirometry techniques and best-practice guidelines for measuring $\dot{M}O_2$ are becoming increasingly accessible (Chabot et al. 2016a). Resources are readily available to construct respirometry chambers, automated pump systems, and even oxygen meters (Svendsen et al. 2016). Studies have even overcome restrictions for working with large animals that have precluded $\dot{M}O_2$ measurement for some species (Graham et al. 1990; Sepulveda et al. 2007; Ezcurra et al. 2012; Payne et al. 2015); although, many species of sharks do not grow larger than 1 m as adults.

Is there utility in estimating $\dot{M}O_2$ to understand and predict elasmobranch species' and populations' responses to stressors? As this review demonstrates, $\dot{M}O_2$ has application to understanding species' responses to various anthropogenic stressors (e.g., climate change, fisheries stressors, and ecotourism encounters), and can ultimately be applied to predict changes in organismal fitness, spatial ecology, and impact on ecosystem function (i.e., via bioenergetics modelling). However, without a foundation of empirical evidence, elasmobranch conservation efforts may be missing critical physiological information underlying species' or populations' responses to current and future anthropogenic stressors (Chin et al. 2010; Lefevre 2016). For instance, we are unaware of any study to date that relates aspects of aerobic performance in elasmobranchs to behavioural traits, such as boldness, that may influence risk-taking or even catchability in fisheries (Redpath et al. 2010; Lennox et al. 2017). Elasmobranchs are certainly a group of fishes that have borne the brunt of anthropogenic influence in the natural world. Diseminating tried-and-tested techniques with tangible deliverables to improve management and conservation of imperilled taxa is paramount to transitioning from an Anthropocene extinction to a "good Anthropocene" (Madliger et al. 2017).

Acknowledgements IA Bouyoucos is supported by an Australian Government Research Training Program Scholarship. JL Rummer is supported by an Australian Research Council (ARC) Early Career Discovery Fellowship

[PDE150101266], a L'Oréal-UNESCO Women in Science Foundation Fellowship (2015–2016), and infrastructure and research allocation from the ARC Centre of Excellence for Coral Reef Studies at James Cook University. We are grateful for the support and constructive feedback from two anonymous reviewers, whose contributions greatly improved the quality of this manuscript.

References

Audzijonyte A, Barneche DR, Baudron AR et al (2018) Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? Glob Ecol Biogeogr. https://doi.org/10.1111/geb.12847

Awruch CA, Simpfendorfer C, Pankhurst NW (2011) Evaluation and use of a portable field kit for measuring whole-blood lactate in sharks. Mar Freshw Res 62:694–699. https://doi.org/10.1071/MF10149

Bangley CW, Paramore L, Shiffman DS, Rulifson RA (2018) Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. Sci Rep 8:6018. https://doi.org/10.1038/s41598-018-24510-z

Barnett A, Payne NL, Semmens JM, Fitzpatrick R (2016) Ecotourism increases the field metabolic rate of whitetip reef sharks. Biol Conserv 199:132–136. https://doi.org/10.1016/j.biocon.2016.05.009

Barnett A, Braccini M, Dudgeon CL et al (2017) The utility of bioenergetics modelling in quantifying predation rates of marine apex predators: ecological and fisheries implications. Sci Rep 7:12982. https://doi.org/10.1038/s41598-017-13388-y

Berenbrink M (2005) Evolution of oxygen secretion in fishes and the emergence of a complex physiological system. Science (80-) 307:1752–1757. https://doi.org/10.1126/science.1107793

Bernal D, Lowe CG (2015) Field studies of elasmobranch physiology. In: Shadwick RE, Farrell AP, Brauner CJ (eds) Physiology of elasmobranch fishes: internal processes. Academic Press, New York, pp 311–377

Bernal D, Carlson JK, Goldman KJ, Lowe CG (2012) Energetics, metabolism, and endothermy in sharks and rays. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edn. CRC Press, Boca Raton, pp 211–237

Bernal D, Reid JP, Roessig JM et al (2018) Temperature effects on the blood oxygen affinity in sharks. Fish Physiol Biochem 44:949–967. https://doi.org/10.1007/s10695-018-0484-2

Bigman JS, Pardo SA, Prinzing TS et al (2018) Ecological lifestyles and the scaling of shark gill surface area. J Morphol. https://doi.org/10.1002/jmor.20879

Bouyoucos IA, Montgomery DW, Brownscombe JW et al (2017a) Swimming speeds and metabolic rates of semi-captive juvenile lemon sharks (*Negaprion brevirostris*, Poey) estimated with acceleration biologgers. J Exp Mar Biol Ecol 486:245–254. https://doi.org/10.1016/j.jembe.2016.10.019

Bouyoucos IA, Suski CD, Mandelman JW, Brooks EJ (2017b) The energetic, physiological, and behavioral response of lemon sharks (*Negaprion brevirostris*) to simulated long-line capture. Comp Biochem Physiol Part A Mol Integr Physiol 207:65–72. https://doi.org/10.1016/j.cbpa.2017.02.023

Bouyoucos IA, Weideli OC, Planes S et al (2018) Dead tired: evaluating the physiological status and survival of neonatal reef sharks under stress. Conserv Physiol 6:coy053. https://doi.org/10.1093/conphys/coy053

Brena PF, Mourier J, Planes S, Clua E (2015) Shark and ray provisioning functional insights into behavioral, ecological and physiological responses across multiple scales. Mar Ecol Prog Ser 538:273–283. https://doi.org/10.3354/meps11492

Brett JR, Blackburn JM (1978) Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. J Fish Res Board Canada 35:816–821

Brill RW, Lai NC (2015) Elasmobranch cardiovascular system. In: Farrell AP, Brauner CJ, Shadwick RE (eds) Physiology of elasmobranch fishes: internal processes. Elsevier, Amsterdam, pp 1–82

Brown JH, Gillooly JF, Allen AP et al (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789. https://doi.org/10.1890/03-9000

Brunnschweiler JM, Payne NL, Barnett A (2018) Hand feeding can periodically fuel a major portion of bull shark energy requirements at a provisioning site in Fiji. Anim Conserv 21:31–35. https://doi.org/10.1111/acv.12370

Butcher PA, Peddemors VM, Mandelman JW et al (2015) At-vessel mortality and blood biochemical status of elasmobranchs caught in an Australian commercial longline fishery. Glob Ecol Conserv 3:878–889. https://doi.org/10.1016/j.gecco.2015.04.012

Carlson JK, Parsons GR (2001) The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. Environ Biol Fishes 61:427–433. https://doi.org/10.1023/A:1011641302048

Carlson JK, Parsons GR (2003) Respiratory and hematological responses of the bonnethead shark, *Sphyrna tiburo*, to acute changes in dissolved oxygen. J Exp Mar Biol Ecol 294:15–26. https://doi.org/10.1016/S0022-0981(03)00237-5

Carlson JK, Goldman KJ, Lowe CG (2004) Metabolism, energetic demand, and endothermy. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 203–224

Chabot D, McKenzie DJ, Craig JF (2016a) Metabolic rate in fishes: definitions, methods and significance for conservation physiology. J Fish Biol 88:1–9. https://doi.org/10.1111/jfb.12873

Chabot D, Steffensen JF, Farrell AP (2016b) The determination of standard metabolic rate in fishes. J Fish Biol 88:81–121. https://doi.org/10.1111/jfb.12845

Chen WK, Liu KM, Liao YY (2008) Bioenergetics of juvenile whitespotted bamboo shark *Chiloscyllium plagiosum* [Anonymous (Bennett)]. J Fish Biol 72:1245–1258. https://doi.org/10.1111/j.1095-8649.2008.01766.x

Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great

Barrier Reef. Glob Change Biol 16:1936–1953. https://doi.org/10.1111/j.1365-2486.2009.02128.x

Claireaux G, Lefrançois C (2007) Linking environmental variability and fish performance: integration through the concept of scope for activity. Philos Trans R Soc B Biol Sci 362:2031–2041. https://doi.org/10.1098/rstb.2007.2099

Clark TD, Donaldson MR, Pieperhoff S et al (2012) Physiological benefits of being small in a changing world: responses of coho salmon (*Oncorhynchus kisutch*) to an acute thermal challenge and a simulated capture event. PLoS ONE 7:e39079. https://doi.org/10.1371/journal.pone.0039079

Clark TD, Sandblom E, Jutfelt F (2013) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J Exp Biol 216:2771–2782. https://doi.org/10.1242/jeb.084251

Cooke SJ, O'Connor CM (2010) Making conservation physiology relevant to policy makers and conservation practitioners. Conserv Lett 3:159–166. https://doi.org/10.1111/j.1755-263X.2010.00109.x

Cooke SJ, Sack L, Franklin CE et al (2013) What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conserv Physiol 1:1–23. https://doi.org/10.1093/conphys/cot001

Cooke SJ, Birnie-Gauvin K, Lennox RJ et al (2017) How experimental biology and ecology can support evidence-based decision-making in conservation: avoiding pitfalls and enabling application. Conserv Physiol. https://doi.org/10.1093/conphys/cox043

Currey LM, Heupel MR, Simpfendorfer CA, Clark TD (2013) Blood lactate loads of redthroat emperor *Lethrinus miniatus* associated with angling stress and exhaustive exercise. J Fish Biol 83:1401–1406. https://doi.org/10.1111/jfb.12216

Dale JJ, Drazen JC, Holland KN (2013) Stingray life history trade-offs associated with nursery habitat use inferred from a bioenergetics model. Mar Biol 160:3181–3192. https://doi.org/10.1007/s00227-013-2305-6

Dapp DR, Walker TI, Huveneers C, Reina RD (2016) Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality. Fish Fish 17:507–524. https://doi.org/10.1111/faf.12124

Del Raye G, Weng KC (2015) An aerobic scope-based habitat suitability index for predicting the effects of multi-dimensional climate change stressors on marine teleosts. Deep Res Part II Top Stud Oceanogr 113:280–290. https://doi.org/10.1016/j.dsr2.2015.01.014

Di Santo V (2015) Ocean acidification exacerbates the impacts of global warming on embryonic little skate, *Leucoraja erinacea* (Mitchill). J Exp Mar Biol Ecol 463:72–78. https://doi.org/10.1016/j.jembe.2014.11.006

Di Santo V (2016) Intraspecific variation in physiological performance of a benthic elasmobranch challenged by ocean acidification and warming. J Exp Biol 219:1725–1733. https://doi.org/10.1242/jeb.139204

Di Santo V, Kenaley CP (2016) Skating by: low energetic costs of swimming in a batoid fish. J Exp Biol 219:1804–1807. https://doi.org/10.1242/jeb.136358

Di Santo V, Tran AH, Svendsen JC (2016) Progressive hypoxia decouples activity and aerobic performance of skate embryos. Conserv Physiol 4:cov067. https://doi.org/10.1093/conphys/cov067

Di Santo V, Kenaley CP, Lauder GV (2017) High postural costs and anaerobic metabolism during swimming support the hypothesis of a U-shaped metabolism–speed curve in fishes. Proc Natl Acad Sci 114:13048–13053. https://doi.org/10.1073/pnas.1715141114

Donelson JM, Salinas S, Munday PL, Shama LNS (2018) Transgenerational plasticity and climate change experiments: where do we go from here? Glob Chang Biol 24:13–34. https://doi.org/10.1111/gcb.13903

Dowd WW, Brill RW, Bushnell PG, Musick JA (2006a) Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model. Fish Bull 104:332–342. https://doi.org/10.1016/j.neuropharm.2005.11.015

Dowd WW, Brill RW, Bushnell PG, Musick JA (2006b) Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change. Fish Bull 104:323–331

Du Preez HH, Mclachlan A, Marais JFK (1988) Oxygen consumption of two nearshore marine elasmobranchs, *Rhinobatos annulatus* (Muller and Henle, 1841) and *Myliobatus aquila* (Linnaeus, 1758). Comp Biochem Physiol Part A Physiol 89:283–294. https://doi.org/10.1016/0300-9629(88)91094-8

Dulvy NK, Fowler SL, Musick JA et al (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3:1–35. https://doi.org/10.7554/eLife.00590

Dulvy NK, Simpfendorfer CA, Davidson LNK et al (2017) Challenges and priorities in shark and ray conservation. Curr Biol 27:R565–R572. https://doi.org/10.1016/j.cub.2017.04.038

Ezcurra J, Lowe C, Mollet H et al (2012) Oxygen consumption rate of young-of-the-year white sharks, *Carcharodon carcharias*, during transport to the Monterey Bay Aquarium. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, pp 17–26

Farrell AP (2016) Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning. J Fish Biol 88:322–343. https://doi.org/10.1111/jfb.12789

Forster J, Hirst AG, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proc Natl Acad Sci 109:19310–19314. https://doi.org/10.1073/pnas.1210460109

French RP, Lyle J, Tracey S et al (2015) High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (*Isurus oxyrinchus*). Conserv Physiol 3:cov044. https://doi.org/10.1093/conphys/cov044

Fry FEJ (1947) Effects of the environment on animal activity. Publ Ont Fish Res Lab 68:1–62

Gaesser GA, Brooks GA (1984) Metabolic bases of excess post-exercise oxygen consumption: a review. Med Sci Sports Exerc 16:29–43

Gallagher AJ, Orbesen ES, Hammerschlag N, Serafy JE (2014) Vulnerability of oceanic sharks as pelagic longline bycatch. Glob Ecol Conserv 1:50–59. https://doi.org/10.1016/j.gecco.2014.06.003

Gallagher AJ, Vianna GMS, Papastamatiou YP et al (2015) Biological effects, conservation potential, and research priorities of shark diving tourism. Biol Conserv 184:365–379. https://doi.org/10.1016/j.biocon.2015.02.007

Gervais C, Mourier J, Rummer JL (2016) Developing in warm water: irregular colouration and patterns of a neonate elasmobranch. Mar Biodivers 46:743–744. https://doi.org/10.1007/s12526-015-0429-2

Graham JB, Dewar H, Lai NC et al (1990) Aspects of shark swimming performance determined using a large water tunnel. J Exp Biol 151:175–192

Green L, Jutfelt F (2014) Elevated carbon dioxide alters the plasma composition and behaviour of a shark. Biol Lett 10:20140538. https://doi.org/10.1098/rsbl.2014.0538

Guida L, Walker TI, Reina RD (2016) The adenylate energy charge as a new and useful indicator of capture stress in chondrichthyans. J Comp Physiol B 186:193–204. https://doi.org/10.1007/s00360-015-0948-y

Hannan KD, Rummer JL (2018) Aquatic acidification: a mechanism underpinning maintained oxygen transport and performance in fish experiencing elevated carbon dioxide conditions. J Exp Biol 221:jeb154559. https://doi.org/10.1242/jeb.154559

Hazen EL, Jorgensen S, Rykaczewski RR et al (2013) Predicted habitat shifts of Pacific top predators in a changing climate. Nat Clim Change 3:234–238. https://doi.org/10.1038/nclimate1686

Heinrich DDU, Rummer JL, Morash AJ et al (2014) A product of its environment: the epaulette shark (*Hemiscyllium ocellatum*) exhibits physiological tolerance to elevated environmental CO_2. Conserv Physiol 2:cou047. https://doi.org/10.1093/conphys/cou047

Hillman SS, Hancock TV, Hedrick MS (2013) A comparative meta-analysis of maximal aerobic metabolism of vertebrates: implications for respiratory and cardiovascular limits to gas exchange. J Comp Physiol B Biochem Syst Environ Physiol 183:167–179. https://doi.org/10.1007/s00360-012-0688-1

Horodysky AZ, Cooke SJ, Graves JE, Brill RW (2016) Fisheries conservation on the high seas: linking conservation physiology and fisheries ecology for the management of large pelagic fishes. Conserv Physiol 4:cov059. https://doi.org/10.1093/conphys/cov059

Illing B, Rummer JL (2017) Physiology can contribute to better understanding, management, and conservation of coral reef fishes. Conserv Physiol 5:cox005. https://doi.org/10.1093/conphys/cox005

Jutfelt F, Norin T, Ern R et al (2018) Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. J Exp Biol 221:jeb169615. https://doi.org/10.1242/jeb.169615

Killen SS, Glazier DS, Rezende EL et al (2016) Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. Am Nat 187:592–606. https://doi.org/10.1086/685893

Killen SS, Norin T, Halsey LG (2017) Do method and species lifestyle affect measures of maximum metabolic rate in fishes? J Fish Biol 90:1037–1046. https://doi.org/10.1111/jfb.13195

Lear KO, Whitney NM, Brewster LR et al (2017) Correlations of metabolic rate and body acceleration in three species of coastal sharks under contrasting temperature regimes. J Exp Biol 220:397–407. https://doi.org/10.1242/jeb.146993

Lefevre S (2016) Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO_2 and their interaction. Conserv Physiol 4:cow009. https://doi.org/10.1093/conphys/cow009

Lefevre S, McKenzie DJ, Nilsson GE (2017) Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. Glob Change Biol 23:3449–3459. https://doi.org/10.1111/gcb.13652

Lefevre S, McKenzie DJ, Nilsson GE (2018) In modelling effects of global warming, invalid assumptions lead to unrealistic projections. Glob Change Biol 24:553–556. https://doi.org/10.1111/gcb.13978

Lennox RJ, Alós J, Arlinghaus R et al (2017) What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish Fish. https://doi.org/10.1111/faf.12219

Lowe CG (2001) Metabolic rates of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). Mar Biol 139:447–453. https://doi.org/10.1007/s002270100585

Lowe CG (2002) Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kāne'ohe Bay, Ō'ahu, HI. J Exp Mar Biol Ecol 278:141–156. https://doi.org/10.1016/S0022-0981(02)00331-3

Lowe CG, Goldman KJ (2001) Thermal and bioenergetics of elasmobranchs: bridging the gap. Environ Biol Fishes 60:251–266

Luongo SM, Lowe CG (2018) Seasonally acclimated metabolic Q10of the California horn shark, *Heterodontus francisci*. J Exp Mar Biol Ecol 503:129–135. https://doi.org/10.1016/j.jembe.2018.02.006

Madliger CL, Cooke SJ, Crespi EJ et al (2016) Success stories and emerging themes in conservation physiology. Conserv Physiol 4:cov057. https://doi.org/10.1093/conphys/cov057

Madliger CL, Franklin CE, Hultine KR et al (2017) Conservation physiology and the quest for a 'good' Anthropocene. Conserv Physiol 5:1–10. https://doi.org/10.1093/conphys/cox003

Madliger CL, Love OP, Hultine KR, Cooke SJ (2018) The conservation physiology toolbox: status and opportunities. Conserv Physiol 6:coy029. https://doi.org/10.1093/conphys/coy029

Marshall H, Field L, Afiadata A et al (2012) Hematological indicators of stress in longline-captured sharks. Comp Biochem Physiol A Mol Integr Physiol 162:121–129. https://doi.org/10.1016/j.cbpa.2012.02.008

McKenzie DJ, Axelsson M, Chabot D et al (2016) Conservation physiology of marine fishes: state of the art and prospects for policy. Conserv Physiol 4:cow046. https://doi.org/10.1093/conphys/cow046

Metcalfe NB, Van Leeuwen TE, Killen SS (2016) Does individual variation in metabolic phenotype predict fish behaviour and performance? J Fish Biol 88:298–321. https://doi.org/10.1111/jfb.12699

Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. Comp Biochem Physiol 113A:51–60. https://doi.org/10.1016/0300-9629(95)02060-8

Morash AJ, Mackellar SRC, Tunnah L et al (2016) Pass the salt: physiological consequences of ecologically relevant hyposmotic exposure in juvenile gummy sharks (*Mustelus antarcticus*) and school sharks (*Galeorhinus galeus*). Conserv Physiol 4:cow036. https://doi.org/10.1093/conphys/cow036

Morrison PR, Gilmour KM, Brauner CJ (2015) Oxygen and carbon dioxide transport in elasmobranchs. In: Shadwick RE, Farrell AP, Brauner CJ (eds) Physiology of elasmobranch fishes: internal processes. Elsevier, London, pp 127–219

Nelson JA (2016) Oxygen consumption rate v. rate of energy utilization of fishes: a comparison and brief history of the two measurements. J Fish Biol 88:10–25. https://doi.org/10.1111/jfb.12824

Norin T, Clark TD (2016) Measurement and relevance of maximum metabolic rate in fishes. J Fish Biol 88:122–151. https://doi.org/10.1111/jfb.12796

Norin T, Clark TD (2017) Fish face a trade-off between 'eating big' for growth efficiency and 'eating small' to retain aerobic capacity. Biol Lett 13:20170298. https://doi.org/10.1098/rsbl.2017.0298

Parsons GR, Carlson JK (1998) Physiological and behavioral responses to hypoxia in the bonnethead shark, *Sphyrna tiburo*: routine swimming and respiratory regulation. Fish Physiol Biochem 19:189–196

Pauly D, Cheung WWL (2017) Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Glob Change Biol. https://doi.org/10.1111/gcb.13831

Payne NL, Snelling EP, Fitzpatrick R et al (2015) A new method for resolving uncertainty of energy requirements in large water breathers: the 'mega-flume' seagoing swim-tunnel respirometer. Methods Ecol Evol 6:668–677. https://doi.org/10.1111/2041-210X.12358

Payne NL, Smith JA, van der Meulen DE et al (2016) Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. Funct Ecol 30:903–912. https://doi.org/10.1111/1365-2435.12618

Payne NL, Meyer CG, Smith JA et al (2018) Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. Glob Change Biol 24:1884–1893. https://doi.org/10.1111/gcb.14088

Peake SJ, Farrell AP (2006) Fatigue is a behavioural response in respirometer- confined smallmouth bass. J Fish Biol 68:1742–1755. https://doi.org/10.1111/j.1095-8649.2006.01052.x

Pecl GT, Araújo MB, Bell JD et al (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science (80-) 355:eaai9214. https://doi.org/10.1126/science.aai9214

Piiper J, Meyer M, Worth H, Willmer H (1977) Respiration and circulation during swimming activity in the dogfish *Scyliorhinus stellaris*. Respir Physiol 30:221–239. https://doi.org/10.1016/0034-5687(77)90032-9

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science (80-) 322:690–692. https://doi.org/10.1126/science.1163156

Pörtner H-O, Bock C, Mark FC (2017) Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. J Exp Biol 220:2685–2696. https://doi.org/10.1242/jeb.134585

Priede IG (1977) Natural selection for energetic efficiency and the relationship between activity level and mortality. Nature 267:610–611. https://doi.org/10.1038/267610a0

Redpath TD, Cooke SJ, Suski CD et al (2010) The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. Can J Fish Aquat Sci 67:1983–1992. https://doi.org/10.1139/F10-120

Roche DG, Binning SA, Bosiger Y et al (2013) Finding the best estimates of metabolic rates in a coral reef fish. J Exp Biol 216:2103–2110. https://doi.org/10.1242/jeb.082925

Romero LM, Dickens MJ, Cyr NE (2009) The reactive scope model—a new model integrating homeostasis, allostasis, and stress. Horm Behav 55:375–389. https://doi.org/10.1155/2010/732586

Rosa R, Baptista M, Lopes VM et al (2014) Early-life exposure to climate change impairs tropical shark survival. Proc R Soc B Biol Sci 281:20141738. https://doi.org/10.1098/rspb.2014.1738

Rosa R, Rummer JL, Munday PL (2017) Biological responses of sharks to ocean acidification. Biol Lett 13:20160796. https://doi.org/10.1098/rsbl.2016.0796

Routley MH, Nilsson GE, Renshaw GMC (2002) Exposure to hypoxia primes the respiratory and metabolic responses of the epaulette shark to progressive hypoxia. Comp Biochem Physiol Part A Mol Integr Physiol 131:313–321. https://doi.org/10.1016/S1095-6433(01)00484-6

Rummer JL, Munday PL (2017) Climate change and the evolution of reef fishes: past and future. Fish Fish 18:22–39. https://doi.org/10.1111/faf.12164

Rummer JL, Binning SA, Roche DG, Johansen JL (2016) Methods matter: considering locomotory mode and respirometry technique when estimating metabolic rates of fishes. Conserv Physiol 4:cow008. https://doi.org/10.1093/conphys/cow008

Schulte PM (2015) The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. J Exp Biol 218:1856–1866. https://doi.org/10.1242/jeb.118851

Semeniuk CAD, Haider W, Cooper A, Rothley KD (2010) A linked model of animal ecology and human behavior for the management of wildlife tourism. Ecol Model 221:2699–2713. https://doi.org/10.1016/j.ecolmodel.2010.07.018

Sepulveda CA, Graham JB, Bernal D (2007) Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. Mar Biol 152:1087–1094. https://doi.org/10.1007/s00227-007-0757-2

Simpfendorfer CA, Dulvy NK (2017) Bright spots of sustainable shark fishing. Curr Biol 27:R97–R98. https://doi.org/10.1016/j.cub.2016.12.017

Skomal G, Bernal D (2010) Physiological responses to stress in sharks. In: Carrier JC, Musick JA, Heithaus MR (eds) Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, pp 457–488

Skomal GB, Mandelman JW (2012) The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comp Biochem Physiol A Mol Integr Physiol 162:146–155. https://doi.org/10.1016/j.cbpa.2011.10.002

Speers-Roesch B, Norin T (2016) Ecological significance of thermal tolerance and performance in fishes: new insights from integrating field and laboratory approaches. Funct Ecol 30:842–844. https://doi.org/10.1111/1365-2435.12652

Stein RW, Mull CG, Kuhn TS et al (2018) Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. Nat Ecol Evol 2:288–298. https://doi.org/10.1038/s41559-017-0448-4

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nat Clim Change 1:2. https://doi.org/10.1038/nclimate1539

Sundström L, Gruber S (1998) Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. Adv Invertebr Fish Telem 371(372):241–247

Svendsen MBS, Bushnell PG, Steffensen JF (2016) Design and setup of intermittent-flow respirometry system for aquatic organisms. J Fish Biol 88:26–50. https://doi.org/10.1111/jfb.12797

Tullis A, Baillie M (2005) The metabolic and biochemical responses of tropical whitespotted bamboo shark *Chiloscyllium plagiosum* to alterations in environmental temperature. J Fish Biol 67:950–968. https://doi.org/10.1111/j.0022-1112.2005.00795.x

Tunnah L, MacKellar SRC, Barnett DA et al (2016) Physiological responses to hypersalinity correspond to nursery ground usage in two inshore shark species (*Mustelus antarcticus* and *Galeorhinus galeus*). J Exp Biol 219:2028–2038. https://doi.org/10.1242/jeb.139964

Van Rijn JA, Reina RD (2010) Distribution of leukocytes as indicators of stress in the Australian swellshark, *Cephaloscyllium laticeps*. Fish Shellfish Immunol 29:534–538. https://doi.org/10.1016/j.fsi.2010.04.016

Wegner NC (2015) Elasmobranch gill structure. In: Shadwick RE, Farrell AP, Brauner CJ (eds) Physiology of elasmobranch fishes: structure and interaction with environment. Elsevier, New York, pp 101–151

Whitney NM, Lear KO, Gaskins LC, Gleiss AC (2016) The effects of temperature and swimming speed on the metabolic rate of the nurse shark (*Ginglymostoma cirratum*, Bonaterre). J Exp Mar Biol Ecol 477:40–46. https://doi.org/10.1016/j.jembe.2015.12.009

Wilson SM, Raby GD, Burnett NJ et al (2014) Looking beyond the mortality of bycatch: sublethal effects of incidental capture on marine animals. Biol Conserv 171:61–72. https://doi.org/10.1016/j.biocon.2014.01.020

Wood CM (1991) Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. J Exp Biol 160:285–308

Wood CM (2018) The fallacy of the P crit—are there more useful alternatives? J Exp Biol 221:jeb163717. https://doi.org/10.1242/jeb.163717