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REVIEW

Too big to study? The biologging approach to understanding the behavioural energetics of ocean giants

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ABSTRACT

Wild animals are under selective pressure to optimise energy budgets; therefore, quantifying energy expenditure, intake and allocation to specific activities is important if we are to understand how animals survive in their environment. One approach toward estimating energy budgets has involved measuring oxygen consumption rates under controlled conditions and constructing allometric relationships across species. However, studying 'giant' marine vertebrates (e.g. pelagic sharks, whales) in this way is logistically difficult or impossible. An alternative approach involves the use of increasingly sophisticated electronic tags that have allowed recordings of behaviour, internal states and the surrounding environment of marine animals. This Review outlines how we could study the energy expenditure and intake of free-living ocean giants using this 'biologging' technology. There are kinematic, physiological and theoretical approaches for estimating energy expenditure, each of which has merits and limitations. Importantly, tag-derived energy proxies can hardly be validated against oxygen consumption rates for giant species. The proxies are thus qualitative, rather than quantitative, estimates of energy expenditure, and have more limited utilities. Despite this limitation, these proxies allow us to study the energetics of ocean giants in their behavioural context, providing insight into how these animals optimise their energy budgets under natural conditions. We also outline how information on energy intake and foraging behaviour can be gained from tag data. These methods are becoming increasingly important owing to the natural and anthropogenic environmental changes faced by ocean giants that can alter their energy budgets, fitness and, ultimately, population sizes.

KEY WORDS: Metabolic rate, Energy budget, Locomotion, Electronic tag

Introduction

Animals require energy for nearly all processes, including body homeostasis, digestion, locomotion, growth and reproduction. Yet, the amount of energy they can gain from the environment during a given period is limited by, for example, food availability, foraging capability, digestion capability and the time required for activities other than foraging. Animals are thus under selective pressure to optimise energy budgets: they are expected to maximise energy gain relative to energy expenditure and allocate energy gain in such a way that the chances of survival and reproduction are maximised

(Alexander, 2003; Stephens and Krebs, 1986). This selective pressure is thought to have shaped many physiological, ecological and morphological traits of animals throughout their evolutionary history. Quantifying energy expenditure, energy intake and energy allocation to specific activities (e.g. locomotion) is, therefore, of central importance for understanding how animals survive in a given environment. Moreover, many environments are rapidly changing owing to climate change and human activities (e.g. urbanisation). Such environmental changes can affect the accessibility of food and the energy balance of animals and, consequently, the fitness of individual animals and population trends (Pagano et al., 2018; Watanabe et al., 2020b; Weimerskirch et al., 2012). Therefore, studying animal energy budgets is important for understanding the causes of population trends and enacting conservation measures if necessary.

An important method when investigating animal energetics is to measure oxygen consumption rates under controlled conditions as a reliable proxy of basal, routine or maximum metabolic rates (see Glossary). Reported values have been compiled to construct allometric relationships across species, allowing us to predict a given species' metabolic rate from simple metrics such as body mass and body temperature (Gillooly et al., 2001; Kleiber, 1932; White et al., 2006). However, the energetics of 'giant' animals, especially those in marine taxa, can hardly be studied in this way owing to logistical difficulties. Before we address this in more detail, we should first consider the question: what is a giant animal? Marine animals tend to be larger than terrestrial animals (Gearty et al., 2018), and criteria for determining gigantism can depend on cofactors such as ancestry and life history. Here, we consider 'ocean giants' to comprise fishes >100 kg, marine reptiles >100 kg and marine mammals >500 kg. The oxygen consumption rates of elephants, the largest extant terrestrial animals, have been measured at various walking speeds with the animals wearing a mask (Langman et al., 1995; Langman et al., 2012). However, applying this method to the largest whales is likely never going to be possible. Similarly, building large respirometers and taking measurements from a swimming 7 m whale shark is logistically difficult, if not impossible. In the case of air-breathing animals, field metabolic rates (see Glossary) can be estimated by using the doubly labelled water method (see Glossary) (Nagy, 1987). However, this method requires animals to be captured twice at a specific interval, limiting its wide application to marine species. Efforts are underway to measure large marine animals' oxygen consumption rates, with examples including the construction of a large flume-type respirometer for fishes (Payne et al., 2015) and experiments with trained toothed whales in aquariums (Kasting et al., 1989; Rosen and Trites, 2013; Worthy et al., 2014). Realistically, however, a comprehensive list of the metabolic rates of ocean giants will not be available in the near future.

Increasingly sophisticated animal-borne electronic tags have allowed researchers to record the behaviour, internal states

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Glossary**Basal metabolic rate**

Metabolic rate of an animal that is resting, awake, not digesting and in the thermoneutral zone (i.e. not paying extra costs for thermoregulation). Called 'standard metabolic rate' for reptiles and fishes.

Doubly labelled water method

A method for estimating field metabolic rate of an animal by injecting stable isotopes of hydrogen and oxygen and tracing the flow of water and carbon dioxide through the body over time.

Field metabolic rate

Metabolic rate of a free-living animal.

Maximum metabolic rate

Metabolic rate of an animal at its maximum level of activity.

 Q_{10}

The factorial increase in metabolic rate caused by a 10°C increase in temperature.

Regional endothermy

The ability of some fishes and reptiles to maintain certain body parts at a temperature higher than the ambient temperature. Also called mesothermy.

Routine metabolic rate

Metabolic rate of an animal performing routine activities.

Stroke volume

The volume of blood pumped from the heart per beat.

Tidal volume

The volume of air inhaled during a normal breath.

and surrounding environment of free-living marine animals, including giant species. This 'biologging' technology provides a new way of studying animal energetics under natural conditions. Parameters recorded by tags (e.g. swim speed, breathing frequency) can be integrated with physical or physiological principles to estimate animal energy expenditure. Such inferences are indirect, as opposed to direct oxygen consumption measurements in the laboratory. Ideally, tag-derived inferences should be validated against oxygen consumption rates in experiments with captive animals, as demonstrated for non-giant species (Lucas et al., 1991; Wilson et al., 2006). However, as discussed above, conducting validation experiments with giant species is difficult or impossible. Without validation experiments, tag-derived energy estimates are qualitative rather than quantitative (Green, 2011) and should be treated cautiously. Despite these limitations, biologging approaches allow us to study the energetics of ocean giants in their behavioural context. Both factors affecting energy expenditure (e.g. locomotor activity) and those affecting energy intake (e.g. feeding rate, type of prey) can be examined by using these approaches.

Here, we review the experimental methods using animal-borne electronic tags for studying the behavioural energetics of ocean giants, for which captive experiments are limited or impossible. Our goal is to show how we could estimate their energy expenditure and energy intake without resorting to respirometry, although measuring oxygen consumption rates using respirometry remains the 'gold standard' for estimating metabolic rates. Ultimately, we aim to encourage more researchers to study the energetics of ocean giants and gain deeper insights into their physiology, ecology and evolution by making use of emerging biologging and remote sensing tools.

Metabolic rate data currently available

As summarised in Fig. 1, few data on the oxygen consumption rates (during resting or routine conditions) of ocean giants are currently available. To our knowledge, the largest body masses for which

oxygen consumption rates have been measured by respirometry are 23 kg for teleosts (juvenile southern bluefin tuna; Fitzgibbon et al., 2008), 126 kg for elasmobranchs (juvenile Greenland shark; Ste-Marie et al., 2020), 430 kg for marine reptiles (leatherback turtle; Paladino et al., 1990), 387 kg for pinnipeds (Weddell seal; Williams et al., 2004), 494 kg for sirenians (West Indian manatee; Irvine, 1983) and 6150 kg for cetaceans (grey whale calf; Wahrenbrock et al., 1974). Frequently cited allometric relationships and body-temperature correcting factors (Q_{10} ; see Glossary) (White et al., 2009, 2006) have used the data for non-giant species (Fig. 1). Extrapolating these relationships to the body size of giant species is highly sensitive to the allometric exponents and Q_{10} value used (Lawson et al., 2019; Payne et al., 2015), and should be done cautiously. Contrary to common perception, the relationship between metabolic rates and body mass might be non-linear on a logarithmic scale (Kolokotronis et al., 2010), further complicating the issue of extrapolation.

If we are to better understand the energetics of ocean giants, more data for their oxygen consumption rates are needed to extend the body size range of allometric relationships and better predict a given species' metabolic rate. Attempts are being made to address this issue. For example, a large flume-type respirometer, in which a giant fish can swim at controlled speeds, has been built; however, its application is currently limited to a 36 kg zebra shark (Payne et al., 2015). Static respirometers, which are logistically less challenging, also work for giant fishes (Ste-Marie et al., 2020). Interestingly, sharks in simple annular static respirometers exhibit swimming kinematics more similar to those of wild individuals and have lower oxygen consumption rates for a given level of body motion (i.e. acceleration and tailbeat frequency) than sharks in flume respirometers (Lear et al., 2019). This finding suggests that static respirometers may elicit more natural swimming behaviour and lower stress on animals, and produce results that are more applicable to wild animals in routine behavioural states. In the case of air-breathing animals, respirometry experiments with trained individuals in aquariums allow direct measurements of giant species' oxygen consumption rates, as demonstrated for adult killer and beluga whales (Kasting et al., 1989; Rosen and Trites, 2013; Worthy et al., 2014). This promising approach should be applied more widely.

Owing to difficulties in studying the energetics of ocean giants in the laboratory, it may be necessary to resort to proxies for energy expenditure that can be recorded in the field by using electronic tags. As discussed above, proxies recorded for giant species are qualitative rather than quantitative and can only be used to tackle specific research questions. With this caveat in mind, below, we discuss several approaches currently available, which can be categorised as kinematic, physiological and theoretical approaches.

Kinematic approaches to estimating energy expenditure**Swim speed**

In marine animals that swim and dive nearly continuously, a major component of metabolic rate elevation above basal levels is locomotion cost. Electronic tag data that quantify marine animals' locomotor activity could thus be used to estimate their locomotion costs and, if calibration equations are available, their total oxygen consumption rates. A relevant parameter is swim speed, which can be measured directly (i.e. using propeller sensors) or indirectly (e.g. from flow noise recorded by acoustic sensors or fine-scale accelerometer 'jiggle') for a range of marine animals, including giant species (Cade et al., 2018; Watanabe et al., 2011).

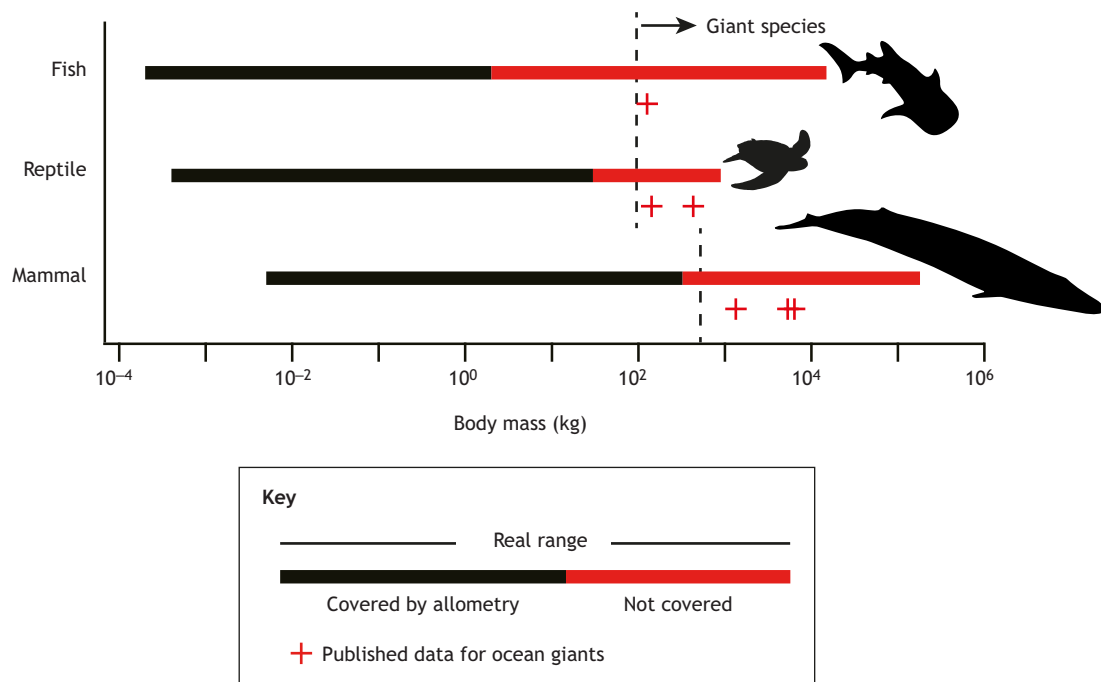


Fig. 1. The coverage of body size by the published allometric relationships of metabolic rates (White et al., 2009, 2006) in relation to real body size ranges in several vertebrate groups. In each group, the upper body size range is not covered by allometry (red bar). Red crosses denote a few giant species (fishes >100 kg, marine reptiles >100 kg and marine mammals >500 kg) for which oxygen consumption rates have been measured by respirometry during resting or routine conditions. These examples include juvenile Greenland shark (126 kg; Ste-Marie et al., 2020), green turtle (170 kg; Enstipp et al., 2011), leatherback turtle (430 kg; Paladino et al., 1990), beluga whale (1341 kg; Rosen and Trites, 2013), killer whale (5318 kg; Worthy et al., 2014) and grey whale calf (6150 kg; Wahrenbrock et al., 1974).

Swim speed data can be converted to metabolic locomotion cost via hydrodynamic theory, although some parameters are often uncertain and need to be assumed (see ‘Theoretical approach’). Swim speed data can also be converted to oxygen consumption rates using calibration equations obtained in the laboratory, which are available for many small fishes (Beamish, 1978) and some non-giant marine mammals (Feldkamp, 1987; Davis et al., 1985). In fishes, the factorial increase in oxygen consumption rates caused by a unit increase in swim speed relative to body length (i.e. body lengths per second) is similar (approximately 2.3-fold) among species with different body sizes (Beamish, 1978). Thus, the locomotion cost of free-living large fishes could be estimated from their swim speed based on captive experiments with smaller fishes. A caveat is that calibration experiments are normally conducted with captive animals swimming horizontally in a tank, whereas large marine vertebrates often exhibit near-continuous diving behaviour in the wild. During dives, buoyancy can either aid or hinder animal movements, depending on body tissue density, water density and swimming direction (Sato et al., 2003; Watanabe et al., 2006; Williams et al., 2000), which complicates the relationship between swim speed and energy expenditure. A reasonable approach is to record both swim speed and tailbeat activity of the animals and set the locomotion cost as zero when they exhibit gliding behaviour aided by non-neutral buoyancy (Watanabe et al., 2019b). Also, animal paths are frequently non-linear, and curved trajectories could incur additional locomotion costs relative to straight-line paths (Hughes and Kelly, 1996; Weihs, 1981; Wilson et al., 2013).

Stroke frequency and body acceleration

Another useful metric for quantifying the locomotor activity of marine vertebrates is stroke (or tailbeat) frequency. It is now

routinely recorded by animal-borne inertial sensors (accelerometers, magnetometers and gyroscopes) (Sato et al., 2007). Stroke frequency can be used to estimate oxygen consumption rates either directly, based on captive experiments (Williams et al., 2017b), or indirectly, by converting it to swim speed (Bainbridge, 1958) and then to oxygen consumption rates. However, it is important to note that animals can modulate the force produced by each stroke (Martín López et al., 2015), potentially causing errors in the estimate of locomotion cost.

Conceptually similar metrics are overall dynamic body acceleration (ODBA) and its variations (Wilson et al., 2020, 2006). These metrics quantify animals’ overall body motion based on acceleration data, defined as the scalar or vectorial sum of the dynamic (or high-pass filtered) accelerations over three axes. ODBA has been calibrated against oxygen consumption rates for a range of fishes (Gleiss et al., 2010) and air-breathing divers (Fahlman et al., 2013), including giant species (Enstipp et al., 2011).

An advantage of using ODBA over stroke frequency is that it could also be applied for non-swimming periods if appropriate calibration experiments are conducted. By contrast, ODBA is sensitive to tag positions (Wilson et al., 2020), meaning that care should be taken when comparing ODBA values among studies. A different metric based on body accelerations combined with gyroscope data has also been proposed (Ware et al., 2016). Unlike ODBA, this metric removes the effect of rotational movements and can provide a better proxy for energy expenditure in animals that frequently rotate, such as sea lions.

Physiological approaches to estimating energy expenditure

Heart rate

Physiological parameters could also potentially be used as proxies for the energy expenditure of ocean giants. One such candidate is

heart rate. Based on the Fick principle of cardiac output, oxygen consumption rates (\dot{V}_{O_2}) can be expressed as:

$$\dot{V}_{O_2} = f_H V_s (C_{aO_2} - C_{vO_2}), \quad (1)$$

where f_H is heart rate, V_s is stroke volume (see Glossary), C_{aO_2} is the oxygen content of arterial blood and C_{vO_2} is the oxygen content of mixed venous blood. This principle states that \dot{V}_{O_2} is proportional to f_H (i.e. f_H is a good predictor of \dot{V}_{O_2}) if the oxygen uptake of a heartbeat [$=V_s(C_{aO_2} - C_{vO_2})$] is constant or changes predictably with changes in \dot{V}_{O_2} . Although this assumption is not strictly met in many cases, positive correlations between heart rates and oxygen consumption rates have been reported for a range of non-giant birds and mammals, including marine taxa (Butler et al., 1992; Williams et al., 1993). However, in marine mammals that routinely dive, the utility of heart rates as a predictor of oxygen consumption rates is complicated by dive responses and other dive-related changes in blood circulation. Heart rates decrease upon submergence ('bradycardia') and increase upon (or before) surfacing ('tachycardia'), primarily to balance central arterial blood pressure against the dramatic changes in peripheral vascular resistance during diving (Blix, 2018). During submergence, stroke volume decreases (Fahlman et al., 2019b; Ponganis et al., 1990). Lungs are compressed by pressure and the pulmonary shunt – the amount of blood bypassing the lung and not participating in gas exchange – increases with depth (Kooyman and Sinnett, 1982). Moreover, blood redistribution during dives is under some degree of cognitive control (McKnight et al., 2019), and heart rates change according to the anticipated dive durations (Elmegaard et al., 2016; Fahlman et al., 2020). For these reasons, heart rates must be averaged over a period longer than a dive cycle (i.e. a dive and the subsequent surface period) if they are to be used as a proxy for energy expenditure (Boyd et al., 1999; Fedak et al., 1988). A few recent studies have recorded heart rates for giant marine mammals (e.g. Goldbogen et al., 2019a; Williams et al., 2017a); however, these records can neither be converted to oxygen consumption rates (owing to the lack of calibration experiments) nor be used as a qualitative proxy for behaviour-specific energy expenditure (owing to complex dive responses). Overall, heart rates are unlikely to be a useful proxy for energy expenditure for air-breathing ocean giants.

In fishes, linear relationships between heart rates and oxygen consumption rates have been reported for non-giant teleosts (Armstrong, 1986; Clark et al., 2010) and elasmobranchs (Scharold and Gruber, 1991), indicating that heart rates can be a good proxy for energy expenditure of giant fishes in the field. In some species, however, variations in oxygen consumption rates for a given heart rate are large, presumably owing to variability in stroke volume and physiological states (e.g. stress level) (Priede and Tytler, 1977; Thorarensen et al., 1996). Despite the potential utility as a proxy for energy expenditure, few studies have recorded the heart rates of fishes in their natural habitats (Lucas et al., 1991; Sureau and Lagardère, 1991), with none studying giant species, primarily because of technical difficulties. For example, heart rate transmitters can only be used in small water bodies owing to limited data transmission ranges (Lucas et al., 1991; Sureau and Lagardère, 1991). Implantable heart rate loggers are available, but their application is limited to specific conditions where tagged fish can be recaptured (e.g. fish in a sea pen; Clark et al., 2008). If we are to record the heart rates of free-living giant fishes, we need to develop a method for detaching heart rate loggers and electrodes from the animals by a time-scheduled release system. Importantly, heart rates and oxygen consumption rates change in a similar manner

with changes in the ambient water temperature in fishes. Heart rates can thus be a better predictor of energy expenditure than kinematic proxies (e.g. body acceleration) when the ambient temperature changes (Clark et al., 2010). Moreover, heart rate increases after feeding in fishes, indicating that digestion cost, in addition to locomotion cost, could be quantified (Armstrong, 1986). Therefore, for giant fishes, heart rate data will complement kinematic proxies and provide important insight into behaviour-specific energy expenditure, even if calibration experiments are impossible.

Breathing frequency

The breathing frequency of cetaceans can be either directly observed in the field or recorded by electronic tags (Goldbogen et al., 2008; Rojano-Doñate et al., 2018; Roos et al., 2016), and it has been used for estimating metabolic rates (Sumich, 1983). This method assumes that oxygen uptake for a given breath, determined by tidal volume (see Glossary) and the difference in oxygen concentration between inspired and expired air, is constant. However, both tidal volume and the difference in oxygen concentration vary from breath to breath, depending on several factors (e.g. activity level, the current oxygen store) (Fahlman et al., 2019a, 2016; Ridgway et al., 1969). Also, the oxygen debt incurred during a dive may not be fully paid back during the subsequent surface period (Fahlman et al., 2008). This means that long-term average values of oxygen uptake per breath must be used for estimating long-term average field metabolic rate for air-breathing divers. Recently proposed models (Fahlman et al., 2016; Roos et al., 2016), where oxygen uptake for a breath varies depending on the conditions, might allow researchers to examine the energy expenditure of air-breathing divers at a finer scale.

Body temperature

As a notable example of giant fish energetics, the metabolic rate of a free-living white shark has been estimated based on simultaneous records of body core temperature and water temperature (Carey et al., 1982). This species shows regional endothermy (see Glossary), and its body core temperature is always higher than the water temperature. An increase in body temperature thus represents metabolic heat production rather than heat gain from the water. However, the metabolic rate estimate given by Carey et al. (1982) is inconsistent with a later estimate based on swim speed and an extrapolation of the metabolic rate of a captive juvenile white shark measured during transport (Semmens et al., 2013). Both estimates are sensitive to assumptions, and it is currently unknown which estimate is more accurate. A key for better understanding the energetics of regionally endothermic giant fishes will be oxygen consumption rate measurements using respirometry for individuals at full adult sizes. Such measurements are not currently available for either teleosts (e.g. bluefin tuna) or elasmobranchs (e.g. lamnid sharks).

Theoretical approach to estimating energy expenditure

As a complementary approach to the kinematic and physiological methods discussed above, theoretical modelling based on physical principles can be used for estimating the costs of locomotion and (in endotherms) thermoregulation. Estimates of locomotion costs can make use of either steady or unsteady models of hydrodynamics. Steady models are applicable when swim speeds are relatively constant, whereas unsteady models can instead be used for animals that rapidly change swim speed, such as lunge-feeding orqual whales.

As the starting point of both models, hydrodynamic drag (D) acting on an animal moving passively in a fluid can be expressed as:

$$D = 0.5\rho SC_D V^2, \quad (2)$$

where ρ is water density, S is the reference area of the animal, C_D is the drag coefficient and V is swim speed (Vogel, 1994). In steady models (Hind and Gurney, 1997), drag equals the thrust force produced by an animal. The mechanical power produced by an active swimmer is the product of D , V and λ ($=0.5\lambda\rho SC_D V^3$), where λ is the ratio of the drag of an active swimmer to that of a passive one. The mechanical power can then be converted into metabolic power by introducing efficiency terms, composed of aerobic efficiency (i.e. the proportion of muscular power transformed from chemical power) and propulsive efficiency (i.e. the proportion of forward thrust power transformed from muscular power) (Hind and Gurney, 1997).

A limitation of this simple model is that efficiency terms, especially aerobic efficiency, are unknown for giant marine species and must be assumed based on experiments performed using distantly related smaller species (Hind and Gurney, 1997). Moreover, efficiency appears to increase with swim speed, given the observation that the oxygen consumption rates of active swimmers do not increase with swim speed as rapidly as V^3 (Feldkamp, 1987; Webb, 1971). Another factor to consider is buoyancy, which can either increase or decrease locomotion costs depending on swimming direction, body volume and the differences between animal tissue density and water density. Several models incorporating this effect have been proposed (Miller et al., 2012; Papastamatiou et al., 2018a). In unsteady models (Hughes and Kelly, 1996; Potvin et al., 2009), V can change with time, as determined by tag measurements. However, this model is rarely applied except in special cases where distinct manoeuvres are thought to dominate energy budgets (Potvin et al., 2012).

Modelling thermoregulation cost in endotherms is more complex than locomotion cost (Hind and Gurney, 1997). However, thermoregulation cost may be a minor component of the energy expenditure of ocean giants, as their heat loss is minimised by their high thermal inertia associated with a low surface-area-to-volume ratio (Lavigne et al., 1990; Ryg et al., 1993). Moreover, the heat produced by muscles associated with locomotion is recycled for thermoregulation (Bostrom and Jones, 2007; Hind and Gurney, 1997). It is possible that body temperature may drop during diving even in endotherms, as reported for penguins (Handrich et al., 1997), potentially leading to decreased metabolic rates via the Q_{10} effect. However, a later study showed that body temperature decreases only slightly in diving seals, except during unusually long dives (Meir and Ponganis, 2010). This finding suggests that metabolic depression via the Q_{10} effect is not an important mechanism and does not need to be considered in the models of marine mammal energy expenditure.

Estimating energy intake

If we are to understand how ocean giants manage their energy budgets, it will be important to gain information on energy intake and foraging behaviour in addition to the proxies of energy expenditure discussed above. Biologging technology helps us to obtain such information, although estimating absolute energy intake (in kJ) is still difficult for most species.

Air-breathing divers

In the case of air-breathing divers, early attempts to examine foraging behaviour relied solely on dive profiles, such as quick

changes in depth ('wiggle'), as signals of feeding events (Hindell et al., 1991). Wiggles are easy to record and can be reasonably accurate, depending on prey types (Bost et al., 2007). Subsequently, various parameters that provide more direct signals of feeding events have been recorded for many species, including ocean giants (Aoki et al., 2012). These parameters include stomach temperature (Wilson et al., 1995), oesophageal temperature (Charrassin et al., 2001), mouth (or beak) opening detected by magnetic sensors (Wilson et al., 2002b), swim speed (Aoki et al., 2012; Wilson et al., 2002a) and head (or jaw) acceleration (Naito et al., 2013). Each method has merits and limitations. For example, oesophageal temperatures can directly detect prey ingestion events (unless water ingestion occurs), but the need for surgical operations in order to gather the data limits wide application of this method. Swim speed and head (or jaw) acceleration can be measured easily by using externally attached tags, but, at best, these signals represent prey capture attempts rather than prey ingestion events. Some of the methods mentioned above can also provide estimates of prey size if calibration experiments with captive animals are conducted (Wilson et al., 1995, 2002b). In toothed whales, an important approach to investigating prey capture events is to record echolocation clicks using acoustic tags (Miller et al., 2004). This method also allows prey size to be estimated by analysing echoes from prey (Wisniewska et al., 2016).

Another important approach that is applicable to most air-breathing divers is to film foraging behaviour using video camera tags (Davis et al., 1999). Camera tags are the only tool that provides direct information on prey type, prey size and foraging tactics (Goldbogen et al., 2017; Watanabe et al., 2020a). A major limitation to the use of camera tags is that recording durations are short (typically <6 h) owing to the high power consumptions of image sensors. However, given that animals consume a narrow range of prey types, recording durations could be effectively extended by linking the prey capture events seen in the footage to particular behavioural signals recorded by other sensors (e.g. head or body movements recorded by accelerometers; Watanabe et al., 2020a; Watanabe and Takahashi, 2013). Moreover, specialised video camera tags that can be triggered by prey capture signals (e.g. head acceleration) allow effective use of limited recording durations (Yoshino et al., 2020). In coordination with animal tagging, prey mapping (using multi-frequency active acoustic signals) in the vicinity of focal animals provides information on prey type, abundance and distribution (Hazen et al., 2009).

Fishes

Compared with air-breathers, efforts to record fish foraging behaviour using electronic tags have been less successful, primarily owing to the difficulties in physically recovering tags from free-living fishes. Several tags have been developed that are meant to be fed to large sharks; these tags detect feeding events based on changes in pH (Papastamatiou et al., 2007) or electric impedance (Meyer and Holland, 2012) in the stomach. However, thus far, these tags have only been deployed on captive animals, and field applications are warranted. Another type of tag, which detects feeding events as drops in stomach temperature, has been used in captive white sharks (Jorgensen et al., 2015). This method has also been applied to the field, where tags were fed to wild white sharks and physically recovered following regurgitation (Jorgensen et al., 2015). Several feeding events were detected, providing proof of concept for this method.

As in air-breathing divers, camera tags can provide direct information on fish foraging behaviour and the prey targeted,

despite limited recording durations (Papastamatiou et al., 2018b). The feeding events confirmed by camera tags can be linked to specific behavioural signals, allowing researchers to characterise foraging behaviour based on long tag records as demonstrated for giant teleosts (Nakamura et al., 2015) and sharks (Watanabe et al., 2019a). Wider applications of this promising approach are warranted.

The most successful examples of recording the feeding events and energy intake of wild fishes are studies on tunas. High fishing pressure on this group of fishes enables the recovery of surgically implanted tags. Because viscera temperature increases following feeding events in tunas (Carey et al., 1984), feeding frequency in the wild can be estimated from viscera temperature records (Bestley et al., 2008). The absolute energy intake of free-living tunas can also be estimated from viscera temperature records, based on captive experiments conducted with similar-sized individuals over a range of water temperatures (Whitlock et al., 2015). This approach,

together with estimates of the geographical position of the animals based on light levels recorded by tags, reveals the spatiotemporal patterns of energy intake during oceanic migrations (Bestley et al., 2008; Whitlock et al., 2015).

Conclusions

This Review has summarised how biologging technology helps us to quantify the energy expenditure and food intake of ocean giants, for which captive experiments are limited or impossible (Fig. 2). There are kinematic, physiological and theoretical approaches to quantifying energy expenditure, with each having its own advantages and disadvantages. Importantly, tag-derived proxies recorded for ocean giants are, in most cases, qualitative rather than quantitative estimates of energy expenditure owing to the lack of validation experiments. It means that, at best, the proxies can only be compared among different behaviours or different conditions within individuals, or among similar-sized individuals exhibiting

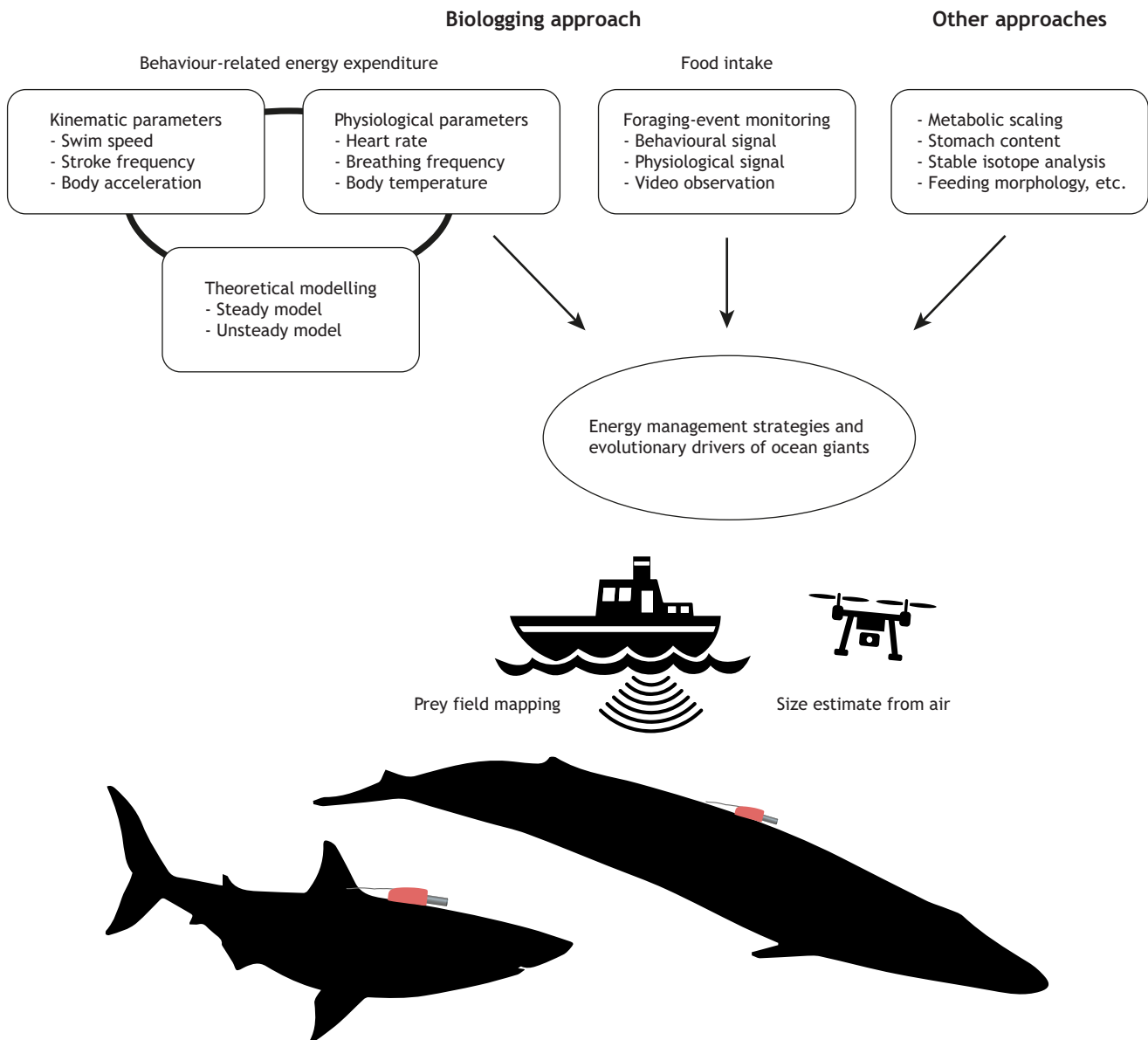


Fig. 2. Conceptual illustration for how we could study the behavioural energetics of ocean giants. Prey field mapping and size estimates from the air are especially important for baleen whales and can be integrated with a biologging approach.

similar behaviour under similar conditions. Despite this limitation, the proxies discussed here can be combined with other behavioural, physiological and environmental data to provide insights into how ocean giants optimise their energy budgets. For example, tag records show that pelicans (albeit not giant animals by our definition) decrease both their wingbeat frequency and their heart rates when flying in formation compared with when flying alone, demonstrating an energetic benefit of formation flight in birds (Weimerskirch et al., 2001). As another example of the utility of these approaches, by combining bioenergetic modelling and food intake estimates based on tag data, energetic efficiency (i.e. energy gain divided by energy expenditure) during a dive has been shown to decrease with body mass in toothed whales but increase in baleen whales (Goldbogen et al., 2019b). This result demonstrates the energetic benefits of being bigger in baleen whales and explains why they have evolved such giant body sizes.

Biologging technology also helps us to understand how increased human activities and ongoing climate change can affect the energetics, fitness and, ultimately, populations of ocean giants. For example, tag records show that white sharks increase activity (as assessed by body accelerations) when interacting with commercial cage-diving vessels, implying that there are negative impacts of wildlife tourism on the energetics of this threatened species (Huveneers et al., 2018). By combining electronic tagging (GPS, accelerometers and cameras), the doubly labelled water method and direct measurements of oxygen consumption rates in the laboratory, it has been shown that polar bears have high energy demands and lose weight quickly when they do not successfully hunt energy-rich prey (i.e. seals) (Pagano et al., 2018). This finding implies that the ongoing decline in the Arctic sea ice and the associated decline in prey availability negatively affect the energetics, fitness and population of this iconic species.

Taken together, we conclude that we can certainly increase our understanding of the energetics of ocean giants by using sophisticated electronic tags, despite the limitation that validation experiments with captive animals are difficult or impossible. An increasing number of studies are using electronic tags to investigate the biology of ocean giants. We believe that, by investigating their energetics based on tag data – while always keeping in mind the inherent limitations discussed in this Review – deeper insights could be gained into the ecological and physiological drivers underlying the evolution of these animals. This approach is increasingly important, because more and more ocean giants face natural and anthropogenic environmental changes that affect their energetics.

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Competing interests

The authors declare no competing or financial interests.

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