

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 • **Q₁₀:** 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 (**Q₁₀**; 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].

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].

184

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.

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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.

284

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 CO₂ 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.

393

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 O₂ partial pressure and SMR [86]),
429 meaning a limited capacity to increase foraging time when needed [16]. Additionally,
430 elevated environmental CO₂ 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 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 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).