Feeding requirements of white sharks may be higher than originally thought

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Quantifying the energy requirements of animals in nature is critical for understanding physiological, behavioural, and ecosystem ecology; however, for difficult-to-study species such as large sharks, prey intake rates are largely unknown. Here, we use metabolic rates derived from swimming speed estimates to suggest that feeding requirements of the world’s largest predatory fish, the white shark (Carcharodon carcharias), are several times higher than previously proposed. Further, our estimates of feeding frequency identify a clear benefit in seasonal selection of pinniped colonies - a white shark foraging strategy seen across much of their range.

Understanding the energetic requirements of organisms in their natural environment is fundamental to ecosystem ecology, as the energetic benefits and costs associated with their activities will heavily influence life-history strategies and trophic relationships. Inherent difficulties in studying marine predatory behaviour in the wild have hindered our understanding of the energetic requirements and associated trophic relationships of apex predators. In the case of pelagic predatory sharks, approaches that provide energetic data are urgently needed, as many of these species are highly vulnerable to overexploitation¹.

White sharks Carcharodon carcharias (Lamnidae) are apex marine predators with a circumglobal distribution. Their longevity, late maturity and low fecundity renders them highly susceptible to overexploitation². The population status of white sharks is poorly known over the species’ range due to a lack of robust abundance indicators, given it is protected throughout much of its range and only caught as a fisheries bycatch species or as part of shark control programs³. Additionally, despite their protected status, white sharks are still regularly incidentally caught in various fishing gear throughout their range⁴–⁶. Even at very low levels of anthropogenic mortality, modelled white shark populations have greatly increased doubling times⁷, and declines in relative catch rates have been reported in parts of their range, e.g. Refs. 3,6. There is however, conjecture surrounding the magnitude of some of these declines⁸–⁹ and some evidence for slight increases in relative catch rates in the last 10–20 years in parts of their range, e.g. Refs 3,4.

Shifting from a predominantly piscivorous diet to one dominated by marine mammals at approximately 3.4 m in total length¹⁰, large white sharks are regular visitors to seal breeding colonies. For example, the Neptune Islands (South Australia) supports the largest seal colony in Australia, and white sharks are most abundant in the area during winter-spring when weaned New Zealand (NZ) fur seals Arctocephalus forsteri are present¹¹.

Energy requirements of large sharks are poorly documented. The only published study of white shark energetics in the wild estimated the field metabolic rate (MR) of a single individual from telemetered muscle temperature data as the individual moved from cold to warm water¹². The authors used their MR estimates to suggest a 943 kg white shark could survive on 30 kg of marine mammal blubber for approximately 1.5 months; a widely cited figure that has perpetuated the assumption that large sharks only need to feed every few weeks to maintain net energy gain.

Rising from estimates of swimming speeds [Fig. 1] and measurements of standard (resting for an obligate ram-ventilator) MR (SMR) in young-of-the-year (YOY) white sharks¹³, with swim-tunnel respirometry data from closely-related shortfin mako sharks Isurus oxyrinchus (Lamnidae)¹⁴ to estimate field routine metabolic
rates (RMR), total daily energy expenditure (TDE), and feeding requirements of white sharks at a NZ fur seal colony, Australia, determined by a radio-acoustic positioning system. Inset, a white shark *Carcharodon carcharias* at the Neptune Islands.

**Results**

Throughout the entire monitoring period, 9,969 swim speed estimates were obtained across all individuals. The distribution of swimming speeds was strongly positively-skewed, so we calculated median swimming speeds as well as mean estimates. The grand mean swimming speed (n = 12) was estimated as 2.91 ± 0.16 m s$^{-1}$ ($U$, 0.81 TL s$^{-1}$), and the median as 2.25 ± 0.14 m s$^{-1}$ ($U$, 0.62 TL s$^{-1}$) [Table 1]. From the mean swimming speed, we estimate the field RMR as 723 mg O$_2$ kg$^{-1}$ h$^{-1}$ or a TDE of 28.2 MJ (daily ration of 1.5–1.9% wet body weight d$^{-1}$) for 428 kg sharks (the average from our

Figure 1 | Movements, swimming speeds and metabolic rates of a white shark. (a) 3.5 h track from a 3.5 m male white shark at the Neptune Islands fur seal colony, Australia, determined by a radio-acoustic positioning system. Inset, a white shark *Carcharodon carcharias* at the Neptune Islands. (b) Swimming speeds ($U$, TL s$^{-1}$) were calculated from locations made at ≤5 s intervals in (a) and used to estimate routine metabolic rate (RMR) (MO$_2$, gO$_2$h$^{-1}$ as per the figure axis label) (see Materials and Methods for details).
Table 1 | Summary of white shark metabolic rate (MR) estimates and the implications for prey intake requirements. Body mass for our study and that of Ref. 13 are given as mean ± s.e.m. All other values for our study are means (grand mean ± s.e.m.) and values in parentheses are medians (grand mean ± s.e.m.). Ref. 13 estimated the range of swimming speeds from video recordings of the sharks swimming in a transport tank. Ref. 12 estimated the shark’s swim speed by proxy; the tracking ship’s course was stated to approximate that of the fish, giving an over-the-ground speed of 3.2 km h\(^{-1}\). Absolute MR and duration of energy balance from 30 kg of blubber was estimated for this study by scaling up to 943 kg using an exponent of 0.79. Ref. 12 used an energy value for blubber of 27.9 MJ kg\(^{-1}\).

| Study       | No. individuals | Body mass (kg) | Swimming speed (m s\(^{-1}\)) | Estimated mass-specific MR (mg O\(_2\) kg\(^{-1}\) h\(^{-1}\)) | Estimated absolute MR (g O\(_2\) h\(^{-1}\)) | Duration (days) that shark is in energy balance from 30 kg blubber |
|-------------|-----------------|----------------|-------------------------------|-------------------------------------------------|---------------------------------------------|-----------------------------------------------------------------|
| Ref. 12     | 1               | 943            | 0.9                           | 60.0                                            | 56.6                                        | 44.1                                                            |
| Ref. 13     | 4               | 29 ± 2         | 0.58 − 0.81                   | 246.0                                           | 55.1                                        | −                                                              |
| **This study** | **12**          | **428 ± 61**   | **2.9 ± 0.2 (2.3 ± 0.1)**     | **723.0 (566.5)**                              | **161.8 (126.8)**                           | **11.6 (14.8)**                                                 |

### Discussion

Our estimate of total daily energy expenditure (TDE) suggests white sharks feed far more frequently than previously estimated\(^\text{12}\) and does not support the proposal that white sharks could survive at energy balance on 30 kg of marine mammal blubber for 1.5 months (44.1 d). Indeed, the mass-specific MR estimated by Refs. 12 for a 943 kg white shark was more than 12-times lower than our estimate for smaller (428 ± 61 kg, mean ± s.e.m., n = 12) sharks (60 versus 723 mg O\(_2\) kg\(^{-1}\) h\(^{-1}\)). Given that absolute MR scales with body size with an exponent of −0.8 for most fish including sharks\(^\text{15,16}\), it is unsurprising that our mass-specific MR estimate is higher than that of a much larger animal. However, if the measurements of SMR in 30 kg sharks\(^\text{15}\) and our measurements of MR in 428 kg sharks are scaled upwards using a mass exponent of 0.79 (Ref. 13), there is strong agreement in absolute MR estimated by Refs. 12 and the one measured by Refs. 13 (56.6 versus 55.1 g O\(_2\) h\(^{-1}\) for 943 kg sharks), whereas our estimate of absolute MR (161.8 g O\(_2\) h\(^{-1}\) for 943 kg sharks) is about three times higher. This suggests that, whereas we have estimated metabolic rate in actively swimming animals (MRM), Ref. 12 is likely to have estimated MR approximated by rest (SMR). Our estimated daily ration of 1.5–1.8% wbw d\(^{-1}\) is highly comparable to the mean ration (estimated directly from the amount of food eaten) for captive YOY white sharks\(^\text{17}\) (1.2% wbw d\(^{-1}\)), after scaling for differences in body mass between the YOY and adult white sharks. Furthermore, our daily ration is comparable to that estimated for free-ranging mako sharks\(^\text{18}\) (2.3–2.8% wbw d\(^{-1}\)), after scaling for differences in body mass between the mako and white sharks.

The new estimate of white shark RMR has implications for answering the likely feeding frequency of this species. Using our estimate of RMR, 30 kg of blubber (27.9 MJ kg\(^{-1}\)) would provide a 943 kg (the weight of the shark examined by Ref. 12) white shark with sufficient energy for approximately 11.6 days, which is about four times less than that calculated by Ref. 12 [Table 1]. The winter–spring water temperature at the Neptune Islands, where we recorded the swimming speeds of white sharks, is 15.35 ± 0.86°C (mean ± s.d.). This is very similar to that recorded by Refs. 12 (14.7–16.7°C) during their measurement of MR, and as such cannot in itself account for the high RMR estimated. However, our RMR estimate takes into account the high levels of activity needed for a white shark to ‘patrol’ a seal colony (e.g. 2.9 ± 0.2 m s\(^{-1}\), grand mean ± s.e.m., n = 12; 0.81 TL s\(^{-1}\)), including burst speeds up to 10 m s\(^{-1}\) [−2.85 TL s\(^{-1}\) for a 3.5 m shark, Fig. 1(b)]. When a median value of swimming speed is used (2.25 ± 0.14 m s\(^{-1}\), grand mean ± s.e.m, n = 12; 0.62 TL s\(^{-1}\)), we get a RMR estimate of 567 mg O\(_2\) kg\(^{-1}\) h\(^{-1}\) (absolute RMR 67.9 g O\(_2\) h\(^{-1}\)), which is comparable to previous estimates of RMR for the related shortfin mako shark\(^\text{14,19}\) (absolute RMR 41.2–44.2 g O\(_2\) h\(^{-1}\))

### Footnotes

1. This work was supported by the Australian Government through the Marine Biodiversity Hotspots Program (‘The Great Australian Bight’ Project).
2. We thank the crew of the R/V ‘Southern Surveyor’ and the late R. Cowan for their support during the field work. Z. Frith, R. Cowan and K. J. Osse are acknowledged for many valuable discussions and assistance. S. Silvain and W. W. L. McFarlane are thanked for assistance with field work. M. A. Scott is thanked for advice on statistical analysis. Y. C. Lee is thanked for constructing an aquarium for shark studies. J. D. Last is thanked for help with statistical analysis. Dr C. McLeod and Dr G. K. Hughes are thanked for advice on the evaluation of the field studies.
3. P. Briscoe is thanked for advice on field technique.
4. The Australian Centre for Field Research (ACFRE) is thanked for assistance with the field work.
5. We are grateful to the Australian Fisheries Management Authority, the South Australian Department of Agriculture, Environment and Water Resources (South Australian Marine Stewardship Council), the Department of Sustainability, Environment, Water, Population and Communities, the Department of the Environment, Water, Heritage and the Arts and the Department of the Environment and Science of the Australian Capital Territory for funding the research. The Northern Continental Shelf Program (NCS) of the Australian Government, and the Australian Centre for International Agricultural Research (ACIAR) are thanked for supporting the project.
6. The authors declare no competing financial interests. This manuscript has been read and approved by all the authors. This study did not involve any human participants and/or animals. The research was carried out in accordance with Australian and South Australian laws governing the use of live animals in research, and with the approval of the Animal Ethics Committee of Flinders University. This article is part of a PhD thesis submitted to the Faculty of Science, Engineering and Technology, Flinders University. This study was supported by an Australian Research Council Discovery Project (DP160100735) and a Discovery Early Career Researcher Award (DE170100905). The authors would also like to thank the following institutions and organizations for their support: Department of Environment and Heritage, Commonwealth of Australia; South Australian Marine Stewardship Council; Australian Centre for International Agricultural Research; and the Northern Continental Shelf Program of the Australian Government. The authors acknowledge the generous support of the following organizations: Australian Institute of Marine Science (AIMS); Australian Museum; Australian National seafood exports.

Given their high metabolic rates, white sharks may target seal colonies to predate on seasonally abundant and more vulnerable weaned pups\(^\text{25}\), rather than adult seals or patchily-distributed fish. Silver seabream is a commonly known forage fish of Australian white sharks\(^\text{24}\), and while the energy density of both prey items are similar (9.4 MJ kg\(^{-1}\) and 8.8 MJ kg\(^{-1}\) for weaned seal pups and silver seabream, respectively), the smaller medium size of silver seabream would necessitate at least one (1.0) successful predation event per day to maintain energy balance, compared to less than one (0.3) if targeting weaned seal pups. However, to contribute any energy toward growth and reproduction, they would need to eat more than one silver seabream per day, but would be in positive energy balance if predating on seal pups every third day. Patchily-distributed reef-associated prey such as C. auratus have been described as ‘less-visitable’ for white sharks\(^\text{25}\) given the prey’s ability to disperse and shelter among complex habitat. Hence, there may be a distinct energetic advantage in targeting one prey item every few days in a predictable (revisitable) habitat such as a seal colony\(^\text{24}\), compared to pursuing and capturing more than one prey item every day in a less-visitable patch (i.e. silver seabream aggregation).

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[References provided in the original document.]

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This study was supported by an Australian Research Council Discovery Project (DP160100735) and a Discovery Early Career Researcher Award (DE170100905). The authors would also like to thank the following institutions and organizations for their support: Department of Environment and Heritage, Commonwealth of Australia; South Australian Marine Stewardship Council; Australian Centre for International Agricultural Research; and the Northern Continental Shelf Program of the Australian Government. The authors acknowledge the generous support of the following organizations: Australian Institute of Marine Science (AIMS); Australian Museum; Australian National University. This study did not involve any human participants and/or animals. The research was carried out in accordance with Australian and South Australian laws governing the use of live animals in research, and with the approval of the Animal Ethics Committee of Flinders University. This article is part of a PhD thesis submitted to the Faculty of Science, Engineering and Technology, Flinders University.
human exploitation25. As an example, our approach could provide a tool for examining the ecological role of mesopredator release through removal of large sharks, such as white sharks. This is a very topical and contentious area of ecological research where further empirical evidence is needed26.

**Methods**

Twelve white sharks *Carcharodon carcharias* (estimated total length (TL) range: 2.8–4.5 m, mean ± s.e.m.: 3.6 ± 0.2) were tagged with acoustic depth transmitters (model V16P-5H, Vemco, Halifax, Nova Scotia) at the Neptune Islands, Australia between December 2009 and September 2011. Tagging was carried out under South Australian (SA) Department of Environment, Water and Natural Resources permits M25738 and M25738-2. SA Department of Primary Industries and Resources exemption 9902364 and Flinders University Animal Ethics Committee approval E287. The three-dimensional positions (latitude, longitude and depth) of tagged sharks were triangulated for up to 19 d (for example see Fig. 1(a)) using a radio-acoustic positioning system (Vemco, Halifax, Nova Scotia. Model VRAP), which covered 0.052 km². Swimming speed (m s⁻¹) was calculated using consecutive location estimates (≤5 s apart). Above 10 m s⁻¹, cavitation limits swimming speeds27. As such only swimming speeds below 10 m s⁻¹ were used (~10,000 speeds representing 82% of data) to calculate a grand mean swimming speed (m s⁻¹) for the 12 sharks. This single value was then converted to *U* (TL s⁻¹) using the mean TL.

To estimate field RMR we modified the relationship for oxygen consumption rate (MO₂, mg O₂ kg⁻¹ h⁻¹) and swim speed (*U*, TL s⁻¹) determined directly for a shortfin mako shark *Isurus oxyrinchus*28:

\[
\text{Log } \text{MO}_2 = 0.58U + \text{Log } (246) \tag{1}
\]

where by the Log value in the intercept 246 in Eq (1) represents the standard (equivalent to resting in an obligate ram-ventrilo) MRO (SMR, mg O₂ kg⁻¹ h⁻¹) calculated during the transport of captive VOY white seals29, the slope 0.58 Eq (1) represents that determined for a shortfin mako shark, and *U* in Eq (1) is the value calculated from our swim speed estimates (TL s⁻¹).

Total daily energy expenditure (TDE, MJ) was calculated from field RMR using an oxycoalorific coefficient of 13.55 kJ g⁻¹ O₂ (Ref. 28). To determine the number of weaned NZ fur seal pups needed to be consumed at this TDE to maintain energy balance and the associated daily ration (% wbw d⁻¹) weaned NZ fur seal pups needed to be consumed at this TDE to maintain energy balance and the associated daily ration (% wbw d⁻¹) weaned NZ fur seal pups needed to be consumed at this TDE to maintain energy balance and the associated daily ration (% wbw d⁻¹)

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