

NOTE

Can threshold foraging responses of basking sharks be used to estimate their metabolic rate?

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ABSTRACT: Empirical and theoretical determinations of minimum threshold prey densities for filter-feeding basking sharks *Cetorhinus maximus* were used to test the idea that threshold foraging behaviour could provide a means for estimating oxygen consumption (a proxy for metabolic rate). The threshold feeding level represents the prey density at which there will be no net energy gain (energy intake equals expenditure). Basking sharks were observed to cease feeding at their theoretical threshold; thus, the assumption underpinning the concept presented here was that over the narrow range of zooplankton prey densities that induce 'switching' between feeding and non-feeding in basking sharks, the energetic value of the minimum threshold prey density is equivalent to the shark's instantaneous level of energy expenditure. Four independent estimates of the lower threshold prey density obtained for *C. maximus* in the English Channel were converted to equivalent rates of oxygen consumption. Best estimates ranged from 62.5 to 91.1 mg O₂ kg⁻¹ h⁻¹ (mean, 80.7 mg O₂ kg⁻¹ h⁻¹, ± 20.1 [95% confidence interval, CI]) for a shark of 5 m total body length (L_T) weighing 1000 kg. Sensitivity analysis using 'low' and 'high' possible values in the model for mouth gape area, proportion of prey filtered, buccal flow velocity, prey energy content and energy absorption, yielded low and high rates of 23.2 and 192.1 mg O₂ kg⁻¹ h⁻¹, respectively. Varying estimated body mass of 1000 kg in the model by ± 200 kg gave an oxygen consumption range of 67.2 to 100.8 mg O₂ kg⁻¹ h⁻¹; a range within the 95% CI of the best estimate mean. For comparison, a new routine oxygen consumption-body mass relationship was determined for sharks (body mass range, 0.35 to 140 kg) and was described by the equation $VO_2 = 0.30M^{0.84}$, where VO_2 is oxygen consumption in mg O₂ h⁻¹ and M is mass in grams. When corrected for likely energy costs associated with filter-feeding, this relationship and 2 other metabolic rate scaling relationships in the literature gave expected rates between 52.0 and 99.2 mg O₂ kg⁻¹ h⁻¹ for a fish of 1000 kg body mass. The threshold-converted and expected oxygen consumption values although derived from different methods show good agreement, an observation that warrants further investigation. To verify the concept it will be necessary to obtain threshold-converted rates of oxygen consumption from a wide size range of basking sharks (1.5 to 10.0 m L_T) to determine whether rates scale predictably with body mass as does actual metabolism.

There are 3 species of filter-feeding shark, the whale shark *Rhincodon typus* of warm-temperate and tropical seas worldwide, the basking shark *Cetorhinus maximus* that inhabits warm-temperate to boreal waters circumglobally, and the megamouth shark *Megachasma pelagios* which occurs in the Pacific and Atlantic, primarily in deep water (Compagno 1984, Yano et al. 1997). They are among the largest marine vertebrates attaining body lengths of up to 14, 10 and 6 m respectively. Comparatively little is known about the biology of planktivorous sharks despite the fact that they are unique within the shark group in that they consume zooplankton directly, which results in them being at the apex of a relatively short food chain with the potential to influence the density and diversity of plankton communities. Although the foraging behaviour of whale sharks (Clark & Nelson 1997) and basking sharks (e.g. Sims & Quayle 1998) has begun to be studied in detail recently, there have been no determinations of the magnitude or rates of vertical energy flux attributable to these species. In this context, measurements of energy expenditure in plankton feeding sharks at different levels of activity would provide important information on the level of zooplankton (energy) intake required by these animals to meet active metabolism, and, set against the calorific value of prey densities utilised by them, would enable calculation of the quantity of energy potentially available for growth. However, measurement of energy expenditure in planktivorous sharks is yet to be attempted.

Numerous investigations have measured metabolic rates in a variety of shark species using the indirect, oxycalorific method (e.g. Pritchard et al. 1958, Hughes & Umezawa 1968, Brett & Blackburn 1978, Bushnell et al. 1989, Sims 1996). The oxygen consumption rates of large species (>1 m in length), how-

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ever, cannot be measured using conventional methods because the size of most water-tunnel respirometers limits experiments to small specimens or juveniles (Graham et al. 1990). The logistical problems associated with capturing large pelagic sharks, keeping them in a respirometer and maintaining them alive for long enough such that near-normal rates of metabolism can be determined have meant only a small number of sub-adult individuals of large, active species have been examined (e.g. lemon shark *Negaprion brevirostris* and shortfin mako *Isurus oxyrinchus*; Graham et al. 1990).

Most commonly the routine oxygen consumption-body mass relationship derived from small to medium-sized fish species has been used to estimate metabolic rates of large sharks indirectly by simple extrapolation (e.g. Stillwell & Kohler 1982). This approach provides only an estimate of routine oxygen consumption and does not take into account species-specific differences in physiology and behaviour, such as the regional heterothermy in certain predatory shark species (e.g. white shark *Carcharodon carcharias*) and its effects on heat conservation, metabolic rate and activity levels. Hence, whilst it is generally accepted that extrapolation of routine oxygen consumption-body mass relationships (to obtain estimates of active metabolism in large sharks) will not provide accurate estimates on a species-by-species basis, there have been no suggestions of other indirect methods that could indicate metabolism in species too large to be kept in the laboratory. Therefore, in the absence of very large tunnel respirometers for measuring oxygen consumption directly or comprehensive oxygen consumption-body mass relationships that include large-bodied shark species, it seems the energy expenditure of filter-feeding sharks must be estimated in other ways.

Whale sharks and megamouth sharks primarily utilise suction or gulp feeding to obtain sufficient particulate prey (Compagno 1990, Colman 1997), where the controlled increase in volume of the shark's buccopharyngeal cavity results in an internal pressure reduction which, when the mouth opens, acts to draw water (containing prey) into the mouth. In contrast, basking sharks feed by swimming forwards with the mouth open to overtake zooplankton prey that are filtered from the passive water flow across the gills by comb-like rakers attached to the gill arches; a strategy known as ram filter-feeding. Basking sharks are dependent therefore on forward swimming speed to regulate rates of prey capture (energy intake). Forward swimming with the mouth open increases drag-induced energy costs compared to normal swimming with the mouth closed, so when prey densities are too low to support feeding at an energetic gain it becomes advantageous to cease feeding. If basking sharks con-

tinued to feed in areas with low prey density for extended periods of time the energy that could be gained from filtered prey would not be sufficient to cover the costs of its collection. The density of zooplankton at which energy intake equals expenditure is termed the threshold prey density, and below this level net energy gain cannot be achieved.

Theory predicts that filter-feeding swimming speed will be lower in higher densities of zooplankton, but will increase as prey becomes sparse in order that optimum rates of prey capture are maintained (Ware 1978, Priede 1985). A recent study on basking sharks demonstrated empirically that individual sharks increase swimming speed in low prey densities and cease feeding at their theoretical threshold prey density determined from energy intake-output calculations (Sims 1999). Below the threshold level, feeding stopped in preference to lower cost (low drag) cruise swimming with the mouth closed. In this paper I suggest a potential method for estimating oxygen consumption rate in the basking shark using determinations of their threshold foraging responses. In the light of the abovementioned study, I reason that, at the threshold prey density which induces 'switching' between feeding and non-feeding in basking sharks, the energy value of the minimum threshold prey density should (after taking into account additional factors) be equivalent to the shark's instantaneous level of energy expenditure at the onset of filter-feeding (i.e. an active metabolic rate). In this study I use the concept of this energetic balance point together with previously published threshold response data (Sims 1999) to estimate oxygen consumption rate in a basking shark of 5 m total body length (L_T). Comparisons are made between this threshold-converted oxygen consumption rate and those derived from 2 new routine oxygen consumption-body mass relationships for sharks, and 2 general fish relationships.

Methods. Threshold foraging behaviour determinations: The minimum threshold prey densities for basking sharks that were used in this study to calculate oxygen consumption were determined from behavioural studies carried out in a 350 km² study area in the English Channel off Plymouth, UK (for map see Sims & Merrett 1997, their Fig. 1). Detailed descriptions of the methodologies used to determine threshold foraging responses are given in Sims (1999). In the latter study 4 independent field methods that related observations of shark behaviour to variations in zooplankton prey density were employed to determine threshold feeding levels empirically. The 4 methods are briefly described here: (1) Swimming speeds of individual basking sharks together with zooplankton sampling along foraging tracks were measured to determine actual feeding responses of sharks to varying prey densities

Table 1. Summary of the empirical minimum threshold prey densities for filter-feeding basking sharks determined by Sims (1999) with threshold-converted rates of oxygen consumption determined using Eq. (1) with 'best' parameter estimates

Empirical threshold estimation method	Threshold zooplankton density (g wet wt m ⁻³)	Oxygen consumption (mg O ₂ kg ⁻¹ h ⁻¹)
(1) Swimming speeds and zooplankton sampling	0.66	85.9
(2) Group tracking and zooplankton sampling	0.64	83.3
(3) Seasonal counts and zooplankton abundance	0.48	62.5
(4) Zooplankton characteristics from feeding/non-feeding areas	0.70	91.1
Mean of empirical estimate	0.62	80.7

encountered. As predicted (Ware 1978, Priede 1985), swimming speed increased with a decrease in zooplankton density because basking sharks adjusted speed to maintain rates of energy gain. The threshold prey density was the point at which sharks switched from cruising (non-feeding) in lower densities to the onset of filter-feeding at higher prey densities. (2) A group of 24 basking sharks feeding in a discrete patch of zooplankton were tracked intermittently over a 250 h period and zooplankton depletion in the feeding area was determined by repeated sampling. The density of zooplankton in the vicinity outside the feeding area was also sampled intermittently over a 400 h period (which encompassed temporally the feeding area observations) at set sampling Stn 1 (see Sims & Merrett 1997, their Fig. 1) and where no sharks were observed surface feeding. The threshold feeding level was taken as the median zooplankton density in the patch when sharks were observed leaving the area, which was coincident with zooplankton density in the patch falling below background levels. (3) The number of surface foraging basking sharks encountered per day was recorded in relation to zooplankton abundance over 60 d periods in each of 2 years. The threshold density using this method was estimated from the median prey density from samples taken at the surface when no further sharks were seen surface feeding in each year. (4) Zooplankton characteristics (density; total number of zooplanktonts; total number of copepods) were determined from samples taken from the paths of foraging sharks during trackings and were compared with samples where sharks had been observed to feed but were absent on sampling days. The 4th estimate of threshold prey density was taken to be the median zooplankton density from samples in areas that did not support feeding activity of basking sharks.

Oxygen consumption calculations: The 4 empirical estimates of threshold foraging level given in Table 1 were each converted into equivalent rates of oxygen consumption ($\dot{V}O_2$) (expressed in g O₂ kg⁻¹ h⁻¹) using the following relationship:

$$\dot{V}O_2 = \frac{(A \cdot u \cdot f \cdot P_F \cdot P_V \cdot T \cdot E \cdot P_E) / 13.6}{M} \quad (1)$$

where A is mouth gape area of the basking shark (m²), u is cruise swimming speed at the 'switching' point (m s⁻¹), f is time spent feeding per hour (s h⁻¹), P_F is the proportion of available prey that was captured by filtration, P_V is the buccal flow velocity as a proportion of forward flow velocity, T is threshold zooplankton density (g wet wt m⁻³), E is the energy value of zooplankton (kJ g⁻¹ wet wt), P_E is the proportion of energy absorbed ('digestible' energy) and M is shark mass in kg. An oxycaloric coefficient of 13.6 kJ g O₂⁻¹ was used (Jobling 1993).

Parameter values were taken from recent investigations on feeding in basking sharks or approximated from data given in the literature. Basking sharks most commonly observed off Plymouth were 5 m L_T (Sims et al. 1997) and were estimated to weigh approximately 1000 kg (Springer & Gilbert 1976, Stott 1980, Kruska 1988). A 5 m L_T basking shark has a mouth gape area (A) of ca 0.20 m² and when feeding continuously spends about 6 s min⁻¹ swallowing filtered zooplankton, hence 54 s min⁻¹ (3240 s h⁻¹) was taken to be the time spent actively filtering (f) (Hallacher 1977, D.W.S. unpubl. data). The mean swimming speed (u) of non-feeding basking sharks was 1.08 m s⁻¹ (Sims 1999). For zooplankton prey of the size encountered by basking sharks, the filtering efficiency was estimated to be 80% ($P_F = 0.8$) (Gerking 1994), and the buccal flow velocity was approximated to be 80% of the forward flow velocity ($P_V = 0.8$) (Sanderson et al. 1994). A zooplankton energy value of 5.04 kJ g⁻¹ wet wt was used (Båmstedt 1986), which represents the mean energy content of calanoid copepods from shallow water and high latitude, the group that makes up 70% of the zooplankton assemblages sampled near feeding basking sharks (Sims & Merrett 1997). The energy absorption efficiency of basking sharks was taken to be the same as the 80% ($P_E = 0.8$) suggested for the lemon shark *Negaprion brevirostris* (Wetherbee & Gruber 1993). Water temperature in the

study area during observations of threshold foraging responses ranged from 13 to 16°C.

Sensitivity analysis: The aforementioned parameter values were used to derive the 'best' estimate of oxygen consumption rate in a 5 m L_T basking shark of mass 1000 kg. In addition, a sensitivity analysis was undertaken to calculate the highest and lowest oxygen consumption rates that could conceivably occur given that some parameter values were, by necessity, approximations. A 'lowest' estimate was calculated using Eq. (1) by substituting best estimate parameter values with lowest possible values suggested from data given in the literature. The mouth gape area (A) of a 5 m L_T shark was reduced from 0.20 to 0.15 m² (Matthews & Parker 1950); the proportion of prey filtered (P_F) was decreased to 70%; buccal flow velocity as a proportion of forward velocity (P_V) was lowered to 60%, the same reduction in buccal flow measured in small-bodied, plankton-feeding paddlefish *Polyodon spathula* (Sanderson et al. 1994). The energy value of zooplankton (E) was lowered to 3.70 kJ g⁻¹ wet wt, the lower mode of energy content sampled for surface-dwelling, high-latitude copepod species (Båmstedt 1986), and the proportion of energy absorbed (P_E) reduced to 60%, the lowest measured in lemon sharks (Wetherbee & Gruber 1993). Swimming speed, feeding time and the minimum threshold density were fixed as these were known with certainty from empirical measurements (Sims & Quayle 1998, Sims 1999). To obtain a 'highest' estimate of oxygen consumption rate, A was increased to 0.24 m² (Parker & Boeseman 1954), P_F and P_E both to 90%, P_V to 100% and E was increased to 6.30 kJ g⁻¹ wet wt, an upper mode for energy content in shallow-water, high-latitude copepods (Båmstedt 1986). Swimming speed, feeding and threshold prey density remained fixed as before. The effect of body mass variation on the best estimate was also examined by calculating oxygen consumption rates using the best estimate parameter values but for sharks of body mass 800 and 1200 kg.

Routine oxygen consumption - body mass relationships: For comparison with the threshold-converted oxygen consumption rates calculated for a basking shark a routine oxygen consumption-body mass relationship for sharks was determined from data given in the literature. Routine metabolic data for 7 species of sharks between 0.35 and 3.51 kg body mass were available for this analysis (6 species from Carcharhiniformes, 1 from Squaliformes). The species used were: *Triakis semifasciata* (Gruber & Dickson 1997); *Negaprion brevirostris* (Nixon & Gruber 1988, Bushnell et al. 1989, Scharold & Gruber 1991); *Carcharhinus acronotus* (Carlson et al. 1999); *Sphyrna tiburo* (Parsons 1990, Parsons & Carlson 1998, Carlson & Parsons 1999); *Scyliorhinus stellaris* (Piiper et al. 1977); *Scyliorhinus*

canicula (Hughes & Umezawa 1968, Sims 1994); and *Squalus acanthias* (Pritchard et al. 1958, Lenfant & Johansen 1966, Brett & Blackburn 1978). A mean routine oxygen consumption rate was calculated for similarly sized individuals in each of the 14 studies, except for *C. acronotus*, for which 3 means from different size groups were calculated from data given in a single study (Carlson et al. 1999), giving an overall n of 16. Routine metabolism in these shark species was defined as the rate at constant, slow swimming speeds. Metabolic rates were standardised to 15°C using a Q_{10} of 2.34 (Carlson & Parsons 1999) for all species except *S. stellaris* and *S. canicula*, for which a Q_{10} of 2.16 was used (Butler & Taylor 1975). Routine oxygen consumption rate (VO_2 , mg O₂ h⁻¹) was related to body mass (M , g) by $VO_2 = aM^b$, where a is a constant and b is the scaling exponent, and fitted by least squares regression after logarithmic transformation of both variables.

A second routine oxygen consumption-mass relationship was determined for these same shark data but this time including estimates of routine metabolism in 3 large individuals of *Negaprion brevirostris* (body mass range, 40 to 140 kg) and a 78 kg bull shark *Carcharhinus leucas* (Schmid & Murru 1994). Routine oxygen consumption was calculated for these large specimens indirectly by difference. The latter authors took measurements of food energy intake (E), estimations of faecal (F) and urinary energy losses (U), and growth increments (P) were recorded over long periods with the amount of energy unaccounted for in the balanced equation $E = R + F + U + P$ being attributed to energy losses via respiration (R) and converted into routine metabolic rates (Schmid & Murru 1994). I converted these rates to equivalent rates standardised to 15°C using a Q_{10} of 2.34 (Carlson & Parsons 1999), and when combined with the data described above, a routine oxygen consumption-body mass relationship was determined by least squares regression after logarithmic transformation of both variables.

In addition, 2 routine oxygen consumption-body mass relationships derived from teleost and shark metabolic data were taken from Parsons (1990) and used for comparisons with threshold-converted rates in addition to the 2 newly derived shark VO_2 -body mass relationships. The scaling relationships were $VO_2 = 13.0(\log M)^{-0.602}$ (derived from 5 shark and 12 teleost species) and $VO_2 = 12.9(\log M)^{-0.866}$ (derived from 5 shark and 8 teleost species), where VO_2 is mass-specific routine oxygen consumption in mg O₂ kg⁻¹ h⁻¹ and M is body mass in grams.

Results and discussion. There are sound theoretical reasons why determinations of minimum threshold feeding level could provide a correlate of active metabolism for basking sharks at the onset of filter-feeding. In order to forage efficiently basking sharks must

select filter-feeding swimming speeds that maximise the difference between energy intake and power output (Ware 1978, Priede 1985), because a shark that swims too slow or feeds in low prey densities will capture insufficient food (energy) to cover the costs of its collection. Recent studies show basking sharks do indeed maximise prey encounter rates by exhibiting selective foraging behaviour on specific zooplankton prey assemblages by concentrating their feeding activity in areas near thermal fronts characterised by high densities of large calanoid copepods (Sims & Merrett 1997, Sims & Quayle 1998). It has also been demonstrated that basking sharks cease surface foraging when the density of zooplankton in feeding areas reaches a lower threshold level (Sims & Quayle 1998, Sims 1999). Sims (1999) demonstrated that the observed threshold prey densities of basking sharks were in close agreement with the theoretical threshold feeding level determined from energy intake-output calculations. This verified that when basking sharks were observed to cease feeding in the wild, it was at a point when the energy extracted from prey balanced the energy that was expended in its capture (Sims 1999).

The minimum threshold prey densities for basking sharks determined by Sims (1999) using 4 independent methods provided the starting point from which the oxygen consumption rate of a 5 m L_T basking shark was estimated in the present study. The assumption underlying these calculations was that the threshold prey density that initiates feeding in cruising (non-feeding) sharks is the point at which the energy they derive from filtered zooplankton is equal to the energy expended at the commencement of filter-feeding. The threshold levels obtained previously (methods 1 to 4; Table 1) when converted using Eq. (1) gave oxygen consumption rates between 62.5 and 91.1 mg O₂ kg⁻¹ h⁻¹, with a mean of 80.7 mg O₂ kg⁻¹ h⁻¹ ± 20.1 (95% confidence interval, CI) (Table 1). Sensitivity analysis of the best estimate showed that substituting the best estimate parameter values for the lowest likely values, the threshold-converted oxygen consumption rate decreased to 23.2 mg O₂ kg⁻¹ h⁻¹, whilst high parameter values yielded a maximum rate of 192.1 mg O₂ kg⁻¹ h⁻¹ (Table 2). This demonstrates that when mouth gape area, proportion of prey filtered, buccal flow velocity, prey energy content and the proportion of energy absorbed remain unknown (i.e. not measured directly), the prediction range for oxygen consumption is large at approximately ± 3 times the best estimate. However, the mouth gape area of a basking shark can be estimated with reasonable accuracy when the body length is known, and the

Table 2. Summary of sensitivity analysis results showing the threshold-converted rates of oxygen consumption using low, best and high parameter values and the effect on estimated oxygen consumption rate of increasing the number of constant (measurable) parameters in Eq. (1)

Body mass (kg)	Parameters used in Eq. (1)	Oxygen consumption (mg O ₂ kg ⁻¹ h ⁻¹)		
		Low	Best	High
800	Constant: <i>u, f, T</i>	29.0	100.8	240.1
1000	Constant: <i>u, f, T</i>	23.2	80.7	192.1
1200	Constant: <i>u, f, T</i>	19.3	67.2	160.1
1000	Constant: <i>u, f, T, E</i>	31.6	–	153.7
1000	Constant: <i>u, f, T, E, A</i>	39.7	–	127.6

energy content of zooplankton prey sampled near foraging sharks can be determined directly by calorimetry. With the best estimates for mouth gape area and prey energy content substituted back into Eq. (1) but with the proportion of prey filtered, buccal flow velocity and the proportion of energy absorbed remaining as low or high estimates, the prediction range for oxygen consumption narrows to between 39.7 and 127.6 mg O₂ kg⁻¹ h⁻¹ (Table 2). Thus, reasonably accurate measurements of mouth gape area and prey energy content in addition to swimming speed, feeding time and threshold prey density increase the precision of the estimate to approximately ± 1.8 times the best estimate.

The best estimate of oxygen consumption rate in a 5 m L_T basking shark was relatively insensitive to a body mass variability of ± 200 kg. Using the best estimate parameter values the rate of oxygen consumption in a 800 kg shark was 100.8 mg O₂ kg⁻¹ h⁻¹ and for a 1200 kg individual 67.2 mg O₂ kg⁻¹ h⁻¹ (Table 2), estimates that fall within the 95% CI of the best estimate (60.7 to 100.8 mg O₂ kg⁻¹ h⁻¹). This suggests that precise estimates of basking shark body mass were not necessary to give broadly accurate estimates of oxygen consumption rate. Overall, the results of the sensitivity analysis demonstrated that relatively large variations in unmeasured parameters (mouth gape area, proportion of prey filtered, buccal flow velocity, prey energy content, proportion of energy absorbed) will still yield threshold-converted oxygen consumption rates of similar magnitude to the best estimate. However, accurate measurements of mouth gape area and prey energy content in addition to swimming speed, feeding time and threshold prey density increase the precision of the best estimate.

The routine (low active) oxygen consumption - body mass relationship for 7 species of shark is given in Fig. 1 and was described by the equation

$$\dot{V}O_2 = 0.27 M^{0.86} \quad (r^2 = 0.89, p < 0.0001) \quad (2)$$

where $\dot{V}O_2$ is in mg O₂ h⁻¹ and M is in grams. The mass scaling exponent of 0.86 found here for 8 species of

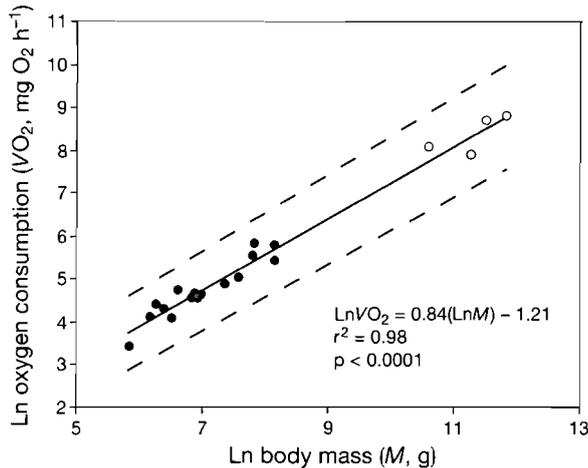


Fig. 1. Routine oxygen consumption - body mass relationship for 8 species of shark (species names and source of data given in the 'Methods' section) described by the linear equation $\ln VO_2 = 0.84(\ln M) - 1.21$ (shark body mass range, 0.35 to 140 kg) (Eq. 3 in text). Dotted lines denote 95% confidence interval. Each data point in the body mass range 0.35 to 3.51 kg (●) represents the mean of routine oxygen consumption rates measured in a number of individuals of a particular species, with each point being derived from a different study (except the 3 data points for *Carcharhinus acronotus*, which were from a single study). These data were described by the linear equation $\ln VO_2 = 0.86(\ln M) - 1.29$ ($r^2 = 0.89$, $p < 0.0001$) (Eq. 2 in text); line not shown for clarity as it lies very close to the fitted line of Eq. (3). Each data point in the body mass range 40 to 140 kg (○) represents a single estimation of oxygen consumption for an individual shark. Oxygen consumption rates were standardised to 15°C using a Q_{10} of 2.34 (Carlson & Parsons 1999) for all species except *Scyliorhinus canicula* and *S. stellaris*, for which a Q_{10} of 2.16 was used (Butler & Taylor 1975)

shark is the same as the 0.86 found for bonnethead sharks *Sphyrna tiburo* (Parsons 1990) and the exponent of 0.86 that was determined for the standard oxygen consumption rate of dogfish *Scyliorhinus canicula* (Sims 1996). For fish generally a mass scaling exponent of 0.7 to 0.9 has been suggested although a value of 0.86 may be appropriate for many species (Brett & Groves 1979, Jobling 1994). A recent analysis of resting oxygen consumption in 69 species of teleost fish determined a mass scaling exponent of 0.80 (Clarke & Johnston 1999). When the estimated routine oxygen consumption rates for 4 large (40 to 140 kg) sharks were included the data were best described by the equation

$$VO_2 = 0.30 M^{0.84} \quad (r^2 = 0.98, p < 0.0001) \quad (3)$$

where VO_2 is in $\text{mg O}_2 \text{ h}^{-1}$ and M is in grams. This demonstrates that the oxygen consumption - body mass relationship alters little in terms of the constant a and the scaling exponent b when estimates of metabolism in sharks that differ in body mass by some 4 orders of magnitude (range, 0.35 to 140 kg) are combined in a

single relationship. This suggests Eqs. (2) & (3) are appropriate for making an extrapolation to estimate the metabolic rate of a 1000 kg basking shark. The data used in the present study to determine Eqs. (2) & (3) represents the majority of metabolic rate data presently available for sharks. Even though in comparison to bony fishes few measurements of oxygen consumption have been made for shark species, the relationships described in Eqs. (2) & (3) are consistent with expected parameter values suggested from previous shark studies (Parsons 1990, Sims 1996).

Substituting a body mass of 1000 kg (for a 5 m L_T basking shark) into Eq. (2) yields a predicted routine oxygen consumption rate of $37.5 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. However, as filter-feeding costs may be between 1.5 and 2 times higher than routine costs at similar swimming speeds (Hettler 1976, James & Probyn 1989), elevating the feeding energy costs by 1.75 gives a predicted rate for filter-feeding oxygen consumption of $65.6 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (range, 56.2 to $75.0 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$). The mean threshold-converted oxygen consumption rate determined in this study for a 5 m L_T basking shark swimming at 0.23 body lengths, L , per second was $80.7 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (range, 62.5 to $91.1 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), which is close to the predicted value (Table 3). Similarly, the oxygen consumption rate range determined from Eq. (3) was 52.0 to $69.3 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (Table 3) and the threshold-converted values fall well within the upper 95% CI derived from Eqs. (2) & (3), for a shark with a body mass of 1000 kg. For additional comparison, 2 general VO_2 -body mass relationships (Parsons 1990) were used to provide a probable range of oxygen consumption rate. The predicted routine (non-feeding) oxygen consumption rates for a 1000 kg fish at 15°C extrapolated from the 2 relationships were 61.3 and $99.2 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ after taking into account increased energy costs associated with ram filter-feeding (Table 3).

Given that the routine oxygen consumption-body mass relationships (Eqs. 2 & 3 and the 2 general relationships) are least squares regression estimates from both shark and teleost data collected under different experimental conditions, and the conversions from threshold foraging responses of basking sharks to rates of oxygen consumption involve making assumptions about some parameters in Eq. (1), it is perhaps surprising, and therefore of interest, that the estimates show good agreement (Table 3). That the threshold-converted rates lie close to the predicted rates from both taxonomic-group-specific and general fish oxygen consumption-body mass relationships is supportive of the concept suggested in the present study that threshold foraging responses could provide a means to determine field estimates of metabolic rate in basking sharks.

Table 3. Comparison of oxygen consumption rate ranges determined from threshold-converted estimates, shark VO_2 -body mass relationships (Eqs. 2 & 3), and from 2 general fish VO_2 -body mass relationships (Parsons 1990)

	Oxygen consumption (mg O_2 kg^{-1} h^{-1})
Threshold-converted estimate	62.5–91.1
Shark VO_2 -body mass relationship (Eq. 2)	56.2–75.0
Shark VO_2 -body mass relationship (Eq. 3)	52.0–69.3
General fish VO_2 -body mass relationships	61.3–99.2

To further test the tentative suggestion raised in this paper, that threshold foraging responses may provide a 'window' on rates of metabolism in basking sharks too large to be examined under controlled conditions, threshold responses of juveniles (1.5 to 2.0 m L_T) compared to sub-adults (3 to 5 m L_T , this study) and large adults (8 to 10 m L_T) should be determined. This comparison will provide a means for verification of this concept because rates of oxygen consumption change predictably with body size (e.g. Sims 1996, Clarke & Johnston 1999). In practice the most ready method for determining threshold foraging responses in individual basking sharks would be to measure swimming speeds in sharks of different body mass under various conditions of food supply. It is at the transition between feeding and non-feeding that an accurate estimate of threshold foraging response to encountered zooplankton can be most reliably made. It has been assumed in the present study that the energy intake at the 'switching' point between feeding and non-feeding is equivalent to the level of energy expenditure. For this to be true, it is expected basking sharks off Plymouth were foraging optimally, because under such conditions they would be expected to make 'correct' decisions about the value of prey patches and whether to continue or cease feeding. The fact that individual and grouped basking sharks were observed to cease feeding at close to their theoretical threshold prey density by Sims (1999) implies that the assumption underlying the concept presented here is entirely reasonable. Therefore, measurements of filter-feeding-cruising swimming speed transitions in individual sharks of known length (estimated mass) responding to prey density gradients would enable individual threshold foraging responses to be determined accurately.

With these data, oxygen consumption rates for a broad size range of basking sharks could be calculated. If individual threshold feeding levels when converted to individual rates of oxygen consumption changed predictably with body mass and with a mass exponent of ca 0.8 to 0.9 (e.g. Parsons 1990, Sims 1996, Clarke & Johnston 1999), then this would indicate correlation between the minimum foraging thresholds of

basking sharks and their use as predictors of oxygen consumption rate during activity. If however, this criteria cannot be satisfied from such measurements it would indicate that foraging responses around the threshold level were not correlated closely with expected rates of energy expenditure and therefore not viable as 'proxy' measures.

Verification of the concept presented here would have broad significance

because a field correlate of metabolic rate in a large filter-feeding species such as the basking shark derived from simple measurements of threshold foraging responses could allow comparisons of metabolic rates between different individuals. However, for these observed differences to be valid, threshold foraging determinations would have to be made on sharks feeding in close proximity, so that variations in environmental factors (except prey density) would be minimised. But if reliable, observed differences could shed light on inter-individual variations in rates of metabolism as a result of different rates of growth or perhaps between males and females that at certain times of the year may have different energy allocation strategies depending on their reproductive status. Finally, although the ram-filter-feeding basking shark has been the species used here to introduce the concept of utilising measurements of threshold foraging responses to estimate active (filter-feeding) metabolism, the idea may also be appropriate for field estimations of metabolism in other surface skim feeders such as right whales *Eubalaena* spp. and bowhead whales *Balaena mysticetus*. As there is a general need to better understand rates of metabolism in planktivorous marine vertebrates and energy fluxes between them and the pelagic environment, further investigations that test the concept outlined here should therefore not be limited to ram-filter-feeding sharks.

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