Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge?

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The minimum threshold foraging response of basking sharks has not been determined despite the widely held view that has been perpetuated in the literature for the past 45 years that this species cannot use low prey densities for net energy gain and so lives on an energetic 'knife-edge'. An early theoretical estimate suggested basking sharks would expend more energy collecting zooplankton at concentrations $< 1.36 \text{ g m}^{-3}$ than could be obtained from it. This led to the claim that basking sharks will feed at an energetic loss for much of the annual cycle as zooplankton abundance outside summer months is too low for net energy gain to occur. Here I show from theoretical calculations and behavioural studies on individual and group-feeding sharks in the English Channel that basking sharks have a theoretical threshold prey density of between 0.55 and 0.74 g m^{-3} and an observed foraging threshold of between 0.48 and 0.70 g m^{-3} (mean = 0.62 g m^{-3}). The close agreement between theoretical and empirical threshold values suggests basking sharks can achieve net energy gain in much lower zooplankton densities than previously thought. The findings imply that this species may not be reliant upon the 'migration-hibernation' energy conservation strategy it is purported to exhibit when seasonal zooplankton abundance decreases below 1.36 g m^{-3} .

Keywords: filter feeding; threshold; *Cetorhinus maximus*; swimming speed; energy budget

1. INTRODUCTION

The basking shark (*Cetorhinus maximus*) is the second largest fish species and occurs in boreal to warm-temperate seas of the continental and insular shelves circumglobally. The biology of this species is little known although they are conspicuous at certain times of the year when they surface feed on zooplankton. Basking sharks feed by forward swimming with a widely opened mouth to overtake particulate prey that are removed from the passive water flow across the gills by long bristle-like rakers on the gill arches, a strategy known as ram filter feeding. *C. maximus* is considered to be the only obligate ram filter-feeding shark, as whale (*Rhincodon typus*) and megamouth sharks (*Megachasma pelagios*) are primarily suction feeders (Diamond 1985; Compagno 1990).

The problem that basking sharks face by adoption of an obligate filter-feeding strategy is that swimming with an open mouth increases the drag incurred (and, thus, energy expenditure) compared to normal swimming with the mouth closed. Consequently, sufficient zooplankton must be obtained to meet the energy costs of its collection before there can be net energy gain. From estimations of zooplankton's energy value and abundance, together with basking shark filter-feeding swimming costs, Parker & Boeseman (1954) calculated that basking sharks would use more energy collecting zooplankton in low densities than they could obtain from it. It was concluded that, unless a basking shark could select and remain in plankton concentrations greater than the low densities

that occur for much of the year in coastal areas, this species would be feeding at a loss (Parker & Boeseman 1954), suggesting these large fish are balanced on an energetic 'knife-edge' (Bone *et al.* 1995).

In view of Parker & Boeseman's (1954) conclusions, it appears that, if basking sharks are to grow and reproduce, they must forage in areas where the zooplankton density is high enough to maximize the difference between the rate of energy intake and power output. Recent studies have shown that basking sharks surface in north-east Atlantic coastal areas to feed on the high abundance of zooplankton that occurs in late spring (Sims *et al.* 1997). They are selective foragers on zooplankton and concentrate their feeding activity along thermal fronts in areas characterized by high densities of large copepods (Sims & Merrett 1997; Sims & Quayle 1998). Therefore, it seems basking sharks can avoid feeding at an energetic loss by foraging near productive fronts. However, despite the concept that basking sharks feed at a loss in all but the highest zooplankton densities available to them during summer months, there have been no direct measurements of the threshold foraging response of basking sharks or theoretical estimates using modern data to shed light on the validity of Parker & Boeseman's (1954) hypothesis. Therefore, the purpose of this study was to test the hypothesis by determining the threshold foraging response of basking sharks from direct observations of the foraging behaviour of individual and grouped basking sharks responding to varying zooplankton densities and to compare the empirical

measurements with a theoretical estimate derived from energy intake–output calculations.

2. STUDY AREA AND METHODS

During a field study of basking sharks (1996–1997) within a 350 km² sea area off Plymouth, UK in the western basin of the English Channel (50° 16' N, 004° 09' W; fig. 1 in Sims & Merrett 1997), I used four methods of determining the threshold foraging response of surface-feeding sharks: (i) measurement of swimming speeds of individual basking sharks together with zooplankton sampling along the foraging tracks; (ii) tracking a foraging shark group and assessing zooplankton depletion in the feeding area over a 250 h period; (iii) counting the number of surface foraging sharks seen per day in relation to zooplankton abundance over 60-day periods in each of two years; and (iv) comparing zooplankton characteristics of samples taken from the paths of foraging sharks with samples where sharks had been observed to feed but were absent on sampling days.

(a) *Zooplankton sampling*

Zooplankton from individual shark feeding paths, group foraging tracks and in the presence and absence of surface-feeding basking sharks were sampled using the same methodology. A single zooplankton sample consisted of a vertical haul, to 10 m deep, of a weighted simple plankton net (net diameter = 0.3 m and mesh diameter = 0.25 mm). Zooplankton were removed from the net receptacle by seawater washing after each haul and were immediately fixed in 4% formaldehyde. The total zooplankton catch in each sample was filtered in the laboratory to remove excess moisture and weighed wet before being carefully resuspended in 70% ethanol. All sample bottles were coded and their provenance withheld from sorters to avoid bias.

(b) *Swimming speed measurements*

I measured the swimming speeds of basking sharks responding to different zooplankton densities because the lower threshold prey density at which basking sharks forage could be estimated from the zooplankton density at which there is a switch from non-feeding, cruising behaviour to that of filter feeding. Measurements were made on six basking sharks (total length range 4.0–6.5 m) between mid-May and mid-June in 1996–1997. All swimming speed determinations on individual sharks occurred between 11.30 and 15.40. The total lengths of individual sharks were estimated using the methodology in Sims *et al.* (1997). Individual basking sharks swimming at the surface were approached slowly and tracked by positioning the 10 m research vessel at a distance of 5–7 m parallel to the shark, with the bow in line with the tip of the shark's snout. At this distance the sharks' behaviour was not affected by the vessel's presence. During tracking, the vessel speed was matched to the sharks' swimming speed by continual fine adjustment of the vessel's speed. Shark swimming speed was measured when they swam on straight courses in two ways: 'through the water' and 'over the ground'.

- (i) A mechanical flow meter (General Oceanics, model 2030R) was used to obtain through-the-water measurements of shark swimming speed. The propeller unit of the flow meter was towed from the vessel at the mid-ship and parallel to the vessel at a distance of 1.5 m and a depth of 0.3–0.5 m. Vessel turbulence did not reach the rotor when in this position as it was forward of and lateral to the

wake. The flow meter had a response threshold of 0.1 m s⁻¹. A digital meter (Solomat 520c) recorded flow meter revolutions and gave continuously updated speed readings in metres per second. Three sharks' speeds were determined between one and six times at the beginning and end of tracking periods lasting between 45.5 and 55.0 min. Determinations were taken at *ca.* 1 min intervals and represented the flow meter-calculated mean of flow speeds during the 1 min period of recording.

- (ii) The speeds of three different sharks when swimming on relatively straight courses were determined using a global positioning system (GPS) to obtain over-the-ground measurements. One shark's speed was recorded from the GPS digital display (Garmin 120S) every 5 s when the vessel remained parallel to the shark as it swam on a straight swimming course. The speeds of two other sharks were measured using an on-board differential GPS (Valsat 03, MLR Electronics) with determinations made every 2–5 min. The effect of current speed on over-the-ground measurements of basking shark swimming speed was accounted for using tidal stream data at tidal recording station C (50° 12.5' N, 004° 05.2' W) given on Admiralty Chart number 1613 (Crown Copyright 1995, Hydrographic Office, UK). During the trackings tidal currents were in the range of 0.05–0.51 m s⁻¹.

Zooplankton samples were taken within 3 m of the feeding path of individual sharks immediately before or after each swimming speed determination and processed as described previously.

(c) *Group tracking*

An aggregation of basking sharks was tracked intermittently within a 52 km² area from 3–12 June 1996 (station 1 was the centre of this area; 50° 18.2' N, 004° 9.2' W). The research vessel stayed within 10–50 m of foraging sharks during each of four tracking periods which lasted for 6.3, 3.3, 4.2 and 0.8 h on the 3, 4, 6 and 12 June 1996, respectively. The group of sharks followed the tidally transported movements of a productive zooplankton patch during this period and covered a minimum distance of 34.6 km (see the track data in Sims & Quayle (1998)). Zooplankton samples within 3–10 m of feeding sharks in this group were taken during each of the four tracking periods in order to estimate the rate of zooplankton depletion by the sharks. These samples were compared with zooplankton samples taken at regular intervals over a 400 h period at station 1. Surface zooplankton samples from station 1 were taken at the start of tracking days, when no basking sharks were present, to provide an estimate of non-feeding (normal background) densities of zooplankton in the area during shark observations.

(d) *Shark counts in relation to zooplankton*

The total number of sharks within each group was counted and expressed as the number sighted per day during 22 trackings of groups of basking sharks in 1996 and 1997. Zooplankton samples within 3–10 m of sharks were taken during trackings with between two and 17 samples per individual track.

(e) *Comparison of zooplankton when sharks were present and absent*

Zooplankton samples taken between May and July 1997 were of two types and were compared: (i) samples taken directly from the path of surface-feeding sharks (shark samples), and

(ii) samples taken at set sampling stations when no sharks were present (non-shark samples). These sample series were taken concurrently over the 42-day period. The samples taken when sharks were absent were from four set stations in the study area with the majority at station 1. The set stations were situated in areas where basking sharks had been seen in abundance in previous studies (Sims & Merrett 1997; Sims *et al.* 1997; Sims & Quayle 1998). Three replicate zooplankton samples were taken at set stations between 07.00 and 08.30 each day. Single zooplankton samples from within 3–10 m of the feeding paths of basking sharks were taken on the same days as sampling from set stations. All samples were initially processed as described previously. In addition to total zooplankton catch, the numbers of zooplanktons in each of the major taxa were counted in all samples. The following species and taxonomic groups were counted: cnidarian medusae, Polychaeta, *Calanus helgolandicus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi*, *Centropages typica*, Malacostraca, Branchiopoda, Chaetognatha, Larvacea, fish eggs and fish larvae. Each zooplankton sample was reduced using a standard plankton splitter to obtain subsamples with between one and four splits made for samples. Validation of this technique by comparison of the number of zooplanktons in each group in a split subsample with the numbers determined from another subsample taken at random from the same original sample showed there to be a mean error of 5.0% (± 5.8 s.e., $n=5$). For each of the calanoid copepod species, only non-naupliar stages (CI–CVI) were counted.

Zooplankton samples were analysed quantitatively using three parameters of zooplankton characteristics, namely zooplankton density (grams per cubic metre), total number of zooplanktons (number per cubic metre) and total number of copepods (number per cubic metre). Differences in the median dispersion between shark and non-shark samples for each of the three parameter-ranked data streams were tested using Mann–Whitney one-tailed *U*-tests with Z -transformation. Significance at the 5% level was tested using the improved normal approximation to the Mann–Whitney *U*-test (Zar 1999).

3. RESULTS

(a) *Swimming speeds*

The mean swimming speed of basking sharks when filter feeding was 0.85 m s^{-1} (± 0.05 s.e., $n=49$ determinations from five different sharks, with mean total length = $4.9 \text{ m} \pm 1.1$ s.d.) compared to a mean non-feeding cruising speed of 1.08 m s^{-1} (± 0.03 s.e., $n=21$ determinations from two sharks, both 4 m total length). As expected (Ware 1978; Priede 1985), basking shark swimming speed decreased with an increase in zooplankton density encountered (figure 1). A logistic function with a fixed lower asymptote was found to produce the best fit to the observed data ($r^2=0.57$ and $p<0.001$) and was described by the relationship

$$U = 1.28 - \frac{0.76}{1 + e^{-1.75(D-1.25)}}, \quad (1)$$

where *U* is swimming speed in metres per second and *D* denotes zooplankton density in grams per cubic metre. The lower asymptote of swimming speed was fixed at 0.52 m s^{-1} , the lowest speed observed and was fitted into the logistic function as the difference between the lowest and highest (1.28 m s^{-1}) speeds (e.g. $1.28-0.52=0.76$).

Figure 1. Surface swimming speeds of six basking sharks (4.0–6.5 m total length) in relation to zooplankton densities encountered during May–June 1996 and 1997. Closed circles denote feeding sharks and open circles denote non-feeding sharks. The curve represents a logistic function with fixed lower asymptote that was fitted by nonlinear least-squares regression.

Equation (1) was used to predict the lower threshold zooplankton density by calculating the zooplankton density predicted for a mean cruising speed of 1.08 m s^{-1} . The observed mean cruising speed was assumed to represent the speed which maximized the distance travelled per unit of energy expended and, therefore, the speed at which there would be greatest likelihood of switching to filter feeding when the lowest favourable zooplankton density was encountered. The mean cruising speed found in this study was only 12.5% greater than the theoretical optimal cruising speed for a 4–5 m fish predicted by the model of Weihs *et al.* (1981). By rearrangement of equation (1) in terms of *D*, the threshold density was calculated to be 0.66 g m^{-3} at the assumed cruise-feed switching speed of 1.08 m s^{-1} .

(b) *Feeding group threshold*

Twenty-three individuals were identified during the 224 h intermittent observation of a feeding group of basking sharks. The changes in zooplankton density at station 1 over the 360 h encompassing the shark feeding observations ranged from 0.94 to 1.92 g m^{-3} , whereas zooplankton sampled in the sharks' foraging area had a greater range, namely 0.47 – 8.29 g m^{-3} (figure 2). The zooplankton density near basking sharks was highest during the first 24 h of observation (1.47 – 8.29 g m^{-3}) and was greater than that at station 1 over the same period. The sample content was much reduced between 24 and 224 h (0.47 – 1.68 g m^{-3}) showing an exponential decline in local zooplankton abundance near basking sharks (figure 2). Nine different sharks made up the surface-feeding group for the first 48 h, while 11 other sharks were seen between 74 and 80 h, although this decreased to three different individuals from 218 to 224 h. Between 74 and 224 h after first tracking the feeding group, the zooplankton densities near sharks were lower than those sampled at station 1 (figure 2). Close observations of these sharks were possible due to calm sea conditions. When the

Figure 2. Change in zooplankton density in the foraging area of a basking shark group (closed circles) compared to background densities at station 1 (open circles) at the centre of the foraging area. The curve illustrating a decrease in zooplankton density near sharks was fitted by eye. The zooplankton density of 8.29 g m^{-3} taken near feeding sharks at 122.5 h is not shown.

zooplankton density near sharks was lower than the background levels ($0.50\text{--}0.80 \text{ g m}^{-3}$) (figure 1), four basking sharks ceased feeding. They swam away from the centre of the foraging area on relatively straight courses. Using zooplankton sample densities when sharks ceased feeding to approximate the threshold foraging response of sharks in the group, the threshold range was $0.47\text{--}0.80 \text{ g m}^{-3}$ (mean $\pm$ s.e. = $0.64 \pm 0.04 \text{ g m}^{-3}$, $n = 8$).

(c) Cumulative number of sharks

Over the three-month study periods in both 1996 and 1997, 70 and 54 basking sharks were sighted, respectively, and ranged from 2.0 to 8.0 m in total length. The maximum increase in the number of surface-feeding basking sharks occurred in early June in both years concomitant with sharp declines in the zooplankton density measured in group foraging areas (figure 3). The cumulative number of sharks in both years reached a plateau after mid-June at a time when zooplankton densities near feeding sharks were measured to be between 0.44 and 0.86 g m^{-3} . No further sharks in either year were seen after the median zooplankton densities sampled near foraging groups had decreased to 0.45 and 0.51 g m^{-3} (figure 3), suggesting a lower threshold zooplankton density had been reached.

(d) Zooplankton where sharks were present and absent

In 1997, 120 zooplankton samples were taken close to surface-foraging basking sharks (shark samples, $n=67$) and from set stations where sharks were absent (non-shark samples, $n=53$). Quantitative statistical analysis showed that the mean zooplankton density was 3.2 times higher in shark samples and that the median density of zooplankton was significantly greater than in non-shark samples (table 1; $t_{0.05(1),\infty}=1.64$, $Z_c'=7.89$ and $p < 0.0005$). The increase in zooplankton density observed near feeding sharks was accounted for by the total number of zooplanktons of all major taxa counted being 2.9 times

Figure 3. Cumulative numbers of basking sharks sighted within the study area in 1996 (solid line) and 1997 (dotted line) in relation to the median zooplankton densities sampled near feeding sharks in 1996 (closed circles) and 1997 (open circles). Each circle represents the median density of between 2 and 17 zooplankton samples (mean $n=7.1$ and total number of samples = 150).

greater compared to numbers where sharks were absent (table 1; $t_{0.05(1),\infty}=1.64$, $Z_c'=7.20$ and $p < 0.0005$). Comparison between the numbers of copepods per cubic metre between shark and non-shark samples demonstrated that, overall, the increase in zooplankton density in areas where sharks foraged was primarily due to a threefold (2.96 times) increase in copepod number (table 1; $t_{0.05(1),\infty}=1.64$, $Z_c'=7.02$ and $p < 0.0005$). On the basis of this analysis it was concluded that, at the time of sampling, the absence of basking sharks in areas where they had previously been observed to feed was due to low abundances of zooplankton, notably copepods. Hence, non-shark samples were assumed to represent unfavourable zooplankton characteristics for foraging sharks. The median zooplankton density of non-shark samples was 0.70 g m^{-3} (table 1) and was taken to be broadly representative of a lower threshold density.

(e) Theoretical estimate of threshold prey density

A 5 m basking shark, the most common shark size seen off Plymouth, was estimated to weigh 1000 kg (Springer & Gilbert 1976; Stott 1980; Kruska 1988). Energy expenditure during routine activity was calculated to be 770.58 kJ h^{-1} using the routine metabolism–weight relationship given in Parsons (1990), which was determined using published data from 17 fish species, including that from three pelagic shark species.

The seawater filtration rate of a 5 m basking shark (mouth gape area *ca.* 0.20 m^2) swimming at an observed speed of 0.85 m s^{-1} was calculated to be $431.83 \text{ m}^3 \text{ h}^{-1}$, allowing for an observed swallowing (prey handling) time of 6 s min^{-1} (Hallacher 1973; D. W. Sims, unpublished data) and assuming the actual buccal flow velocity to be 80% of the forward swimming velocity (Sanderson *et al.* 1994). The amount of energy required from zooplankton to meet the energy expenditure from activity was found by dividing the energy costs of routine metabolism by the filtration rate. Using efficiencies of 80% for both zooplankton filtration (Gerking 1994) and energy

Table 1. *Zooplankton characteristics in areas where feeding basking sharks were present (n=67) and absent (n=53) during May–July 1997*

(s.e. denotes one standard error of the mean.)

	density (g m ⁻³)	total zooplankton (number m ⁻³)	total copepods (number m ⁻³)
sharks present			
mean	2.41	2605.31	1796.29
s.e.	0.24	244.93	180.66
median	1.80	2324.62	1481.87
sharks absent			
mean	0.75	894.07	606.37
s.e.	0.04	86.55	67.16
median	0.70	729.62	472.28

absorption in sharks (Wetherbee & Gruber 1993), a 5 m basking shark would need to obtain 2.79 kJ m⁻³ to avoid feeding at a loss. Copepods make up 70% of the zooplankton where basking sharks forage (Sims & Merrett 1997) and have a mean energy content of 5.04 kJ g⁻¹ wet weight (Båmstedt 1986). Assuming a similar energy density for the remaining 30% of zooplankton (observed to be mostly other Crustacea), the theoretical prey density at which a 5 m basking shark would avoid feeding at a loss was 0.55 g m⁻³.

However, this theoretical estimate of threshold prey density is largely dependent on the estimated costs of basking shark swimming activity which have not been determined for this species by direct measurement for obvious logistical reasons. As filter-feeding costs may be between one-and-a-half and two times higher than routine activity costs at similar swimming speeds (Hettler 1976; James & Probyn 1989), elevating the feeding energy costs of a 5 m basking shark by a factor of 1.75 gives a threshold prey density of 0.74 g m⁻³. These two estimates at different levels of energy expenditure were taken as probable limits to the theoretical threshold foraging response of basking sharks.

4. DISCUSSION

This study is the first to determine the threshold foraging response of basking sharks empirically, enabling a hypothesis which has stood untested for 45 years (that basking sharks forage at a loss in low zooplankton densities) to be addressed directly. Using behavioural and zooplankton sampling studies over a variety of spatial scales to assess the threshold foraging behaviour of basking sharks on zooplankton, this study shows that threshold responses of basking sharks occurred in the zooplankton density range 0.48–0.70 g m⁻³ with a mean of 0.62 g m⁻³, values which agreed closely with the theoretical threshold prey density calculated for a 5 m total length basking shark which ranged from 0.55 to 0.74 g m⁻³. Basking sharks tracked through prey densities < 0.45 g m⁻³ did not feed, which further supports a threshold prey density for basking sharks close to 0.5–0.6 g m⁻³. These results demonstrate that foraging basking sharks off Plymouth cease surface filter feeding

when surface prey densities approach the theoretically predicted lower threshold, an observation that suggests they are able to derive net energy gain from prey densities down to ca. 0.5–0.6 g m⁻³.

The new threshold estimates provided by this study are lower than the threshold prey density calculated by Parker & Boeseman (1954) solely on the basis of theoretical considerations of shark swimming costs and zooplankton energy content. The latter authors calculated that a 7 m basking shark swimming at ca. 2 knots (1.03 m s⁻¹) would need to consume 2.02 kg of zooplankton per hour to meet the energy costs of its collection (2.77 kJ h⁻¹). They estimated this shark would filter 1484 m³ of seawater per hour (Parker & Boeseman 1954), which gave a threshold zooplankton density of 1.36 g m⁻³. This calculated value is 2.2 and 2.5 times higher, respectively, than the mean empirical and theoretical estimates determined in the present study. However, the energy costs of swimming activity calculated by Parker & Boeseman (1954) were one to two orders of magnitude lower than present-day estimates based on determinations of the oxygen consumption rate in large sharks (Graham *et al.* 1990; Parsons 1990). Similarly, the energy content of copepod-dominated zooplankton used in their calculations was three orders of magnitude lower than present-day accepted standard values (Båmstedt 1986; Mauchline 1998). In addition, inaccuracy in Parker & Boeseman's (1954) estimate for energy intake by basking sharks was compounded because they did not take into account inefficiencies associated with filter feeding, namely buccal flow velocity was assumed to equal forward swimming velocity, all zooplankton encountered was assumed to be captured, swallowing (prey handling) time was not considered and 100% of encountered energy (prey) was assumed to be absorbed by the shark. Although Parker & Boeseman's (1954) threshold estimate is only roughly double those in the present study and was probably as accurate as was possible given the constraints in knowledge and methodologies at the time, it is now clear that the parameter values used by Parker & Boeseman (1954) were not accurate and, in turn, that the threshold prey density estimate of 1.36 g m⁻³ cannot now be considered to be correct.

Empirical and theoretical estimates in the present study both support a threshold zooplankton density for foraging basking sharks close to 0.5–0.6 g m⁻³, a significantly lower value than previously thought. Although Parker & Boeseman's (1954) conclusion that basking sharks would not forage at densities < 1.36 g m⁻³ has not been formally tested in field or theoretical investigations until now, the present finding that basking sharks are apparently able to use lower prey densities for net energy gain is an important one in terms of how it now influences our interpretation of this species' behaviour outside summer months.

The Parker & Boeseman (1954) hypothesis, that basking sharks are unable to feed in low zooplankton densities because they would not achieve net energy gain, is a view that has been perpetuated in the literature on this species for nearly half a century (e.g. see the review of Kunzlik 1988). Since the early work that formulated these ideas (Matthews & Parker 1950; Parker & Boeseman 1954; Matthews 1962), it has been largely

accepted that, in autumn, when the zooplankton levels in coastal areas decrease, basking sharks migrate into deep water where they become inactive and remain resting on the bottom in a hibernative state. It was suggested that the main determinant for offshore migration and hibernation of basking sharks during winter was that the standing stock of winter zooplankton in coastal areas was insufficient to support the metabolic costs of feeding activity (Parker & Boeseman 1954). The latter authors also found that some winter-caught basking sharks were rakerless but had a new set of rakers developing under the gill arch epidermis. The conclusion was that, because basking sharks would feed at a net energy loss on zooplankton during winter months, they shed their gill rakers, swim offshore into deep water and hibernate for four months to conserve energy (Parker & Boeseman 1954; Matthews 1962). It was proposed that development of new rakers occurred during the winter hibernation and erupt through the gill arch epidermis in early spring in time for summer foraging (Parker & Boeseman 1954).

The results of the present study question the validity of this 'hibernation' hypothesis on the grounds that basking sharks, off Plymouth at least, forage for long periods in low prey densities ($<1.36 \text{ g m}^{-3}$). The results of the present study strongly suggest that basking sharks are capable of using lower prey densities than 1.36 g m^{-3} for maintenance of growth rates. The implication of this finding is that, if zooplankton densities between 0.55 and 1.36 g m^{-3} occur in north-east Atlantic waters outside summer months, then foraging areas of sufficient productivity to support basking shark feeding and growth may not be as spatio-temporally limited as suggested by Parker & Boeseman (1954). Zooplankton abundance in the north-east Atlantic is less during winter than summer, but the concentrations above the threshold density for shark feeding shown in this study (0.62 g m^{-3} , ca. 400 copepods m^{-3}) are present off Plymouth in winter (Harvey *et al.* 1935; Digby 1950; November–February range 651–2792 copepods m^{-3}). In addition, the threshold prey density found in my study is also lower than the winter zooplankton biomass estimate of 0.84 g m^{-3} adopted by Parker & Boeseman (1954) in their analysis. Therefore, basking sharks may not be limited to feeding on high prey densities in the summer alone.

However, the observation that basking sharks found in winter do not have rakers seemingly provides evidence against the suggestion arising from the present results that basking sharks could exploit, without net energy loss, threshold prey densities characteristic of temperate seas during winter. However, a significant proportion of basking sharks in winter have been found with full sets of gill rakers and zooplankton prey in their stomachs (Van Deinse & Adriani 1953; Parker & Boeseman 1954). This suggests the accepted chronology of raker shedding in October–November, new raker development during December–February and eruption of new rakers in spring does not apply to all individuals in the population. Basking sharks may in fact have a shorter raker development time which would account for sharks in winter possessing rakers and having food in their stomachs. These observations, taken together with the present study,

indicate basking sharks probably use low prey densities both within and outside of the summer months. In the light of these results, the purported 'hibernation' behaviour of this species for four months (due to an apparent inability to achieve net energy gain in low prey densities) is probably not a tenable explanation of the cause of their apparent offshore migration and seasonal deep water habit.

Female basking sharks with recently healed mating scars have been observed at the start of summer foraging (Matthews 1950) while pregnant individuals are virtually unknown, observations which suggest breeding grounds lie offshore and that seasonal migration of sexually mature individuals occurs primarily for courtship and mating. In addition, as some basking sharks do possess gill rakers in winter, the fact that significant concentrations of late stage, energy-rich calanoid copepods overwinter in deep water off the north-east Atlantic continental shelf (Kaartvedt 1996; A. D. Bryant, personal communication) may also be an important ultimate factor driving the offshore migration of sexually immature basking sharks.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.