

# 1 Powering ocean giants: the energetics of shark and ray megafauna

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20 Bioenergetics model, ocean deoxygenation, megafauna, metabolism, trophic ecology, warming

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## 28 Abstract

29 Shark and ray megafauna play crucial roles as top predators in many marine ecosystems, but  
30 are currently among the most threatened vertebrates and, based on historical extinctions,  
31 may be highly susceptible to future environmental perturbations. However, our  
32 understanding of their energetics lags behind that of other taxa. Such knowledge is required  
33 to answer important ecological questions and predict their responses to ocean warming,  
34 which may be limited by expanding ocean deoxygenation and declining prey availability. To  
35 develop bioenergetics models for shark and ray megafauna, incremental improvements in  
36 respirometry systems are useful but unlikely to accommodate the largest species. Advances  
37 in biologging tools and modelling could help answer the most pressing ecological questions  
38 about these iconic species.

## 39 Glossary

- 40 • **Mesothermy:** Some elasmobranchs are able to retain heat generated by metabolic  
41 processes to keep certain body parts warmer than the surrounding water, e.g.  
42 elevated temperature of the brain, eyes and body musculature of some sharks may  
43 maintain physiological performance in colder waters. Sometimes referred to as  
44 'regional endothermy'.
- 45 • **Metabolic scope:** Also known as maximum factorial scope; the difference between  
46 maximum aerobic metabolism and standard aerobic metabolism. Metabolic scope  
47 indicates the capacity to perform energy-using processes, such as locomotion or  
48 digestion, beyond SMR, and is dictated by the rate of oxygen supply to organs. This  
49 supply is dependent on an animal's physiology and ambient environmental

50 conditions. Metabolic scope is distinguished from routine factorial scope, which is  
51 the ratio of daily energy use to standard metabolic rate.

52 • **Obligate ram ventilation:** Many large elasmobranchs lack the anatomical features  
53 to pump water over their gills, and hence rely on moving their entire body to  
54 oxygenate their gills. This requires them to constantly move forwards through the  
55 water.

56 • **Q<sub>10</sub>:** The factorial increase in metabolic rate associated with a 10 °C increase in  
57 temperature.

58 • **Respirometry:** Indirect calorimetry via respirometry quantifies the aerobic  
59 respiration of an animal by measuring its oxygen consumption. By estimating the  
60 substrates being metabolised (commonly 70% carbohydrate, 20% lipid and 10%  
61 protein), these measurements of oxygen consumption can be converted to energy  
62 expenditure.

63 • **Standard Metabolic Rate (SMR):** The minimum energy expenditure of an  
64 ectotherm for body functioning and maintenance. As locomotor activity is essential  
65 for respiration in obligate ram ventilators, measures of their SMR include some  
66 locomotor costs.

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## 75 The value of measuring the energetics of large sharks and rays

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77           Understanding how megafauna are able to maintain energy balance has intrigued  
78 physiological ecologists for decades. Fundamental to this research is the measurement, or  
79 at least estimation, of metabolic rates. The ability of megafauna to sustain energy balance  
80 has been explored in extinct groups of large vertebrates, such as dinosaurs [1], as well as  
81 some of the largest extant vertebrates such as whales [2, 3], and may help inform our  
82 understanding of the evolution of body size [4, 5]. Large sharks, rays and skates  
83 (elasmobranchs) are a group of megafauna that include the largest fish and have a range of  
84 diets spanning plankton, fish, reptiles and marine mammals. They also include many species  
85 threatened with over-fishing and climate change [6, 7]. Yet how energy balance is  
86 maintained across this diverse group remains poorly understood. Given these long-standing,  
87 unresolved questions and the advent of new technology and methods, it is timely to review  
88 current knowledge of the metabolic rates of large elasmobranchs and examine how our  
89 understanding of this group is changing.

90           Logistical problems of working with large elasmobranchs means there are few  
91 studies that quantify their energy use [8]. These species are too large for housing in the  
92 laboratory, and, unlike marine mammals, do not surface to respire where they can be easily  
93 accessed. Further, the few existing bioenergetics models (**Box 1**) for elasmobranch  
94 megafauna extrapolate from species that are orders of magnitude smaller [9] (Figure 1B). In  
95 fact, the heaviest elasmobranch for which metabolic rate (MR) – a key aspect of energetics  
96 – has been measured is only 47.7 kg, despite many elasmobranchs weighing >1,000 kg, with  
97 the whale shark (*Rhincodon typus*) reaching 34,000 kg. Further, the thermal sensitivity of MR  
98 (**Q<sub>10</sub>**; see Glossary) varies substantially across ectotherms [10] and is not well established for

99 elasmobranchs (Figure 1C). This enormous uncertainty in MR for large elasmobranchs  
100 hinders our ability to answer important ecological questions concerning this group, which  
101 includes several unusual species: the largest ectotherm, the planktivorous whale shark; the  
102 longest-lived vertebrate (392 years) - the Greenland shark (*Somniosus microcephalus*) [11];  
103 and some of the largest apex predators including the white shark (*Carcharodon carcharias*).

104 Large elasmobranchs are also disproportionately at risk of extinction within an  
105 already vulnerable group [6]. The class Chondrichthyes (that contains about 1050 species, of  
106 which 96% are elasmobranchs) has the lowest proportion of non-threatened species of any  
107 vertebrate group based on IUCN Red List criteria [6]. Ocean warming is also expected to raise  
108 the MR of ectotherms [12], which will impact energy balance and reproductive performance  
109 [13]. In previous mass extinctions, large ectotherms and top predators were among the  
110 animals most affected by ocean warming and the resultant water deoxygenation [14, 15].  
111 Ocean deoxygenation limits **metabolic scope**, prey availability and ‘aerobic habitat’ - zones  
112 with sufficient oxygen to meet metabolic demands [16, 17].

113 Current climate change predictions mimic conditions of past extinctions, suggesting  
114 the largest ectotherms are again likely to be heavily impacted [14, 16, 17]. Most large shark  
115 species went extinct during warming at the end-Cretaceous period, while smaller sharks  
116 survived [14]. Nine of the 15 largest extant ectotherms are elasmobranchs. Unlike other  
117 animals, most large elasmobranchs must move continuously, which requires from 34% to  
118 almost 100% of their metabolic scope, limiting growth, reproduction and foraging ability  
119 when MR is elevated [18]. Prey availability could also be impacted by climate change, with  
120 mean global zooplankton biomass predicted to fall by ~14% this century [19], and in some  
121 areas by 50% [20]. Some large elasmobranchs are hypothesised to rely on efficient foraging  
122 behaviours to overcome an apparent ‘energy-budget paradox’ caused by high feeding costs

123 and sparse prey orders of magnitude smaller than themselves [21, 22]. Large elasmobranch  
124 species may therefore be sensitive to a range of environmental perturbations, and the  
125 effects of such perturbations may be mediated by changes in their energy balance.

126         Although investigating the energetics of large elasmobranchs is challenging, it  
127 remains an important goal in light of their critical role in food webs and the need to  
128 understand their response to climate change [23]. Here, our aim is to promote energetics  
129 research in elasmobranch megafauna and to provide a roadmap for the most promising  
130 research methods and most pressing questions concerning the energetics of this group. This  
131 will enable an understanding of how metabolism, locomotion and feeding affect their  
132 growth, reproduction, ecology, and ultimately their fitness, which will provide the basis for  
133 population and ecosystem models [24].

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Box 1. What is a bioenergetics model?

A bioenergetics model describes the energy requirements of an animal and how energy is distributed to processes in the body (i.e. the animal's 'energetics') [25]. It has four main component processes: **standard metabolic rate (SMR)**; active metabolic rate (cost of activity); food assimilation (specific dynamic action); and growth and reproduction (Figure 1). If the consumption rate is known, bioenergetics models are commonly used to predict and assess rates of growth and reproduction [26], both of which are crucial for survival at the individual and population level. However, growth and reproduction can be depressed in times of elevated energy demand, a situation predicted under future ocean warming [25].

An animal's energy requirements can increase in a number of ways, but is most commonly due to elevated SMR or activity levels. In ectotherms, SMR increases approximately exponentially with temperature [12]. Activity levels may increase with migration, changed prey availability, predator evasion, mating behaviours, weather patterns, tidal state, temperature, or human interference [27-31]. Consequently, an individual must either increase its food consumption to meet these new energy requirements, or energy must be diverted away from growth or reproduction and towards SMR or activity costs [13, 25]. Animals may be able to increase their total energy intake by consuming more energy-dense food, rather than consuming greater biomass [32], however energy-dense diets are often lacking in sufficient nitrogen for synthesising proteins [33].

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## 168 What can we learn from the energetics of megafauna?

### 169 Terrestrial megafauna and hard-to-study species

170 Although megafauna are difficult to study because they are often highly mobile, too  
171 large for captivity, dangerous to handle, or live in extreme environments, energetics studies  
172 can reveal how these animals survive, especially in unusual environments or with unusual  
173 life histories. For example, energetically-economical long-distance travel and foraging are  
174 achieved through morphological adaptation in large sea-birds that stay airborne for months  
175 [34], and through migratory and feeding behaviour strategies in African elephants  
176 (*Loxodonta africana*) [35] and blue whales (*Balaenoptera musculus*) [2]. Likewise, MR  
177 measurements have shown how energetic costs of prey capture are linked to hunting  
178 success and hence population viability at small population sizes in endangered species  
179 including cheetah (*Acinonyx jubatus*) and puma (*Puma concolor*) [36, 37]. Similarly, MR  
180 measurements can help identify challenges and threats that animals face with climate  
181 change. The measured MR of free-living polar bears (*Ursus maritimus*) has revealed  
182 unusually high energy requirements associated with carnivory, and hence how increased  
183 search costs for prey due to sea ice loss linked to warming threatens their survival [38].

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### 185 Elasmobranchs

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187 Although energetics studies of large elasmobranchs are challenging, they have  
188 increased our fundamental understanding of how these species survive. Megafauna,  
189 particularly ectotherms, may have advantages for feeding on widely dispersed prey, since  
190 energy reserves of larger individuals sustain them for longer because of their lower mass-



191 specific SMR [39]. Conversely, filter-feeding and **mesothermy** appear as the two key  
192 evolutionary pathways for the largest elasmobranchs, but also puts them at greater  
193 extinction risk due to potentially unsustainable metabolic demands if prey availability  
194 declines in changed environmental conditions [40]. Human activities are probably already  
195 having direct consequences on the energetics of elasmobranchs; for example tourism  
196 operations cause reef sharks (*Triaenodon obesus*) to be active during times they normally  
197 rest, increasing energy expenditure [29].

198         Many energetics studies of elasmobranchs have focused on how they minimise  
199 transport costs. Locomotion is energetically costly, yet many megafauna regularly migrate  
200 thousands of kilometres. Understanding long-distance migrations, and how climate change  
201 impacts them, is a key research topic for marine megafauna [41]. Studying energetics of  
202 animals has informed why they move to areas that yield the greatest net energy gain. For  
203 example, movement patterns of many terrestrial and marine animals are partially driven  
204 by the energetic demands of traversing different environments [35, 42]. It is proposed that  
205 ectotherms choose habitats with high food availability regardless of temperature to  
206 maximise net energy gains when feeding, but preference colder areas to minimise energy  
207 expenditure when not feeding [30, 43, 44]. For example, basking shark (*Cetorhinus*  
208 *maximus*) movements are both thermally driven and dependent on prey (zooplankton)  
209 biomass [45, 46].

210         Energetics has provided insights into the underlying reasons for long-distance  
211 migrations in elasmobranchs. When the purpose of migration is primarily to improve  
212 foraging, then marine megafauna ensure that the energy gained through better feeding  
213 conditions exceeds the energetic cost of migration, in a number of ways. For example,  
214 whale sharks may reduce locomotor costs by 32% by adjusting swimming patterns while

215 foraging [22]. Most sharks are negatively buoyant and are able to use a passive, downward  
216 glide to cover considerable horizontal distances without expending energy on swimming  
217 (e.g. [47, 48]) and reduce the cost of vertical movements, in which they may dive 2000 m in  
218 search of prey [49, 50]. Blue sharks (*Prionace glauca*) remain at ~400 m when migrating to  
219 reduce their cost of transport [51]. Their MR in this cool water is estimated to be 40% of  
220 that in warmer surface waters, though such estimates are based on the measured  
221 temperature dependence of metabolism in other ectotherms [51]; no data are available  
222 for blue sharks. Although energetics studies have improved our understanding of the  
223 behaviour, morphology and ecology of elasmobranch megafauna, several methods must  
224 be developed further to fill the information void regarding fundamental energy use.

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## 227 Future Research

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229 Building on recent methodological advances in measuring the energetics of  
230 marine megafauna

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232 Mega-flumes and respirometry: measuring the metabolism of large animals

233 **Respirometry** remains the primary method for measuring the MR of water-breathers,  
234 as other methods used for terrestrial and aquatic air-breathing species are not applicable  
235 (Box 2). Advances in laboratory infrastructure, animal husbandry, and capture and transport  
236 techniques have allowed researchers to perform respirometry on increasingly large marine  
237 animals [52]. The MR of freely-swimming elasmobranchs up to 47.7 kg has been measured

238 using large (up to ~3,800 L) respirometers [9]. The main issue with this method remains the  
239 size-limitation of laboratory respirometry systems. To understand allometric scaling of MR  
240 in elasmobranchs (Figure 1B), the MR of incrementally larger individuals may be measured  
241 with larger systems or opportunistic methods. For example, the MR of white sharks up to  
242 36.2 kg was measured in an 11,360-L transport tank en-route to an aquarium [53].

243 Besides SMR, another key component of bioenergetics is the energy cost of activity.  
244 Total activity cost (e.g. daily) can be determined if the cost of transport (COT) per unit  
245 distance or swimming effort is known. Total activity cost is often estimated as a constant  
246 value proportional to SMR, although this is usually a spurious assumption [54]. Total activity  
247 cost can be quantified using a combination of laboratory and field techniques [55]. In water-  
248 breathers, this is usually achieved using a swim-tunnel ('flume'), which comprises a closed  
249 system where water is circulated at specific speeds, and the subject animal swims to hold its  
250 position while its MR or COT is monitored [9]. Until recently, the largest elasmobranch for  
251 which COT was measured was a 9.5-kg mako shark (*Isurus oxyrinchus*) in a 3,000-L flume  
252 [56]. The 'mega-flume' is a 26,000-L sea-deployable flume that was originally tested by  
253 measuring the COT of a 36-kg zebra shark (*Stegostoma fasciatum*) [9], and this remains the  
254 largest animal that it has been used to measure. Flumes are yet to overcome the logistical  
255 challenges required to measure COT in the largest sharks, including the potential of stress to  
256 inflate MR and that animals may require training to swim in a flume appropriately [57].  
257 Although flumes can be used to calibrate a measure of activity to then quantify total activity  
258 cost in free-ranging animals (see below), similar results may be achieved in simple  
259 respirometry setups relying on volitional activity by the animal [58]. Flumes may overcome  
260 their logistical challenges and continue to increase in size, allowing COT measurements of

261 larger animals, but are unlikely to accommodate an animal >10 m in length such as a whale  
262 shark.

263 -----

264 *Box 2. What can we learn about elasmobranch energetics from other megafauna?*

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266 **What can we learn from other megafauna?**

267 One approach to gain insights into the energetics of elasmobranchs is to compare them with other  
268 species exhibiting similar traits (Table I) and for which energetics is more easily measured. For  
269 example, feeding, reproductive costs and costs of activity can be more easily measured in air-  
270 breathers such as cetaceans (whales, dolphins and porpoises; see below).

271 **Feeding:** A shared zooplankton diet between some elasmobranchs and cetaceans implies similar  
272 problems in energy acquisition, including patchy prey, high feeding costs, minimum prey density  
273 requirements, and declining zooplankton biomass in the future [19, 59]. The assumed energy cost of  
274 whale lunge-feeding is used to estimate minimum prey intake from feeding events [60]. A similar  
275 approach could be used for sharks hunting large vertebrate prey, whereby the estimated cost of  
276 hunting attempts could define the required success rate.

277 **Reproductive costs:** Although elasmobranchs exhibit diverse reproductive methods, many large  
278 species produce a few, well-developed offspring, similarly to cetaceans. Therefore both may have  
279 similar gestation costs, although parental energy input differs substantially due to lactation costs in  
280 cetaceans [61].

281 **Cost of activity:** Although SMR cannot be extrapolated from mammals to fish [62], activity cost may  
282 be estimated using kinematic modelling [63], and these groups may have similar costs of transport  
283 per unit body weight.

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285 Table I: Similarities and differences in traits of elasmobranch and marine mammal megafauna. Marine  
 286 mammals represent the largest group of non-elasmobranch marine megafauna, and of these, the cetaceans  
 287 are the most morphologically and ecologically similar to large elasmobranchs.

Trait	Large elasmobranchs	Marine mammals
Oxygen exchange	Water (gills), most must swim continuously	Air (lungs), no swimming required
Energy storage	Primarily in liver as lipids	Subcutaneous fat (blubber)
Thermoregulation	Mostly ectothermic	Endothermic
Fecundity	Mostly low	Low
Diet	Largest are planktivores, some are highly active hunters	Largest are planktivores, some are highly active hunters
Buoyancy	Changes with body size and habitat. Large or deep-sea sharks may be neutral or slightly positive, others are slightly negative	Generally positive at surface, may decrease with depth as is influenced by lung volume
Parental care	None (but offspring may be large at birth)	Substantial in most species, and offspring large at birth
Migrations	Some long distance (1000s of km)	Some long distance (1000s of km)

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290 **Currently non-transferable methods**

291 Unfortunately, many insights into the energetics of non-elasmobranch megafauna have been  
 292 derived using methods that are inapplicable to elasmobranchs.

293 **Surfacing rates to estimate MR:** Air-breathing marine megafauna surface for respiration, offering an  
 294 opportunity to estimate their MR that is not possible with water-breathers. Specifically, MR for  
 295 cetaceans can be estimated from respiration timing, pre-existing oxygen stores, tidal lung volume  
 296 and oxygen extracted from inspired air (measured) [3].

297 **Doubly-labelled water (DLW):** DLW is used to quantify energy use in wild terrestrial megafauna (e.g.  
 298 polar bears [38] and cheetahs [37]), whereby stable isotopes of oxygen and hydrogen trace the flow  
 299 of CO<sub>2</sub> and water through the body to quantify MR. Unfortunately, the DLW method is unsuitable for  
 300 fish due to high water fluxes between the body and environment.

301 **MR estimates from fish otoliths:** A new method of determining energy use in teleosts has been  
302 developed using isotopic composition of carbon found in ear bones (otoliths) [64]. This method has  
303 provided total MR estimates to a resolution of approximately 15 d [64]. Elasmobranchs lack the  
304 calcified structures necessary for this analysis.

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306 **Using captive elasmobranchs and back-calculating metabolic costs**

307 Commercial aquaria may be valuable for determining fundamental relationships such  
308 as allometric and thermal scaling of MR in the largest elasmobranchs. Some aquaria house  
309 many large elasmobranchs, including the largest ectotherm, the whale shark. Harnessing  
310 these commercial enterprises can advance our understanding of the charismatic megafauna  
311 they display, without the need for capturing wild animals. Existing infrastructure may allow  
312 large animals to be isolated and their MR measured via respirometry, providing a solution to  
313 the size-limitation of traditional laboratory respirometry systems. However, issues remain in  
314 obtaining MR measurements that reflect a normal existence in the wild [58].

315 Captive elasmobranchs can provide insight into energy requirements without the need  
316 for directly measuring MR. If the food intake, growth, and assimilation costs (dependent on  
317 diet composition) of an individual are monitored, the remaining energy devoted to MR can  
318 be calculated (Box 1). This has been partially achieved in captive white sharks; in a simple  
319 bioenergetics model, assimilation costs were assumed constant (27%) and the food  
320 consumption and mass of individuals were tracked [65]. The model estimated that  
321 metabolism (SMR + activity cost) and growth accounted for 45% and 28% of energy use,  
322 respectively [65]. However, white sharks in captivity grew at twice the rate of wild sharks,  
323 suggesting energy allocation to growth is probably higher in captive sharks due to reduced  
324 activity and/or, as is commonly the case, energy ingestion may typically be a limiting factor

325 for growth [65]. Nevertheless, this 'back-calculation' method can estimate feeding  
326 requirements to maintain growth rates, indicate metabolic sensitivity to temperature, and  
327 provide insight into the interplay between reproductive rate and body size [66].

### 328 Using new biologgers in the field to estimate the energy expenditure of locomotion

329 Advances in biologging technology have allowed researchers to progress from  
330 describing animal movement or behaviour patterns to explaining their underlying causes.  
331 Growing demand and commercial viability has seen a surge in development and use of new  
332 animal-borne sensors, along with attachment and retrieval methods, to explore the activity,  
333 behaviour, movement and physiology of wild animals [73] (Figure 2, **Box 2**). For example,  
334 combined with respirometry, animal activity measures can provide proxies of energy  
335 expenditure [67]. In the laboratory, data loggers can calibrate an activity measure, often  
336 body acceleration or tail-beat frequency, against MR by simultaneously measuring both at  
337 multiple swim speeds [68]. The same activity measure can then be recorded in free-ranging  
338 animals via animal-borne loggers, enabling activity energy cost to be quantified [55, 68].  
339 While activity measures enable an understanding of total energy use (e.g. [69]), they can  
340 also elucidate costs of fine-scale behaviours including differences with swimming patterns  
341 [28], time of day [55], weather [31], tides [27] or tourism operations [29]. The rigid fins of  
342 large sharks represent ideal surfaces for sensor attachment, allowing a range of data to be  
343 measured. However, the reliance on laboratory calibration of such devices inherits the same  
344 problems as traditional respirometry for megafauna, in that the required laboratory systems  
345 are size limiting. Calibration with larger elasmobranchs will require advances such as the  
346 mega-flume or other large respirometry setups [9]. However, the MR-activity relationship

347 may shift reliably with body mass, which would allow extrapolations from smaller animals  
348 with similar morphologies [70].

349 Heart rate is commonly included in terrestrial and aquatic biologging studies to  
350 estimate activity cost and total energy expenditure. For example, heart rate measurements  
351 have shown unexpected efficiencies in birds on long-distance migrations [34], a low daily  
352 activity cost in great cormorants (*Phalacrocorax carbo*) allowing them to survive Arctic  
353 winters [71], and unusual energy usage in narwhals (*Monodon monoceros*) following net  
354 entanglement [72]. However, the use of heart rate sensors in free-ranging fish has lagged  
355 behind other taxa [73]. Traditionally, the variation among individuals in the MR-heart rate  
356 relationship was thought to be greater in fish (including elasmobranchs) than other taxa  
357 [74], which may have slowed the development of commercially-available heart rate sensors  
358 for fish [73]. However, more recent work suggests there is a reliable relationship between  
359 heart rate and MR (e.g. [75]). As with activity, heart rate must first be calibrated in the  
360 laboratory before being employed as a quantitative measure in the field, thus making it  
361 problematic for megafauna for the reasons described above. Additionally, loggers must be  
362 physically retrieved by re-capture; a difficult task for large elasmobranchs that traverse  
363 oceans.

364 Swim speed has occasionally been used as a proxy for activity energy cost in  
365 bioenergetics models (e.g. [76]) and has provided useful qualitative insights into  
366 elasmobranch energetics (e.g. [77]). Swim speed is an essential parameter of kinematic  
367 modelling (KM), a promising approach that uses hydrodynamics to estimate transport cost.  
368 KM estimates forces such as lift and drag produced as an animal of known morphology  
369 moves through water at a certain speed. In combination with estimates of muscle efficiency,  
370 KM can be used to infer activity cost [63]. This modelling can outline differences in activity



371 cost of different movements within individuals and environments, and can be incorporated  
372 into bioenergetics models if data on SMR, prey capture and prey energy content are  
373 available [63]. KM is also useful in understanding the evolution of morphology associated  
374 with different lifestyles. For example, similarly to seabirds with high aspect-ratio wings,  
375 pelagic sharks in oligotrophic environments have disproportionately large pectoral fins that  
376 reduce the cost of a high cruising speed needed to search vast areas for prey [63].  
377 Additionally, the kinematics of breaching events may provide insights into maximum  
378 movement speeds, power outputs and energy expenditure [78]. However, KM remains  
379 vulnerable to uncertainty of influential parameters that are difficult to measure, such as  
380 hydrodynamic efficiency (see **Outstanding Questions**), for which more work is required  
381 before reliable comparisons can be made between species and morphologies. Nevertheless,  
382 if swim speed measurements are obtained for more large elasmobranchs, KM can provide  
383 insights into activity cost without laboratory calibration, such as relative cost of activity or  
384 environmental influence on activity levels [63].

385       Finally, machine-learning and artificial intelligence are already being used to identify  
386 elasmobranch behaviour based on an acceleration signature [79]. Future use of machine-  
387 learning, especially in conjunction with improved biologging sensors and an understanding  
388 of activity cost, will allow for an array of pattern recognition in energy use of wild animals;  
389 comparable to machine-learning that out-performs human specialists in diagnosing disease  
390 [80]. This may elucidate fine-scale differences in energy use linked to particular behaviours  
391 or prey availability, or prediction of metabolic responses to complex environmental  
392 conditions associated with future warming and deoxygenation.

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## 394 Energetics of large elasmobranchs in the Anthropocene

395 By building on recent methodological advances in measuring the energetics of  
396 marine megafauna, a suite of important questions can be answered related to the long-term  
397 survival of elasmobranch megafauna in the Anthropocene.

## 398 Warming and elasmobranch movement

399 Unlike most other ectotherms, the relative increase of SMR with warming in  
400 elasmobranchs is not well established (Figure 1C), making it difficult to predict how growth,  
401 reproduction or activity may change as oceans warm. Further, activity cost increases with  
402 warming, but not necessarily in line with SMR [54]. Warming raises activity cost in multiple  
403 ways: energy cost of transport per unit distance increases [63], the speed at which minimum  
404 cost of transport occurs increases (therefore increasing absolute energy use)[63], and  
405 activity rates may increase [54, 81]. Animals may be able to buffer against these effects by  
406 increasing rest periods or tracking optimal temperatures [81], e.g. some elasmobranchs  
407 avoid warm surface waters once a temperature threshold is met [82]. However, **obligate**  
408 **ram ventilating** elasmobranchs may have limited ability to reduce activity, and optimal  
409 temperatures may no longer coincide with suitable prey habitats, aggregation sites,  
410 spawning grounds, or migration patterns [83]. Any unavoidable increases in activity cost  
411 may strain the already limited metabolic scope of obligate ram ventilators, reducing their  
412 ability for growth and reproduction [18]. Understanding plasticity in thermal responses will  
413 be important for predicting resilience of ectotherms to climate change and the sustainability  
414 of long-distance migrations [10].

## 415 Ocean deoxygenation

416 Accelerating water deoxygenation, now seen in all oceans, is considered one of the  
417 most significant ecological consequences of climate change [84]. Future deoxygenation is  
418 predicted to mimic conditions during the end-Permian period, when a collapse of suitably  
419 aerobic habitat caused the largest marine extinction in history [16]. Although similarities in  
420 modern climate change to conditions seen in multiple previous extinctions of large sharks  
421 suggest elasmobranch megafauna are particularly vulnerable to the effects of ocean  
422 deoxygenation and warming [14], further work is needed to understand their metabolic  
423 responses to these changing conditions and their ability to find suitably oxygenated  
424 habitats.

425 Lower levels of dissolved oxygen have far-reaching effects on animal physiology and  
426 behaviour, including the ability to maintain energy balance [85]. Reduced oxygen partial  
427 pressure and increased oxygen demand in warmer water (due to elevated SMR) reduces  
428 the 'metabolic index' of ectotherms (the ratio between O<sub>2</sub> partial pressure and SMR [86]),  
429 meaning a limited capacity to increase foraging time when needed [16]. Additionally,  
430 elevated environmental CO<sub>2</sub> associated with deoxygenation can increase metabolic  
431 demands of maintaining pH homeostasis, and activity may increase with low dissolved  
432 oxygen as animals move to find oxygenated water [85]. Deep anoxic zones can limit the  
433 diving of water-breathers, but do not directly affect air-breathers [87]. Therefore, deep-  
434 diving water-breathers may miss opportunities to hunt hypoxia-tolerant prey [85, 87].  
435 Historically, as the ratio between dissolved oxygen supply and demand declines, animals  
436 that have been most susceptible include those with high energy requirements (e.g. highly  
437 active sharks), a reduced available metabolic scope (e.g. obligate ram ventilating

438 elasmobranchs) [18], and the largest ectotherms [16]. The five largest extant ectotherm  
439 species are elasmobranchs, and future research needs to examine if their size, energy use  
440 and lifestyle are sustainable with declining ocean oxygen levels. For example, it would be  
441 valuable to determine the reliance of elasmobranchs on deep cooler waters for energy  
442 acquisition or reducing MR (Figure 2), that may become hypoxic and uninhabitable.

443

#### 444 Concluding remarks

445 Elasmobranchs play important roles as top predators in ecosystems, but are threatened  
446 by fishing and climate change. More work is needed to understand fundamental  
447 physiological traits and the vulnerability of elasmobranch megafauna compared to other  
448 marine life. Of particular importance is their metabolic response to elevated temperatures  
449 and body size, reliance on deep waters that may become hypoxic, and ability to increase  
450 energy acquisition under climate change. By obtaining fundamental metabolic relationships  
451 (e.g.  $Q_{10}$ ) for large elasmobranchs, biologging and modelling can enable a better  
452 understanding of their energetics without the need for size-limiting laboratory systems. MR  
453 data for large elasmobranchs is difficult to obtain, but similar data in other hard-to-study  
454 groups has provided crucial insights into their ecology [38]. Collaboration between  
455 researchers in different fields may be key to predicting future impacts of climate change on  
456 the largest ectotherms. Already, work between ecologists and physicists has used kinematic  
457 modelling to understand energy use [63, 78], and machine-learning may be incorporated  
458 into existing work between physiologists and oceanographers to understand future ocean  
459 warming and deoxygenation scenarios, and how this will affect animals with extreme traits.

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679 **Figure 1. Extrapolation to obtain metabolic rate estimates for large elasmobranchs.** To  
680 calculate the MR of large animals, smaller species or juveniles of the same species are  
681 commonly used to calculate the allometric scaling of MR, and the trend extrapolated (e.g.  
682 [18, 69]). Choice of proxy species is important, as metabolism is affected by physiology,  
683 morphology, activity levels, swimming style, thermal acclimation, and endothermy [9, 54, 62].  
684 How MR scales with body mass is an on-going debate (e.g. [62, 88]), and small errors can  
685 result in large differences in MR estimates when extrapolating to megafauna [9]. Similarly,  
686 the sensitivity of MR to temperature ( $Q_{10}$ ) for elasmobranchs is not well established  
687 compared with other taxa [18, 26, 58]. Pictured (A) a whale shark (*Rhincodon typus*); the  
688 world's largest ectotherm. (B) The range of SMR estimates for large sharks based on the  
689 common range of allometric scaling exponents ( $b = 0.67-0.89$ ), with all other parameters held  
690 constant (temperature=20°C,  $Q_{10}=2.1$ ). For example, the estimated SMR of a 10,000 kg whale  
691 shark is likely to be between 69 and 523  $\text{kJ h}^{-1}$  (>7-fold range). (C) The range of inferred SMR  
692 for a 10,000 kg whale shark within its natural temperature range based on  $Q_{10}$  values  
693 described in the literature for sharks ( $Q_{10}=1.3-2.9$ ) [18, 89], teleosts ( $Q_{10}=1.83$ ) [90] and the  
694 mean across ectotherm taxa ( $Q_{10}=2.19$ ) [91], with other parameters kept constant ( $b=0.70$ ).  
695 At 30°C, estimated SMR ranges from 45 to 502  $\text{kJ h}^{-1}$ . Photo and silhouettes reproduced from  
696 Simon Pierce (simonjpierce.com; (A)), and Natasha Sinagina, T. Michael Keeseey, Steven Traver  
697 (phylopic.org; (B, C)).

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701 Figure 2. Estimating metabolic rate for free-living sharks using data from animal-borne  
702 tags. It is now possible to track sharks routinely (e.g. via satellite or by using acoustic tags)  
703 while obtaining continuous data that enable changes in MR over time to be estimated. (A) A  
704 blue shark (*Prionace glauca*). (B) Tracks of seven individuals that moved in and out of the Gulf  
705 Stream [51]. When in warm waters of the Gulf Stream, the sharks tend to dive and occupy  
706 deeper, relatively cool waters (~400 m). In surface waters of the Gulf Stream, the MR of  
707 sharks is estimated to be 2.5x higher than at depth, once body temperature equilibrates with  
708 water temperature [51]. (C) Simulated biologging data on the depth of blue sharks and  
709 associated water and body temperatures. Water temperature is taken from dive profiles of  
710 blue sharks [51], with resulting body temperature based on the measured thermal inertia of  
711 leopard sharks (*Triakis semifasciata*) and ocean sunfish (*Mola mola*) during short dives [92,  
712 93]. The rate of change in body temperature (thermal inertia) will depend on animal body  
713 size and gill surface area (where most heat-loss occurs in fish), the difference in temperature  
714 between the body and surrounding water, and heat generated by metabolism. Some sharks  
715 demonstrate mesothermy, and so their heat loss may differ. Thermal inertia has not been  
716 measured in large, fully ectothermic elasmobranchs, but likely causes substantial differences  
717 between water and body temperature of large elasmobranchs that traverse the water  
718 column. (D) Simulated data to illustrate how instantaneous estimates of MR could be  
719 achieved by integrating animal-borne sensor data such as body temperature and  
720 acceleration. For example, metabolic costs of blue sharks diving to cooler waters can be more  
721 accurately determined if their body temperature and swimming effort are considered; the  
722 sharks likely have a low cost of activity as they passively glide to descend, but increase activity  
723 costs at depth as they forage and then return to the warmer surface (see reviews on

724 elasmobranch biologging [94, 95]). Reproduced from Mark Conlin/NMFS (A) and [51] under  
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753 **Box 1 Figure I. (A) A bioenergetics model calculates total daily energy expenditure by summing the**  
754 **energy costs of four broad body processes.** These components may be simple (a single number for  
755 each) or more complex (multiple interdependent equations). Generally, four components are  
756 measured (SMR, active metabolic rate, assimilation, and growth and reproduction) and summed to  
757 calculate total energy requirements. Food consumption is then assumed to be equal to those total  
758 energy requirements. Alternatively, consumption is measured directly and then any other single  
759 unknown component can be estimated. **(B) The mass-balance equation of a bioenergetics model.**  
760 Processes on the left sum to the daily energy requirements, but are also dependent on consumption  
761 level. For example, if warmer temperatures cause an increase in SMR, the animal must either  
762 consume more energy or compensate (keeping consumption constant) by devoting less energy to  
763 another process (usually growth or reproduction). Silhouette reproduced from Dmitry Bogdanov  
764 (vectorized by T. Michael Keeseey).