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Searching speeds and the energetic feasibility of an obligate whale-scavenging fish

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Abstract

Two recently published models reach opposite conclusions on the energetic feasibility of a scavenging fish that specialises on whale carcasses. We argue that the key difference between these models is in their estimate of the likely searching speed of such a hypothetical scavenger. Neither of the previous models considers that although faster searching will allow food sites to be found more quickly, it will also reduce the time between meals that the fish can survive on its reserves. Hence, we present a novel model that encapsulates this trade-off, and use this model to predict the optimal searching speed for such a hypothetical scavenger. The model predicts that the optimal speed should increase with mass and be in the range $0.1\text{-}0.2\text{ms}^{-1}$ for fish of the range of sizes found for the ubiquitous grenadier *Coryphaenoides armatus*. These values accord with most estimates of the swimming speeds for this species. Hence we conclude that rejection of a whale-carcass feeding specialist fish on energetic grounds is premature. Although we see no reason to dismiss such a specialist on energetic grounds, we argue that such a fish will be unlikely on ecological grounds, although a deep-sea fish that gathered much of its energy from scavenging at relatively large food packages on the ocean floor should be feasible.

Smith & Baco (2003) concluded that whale carcasses are too sparse a resource to allow a scavenging fish to specialise solely on this food source. Their argument, based on a simple mathematical model, is that such a whale-specialist would have only a 50% chance of finding a whale carcass after 700 days of searching, and 700 days is likely to be well in excess of their maximum fasting time. This seems at odds with the conclusion of Ruxton & Houston (2004) that an oceanic obligate scavaging fish would be entirely energetically possible. It is this apparent conflict that this manuscript sets out to explore. The main difference between the two published models lies in the assumptions they make about the searching speed of the fish. Smith & Baco assume 0.016ms^{-1}, whereas Ruxton & Houston (2004) use an allometric equation which predicts 0.41, 0.47 and 0.5ms^{-1} for 0.5kg, 1kg and 1.5kg fish respectively. Smith & Baco's estimate comes from the work reported in Collins et al. (1998). These authors studied the movement of the ubiquitous grenadier fish *Coryphaenoides armatus* during dispersal from an artificial food fall having ingested an acoustic tag. The fish were followed to a range of up to 600m from the food fall, taking up to 12 hours. Although the 2-dimensional path of the fish was determined, the speed quoted by Collins et al. (1998) is the radial distance away from the food fall divided by the time since departure from the bait. Several other estimates of swimming speeds are available for this species. The most recent estimates of swimming speeds in *C. armatus* that we could find are those of Priede et al. (2003) based on video measurement of tail beat frequencies converted to speeds by a previously published general relation for anguiliform and subcarangiform swimmers. This gave mean values of 0.23 and 0.27ms^{-1} for two different trials. This measurement represents speed through the water, which may be different from speed across the ground if currents are substantial. Also, these measurements were made in the vicinity of a food source, which may have induced increased activity levels over normal searching behaviour. Collins et al. (1998) measured speed across the ground in video images of this species in the vicinity of an artificial food fall, as well as by acoustic methods. The mean swimming speed recorded in this study was 0.088ms^{-1}. This compares with previous estimates obtained by similar methods of 0.09ms^{-1} (Bagley et al. 1994; Priede et al. 1994) and 0.09ms^{-1} (Smith et al. 1997). From these it seems that (since 0.5-1.5kg are representative masses for *C. armatus*: Smith 1978; M.A. Collins et al. unpublished data), that the value for searching speed used in Ruxton et al. is likely to be an overestimate, by at least a factor of two. However, the value used by Smith & Baco, is potentially as much as ten times lower than other plausible estimates of the over-ground speed of this species.

It is now logical to ask how important searching speed is to the probability of finding a whale carcass within a specified time. If we assume (as both Ruxton & Houston, 2004 and Smith & Baco, 2003 do) that whale falls are distributed randomly over the ocean bed and the fish moves so as to avoid re-searching previously covered ground, an expression for the probability of encountering a whale fall can be derived from simple geometric reasoning (e.g. Gerritsen & Strickler 1977; Baird & Jumper 1995). Specifically, the probability of encountering a whale after searching for time T, $P(T)$ is given by

$$P(T) = 1 - \exp(2dv\rho T), \qquad (1)$$

where ρ is the density of whale falls, v is the mean search speed and d is the distance at which a whale carcass can be detected. In Figure 1, we take the values for ρ and d from Smith & Baco ($\rho = 0.001\text{km}^{-2}$; $d = 500\text{m}$), and plot P as a function of v for various values of time interval (T). We see that if 0.1ms^{-1} is an appropriate estimate of search speed, then this changes Smith & Baco's calculations and conclusions quite considerably, in that the probability of finding a whale by the time 700 searching days has elapsed is 0.998, dropping to 0.82 for 200 days and 0.58 for 100 days. We chose 700 days for commonality with the arguments of Smith & Baco, and 200 days because Smith (1978) estimated that the energy stored in the lipid and glycogen that he found in three specimens of *C. armatus* that he dissected could last the fish 186 days (based on his estimate of their metabolic rate). It is important to note that Smith's fish were lured to a bait that they could not eat before being trapped, so there is no reason to expect that these fish had fed recently before being caught, and so no reason to expect their stored energy to represent a maximum value of a fish having just fed. Indeed the study of Drazen (2002a) found that lipid levels were very variable between individuals and suggested that Smith's values might be relatively low. Further, since scavengers are likely to be able to feed to satiation on discovering a whale carcass, Smith's estimates of energy reserves are likely to be a conservative estimate for our purposes.

However, it is worth considering that active searching is energetically expensive, and expense will rise with searching speed. Hence, although faster searching will allow food sites to be found more quickly, it will also reduce the time that the fish can survive on its reserves. We can quantify this by replacing T in our original equation by an expression for the time that a fish can survive on its stored reserves (T_{max}):

$$T_{\max} = \frac{E}{S + C(v)},\tag{2}$$

where E is the total amount of stored energy (in Joules), S is the standard metabolic rate when not in motion (in Watts) and C is the additional cost (in Watts) of travelling as speed v. It is possible to estimate all of these factors. Smith (1978) investigated the composition of three *C. armatus* specimens, weighing 0.5, 0.7 and 1.2kg. He detected no obvious pattern in composition with size, and estimated that on average 0.73% of the mass was neutral lipid and 0.17% was glycogen. He argued that these are likely to be the two main energy stores, and suggested that their energetic values where 39kJ per gram for lipids and 18kJ for glycogen. Taken together these assumptions and measurements can be used give an expression for E (in Joules) as a function of mass in kilograms (M). One kg of fish equates to 7.3g of lipid and 1.7g of glycogen, which multiplying by the energy values and adding gives 315300J. Since, we assume that the energy stores scale linearly with mass, we can use the following expression for E:

$$E = 315,000M\tag{3}$$

If we assume that the three fish that Smith (1978) measured metabolic rates for were relatively inactive, then we can use his data to provide the following relation (adapted from Bailey et al. 2002, using the conversion 1ml 0_2 = 19.4J from Drazen 2002b):

$$S = 0.015 M^{0.65} \tag{4}$$

There are a number of published relations for *C* (based either on theoretical arguments or empirical measurements over a range of species), of which perhaps the most commonly cited one is that of Ware (1978):

$$C = 1.17 M^{1.44} v^{2.42} . \tag{5}$$

To explore the validity of this equation for *C. armatus* we can utilise the only energetic expenditure measurement that is available for a *C. armatus* swimming at known speed: Bailey et al. (2002) estimated the energy expenditure of a 1.5kg fish swimming at 0.1ms^{-1} as 0.029W (again using 1ml 0_2 = 19.4J from Drazen 2002b). If we substitute *M* = 1.5 and *v* = 0.1 in eqns. (4) & (5), then we get *S* = 0.020W and *C* = 0.008W, giving a combined estimated energy expenditure rate of 0.028W, which is close to Bailey et al.'s measured value. That locomotion can be achieved with such a modest increase in metabolism (*C*(0.1) = 0.4*S*) may seem initially surprising, but since a 1.5kg *C. armatus* might be around 70cm long (M.A. Collins et al, unpublished data), a velocity of 10ms^{-1} represents only 0.15 bodylengths per second. It is also worth noting that the metabolic rates measured for *C. armatus* by Smith (1978) and Bailey et al. (2002) suggest that this species does have a very low metabolism: being only 15-30% of measurements of similar sized Atlantic cod (*Gadus morhua*) at similar temperatures (Sanders 1963; Claireaux et al. 2000). Very few measurements of metabolic expenditure during such slow swimming are available. Webber et al. (1998) measured the metabolic cost of swimming at speeds between 0.07 and 0.65ms^{-1} for Atlantic Cod (*Gadus morhua*) with a mean weight of 1.9kg in water at 5°C. They estimated *C*(0.1) to be 0.2*S*, *C*(0.2) to be 0.6*S* and C(0.6) to be 2.9*S*, suggesting that although fast swimming is energetically expensive, our estimate of a modest energetic expense to slow swimming may not be unrealistic.

By combining equations (1) – (5), we are now able to estimate the probability of finding a whale carcass before a fish's energy reserves run out, as a function of search speed and size (see Figure 2). This suggests that the probability of finding a food item before starvation is maximised at intermediate speeds, with slow speeds not allowing sufficient ground to be covered and high speeds causing energetic reserves to be used too quickly (see Figure 3). This optimal speed increases with mass and is in the range 0.1-0.2ms^{-1} for fish of the range of sizes found for *C. armatus*. However, no matter the size of fish, search speeds within this range yield probabilities of finding a food site in time to avoid starvation always higher than 75%. We can see that *C* increases faster than *S* with increasing mass, so the costs of travel are proportionately higher for larger fish. *C* for a 1.5kg fish travelling at 0.2ms^{-1} is equivalent to 2.2 times the resting metabolic rate (*B*). Estimates of metabolic scope in Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*) at 4-5°C range from 2.5-4 times resting metabolic rate (e.g. Bushnell et al. 1994; Claireaux et al. 2000). Thus it seems that the continuous search speeds that we postulate here could be within the metabolic scope of the animals involved, and certainly involve speeds similar to those that have been observed empirically.

In summary, we conclude that rejection of a whale-carcass feeding specialist fish on energetic grounds is premature. We believe that this paper sets out an energetically plausible scenario for the survival of such a specialist. However much remains

unknown about the lifestyles of deep-water fishes, and in particular the searching behaviour of species like *C. armatus* is still uncertain. To keep our models simple, we have assumed that scavengers avoid re-searching parts of the environment that they have only recently searched. This assumption is biologically plausible, since this behaviour maximises the rate of encounter with food (assuming food falls are essentially independent random events), and can be achieved most easily in still water by swimming continuously in one direction without frequent turns. However, if water-currents are heterogeneous in space and/or time, then avoiding re-searching already explored parts of the environment may be more challenging to achieve. There is a pressing need for empirical work using tags that can allow fish to be tracked over weeks and months. Such technology is already being exploited for fish in shallower waters (e.g. Hunter et al. 2004a&b), and (although logistically challenging), the transfer of this technology to the deep sea would be very fruitful. The theory presented here makes very clear quantitative predictions (such as the expected variation in search speeds in fish of different sizes), which such empirical data could critically test.

Although we see no reason to dismiss a whale-carcass feeding specialist on energetic grounds, we would consider such a fish to be highly unlikely on ecological grounds. These fish are also predatory, and the relative importance of live prey and scavenged material is uncertain. Stomach contents are difficult to obtain from deep-living fish as they typically regurgitate during decompression, and scavenged flesh will probably be difficult to identify. The chances of obtaining stomach contents from a deep-sea fish that has fed sufficiently recently for those contents to be identified as carrion is unfortunately slim, even if scavenged material was energetically very important.

Smith & Baco's calculations were part of a wider review of the ecology of whale falls at the deep-sea floor, and for this reason the focused only on whales as food for their putative scavenger. We can think of no circumstances where an individual would be physiologically able to access whale carcasses but not those of other sea mammals, fish and squid that will also fall onto the sea floor. Although such smaller carcasses may be available for less time, be more challenging to detect, and may provide less substantial meal sizes, it seems ecologically unlikely that a fish actively searching for whale carcasses would not periodically find and exploit such a food source. The key consequence of a whale-specialist being energetically feasible is in supporting the argument that a deep-sea fish that gathered much of its energy from scavenging at relatively large food packages on the ocean floor should certainly be energetically feasible.

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Figure Captions

Figure 1: The probability of finding a food site within a specified time, as a function of search speed (using eqn (1) with $\rho = 0.001 \text{km}^{-2}$ and $d = 500\text{m}$). The solid vertical line indicates the point where search speed is 0.1ms^{-1}, discussed in the text.

Figure 2: Probability of finding a food site before reserves are exhausted, as a function of search speed v and individual mass M (using eqns (1) – (5) with $\rho = 0.001 \text{km}^{-2}$ and $d = 500\text{m}$).

Figure 3: The time in days that a fish can survive on its reserves (T_{max}), as a function of search speed v and individual mass M (using eqns (2) – (5)).
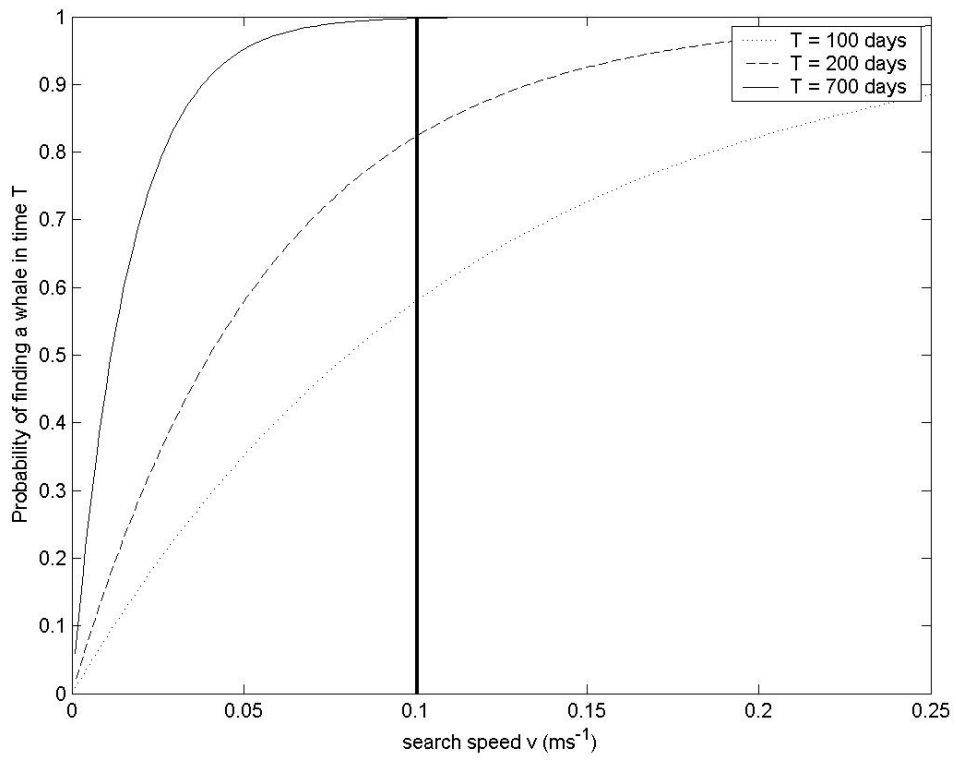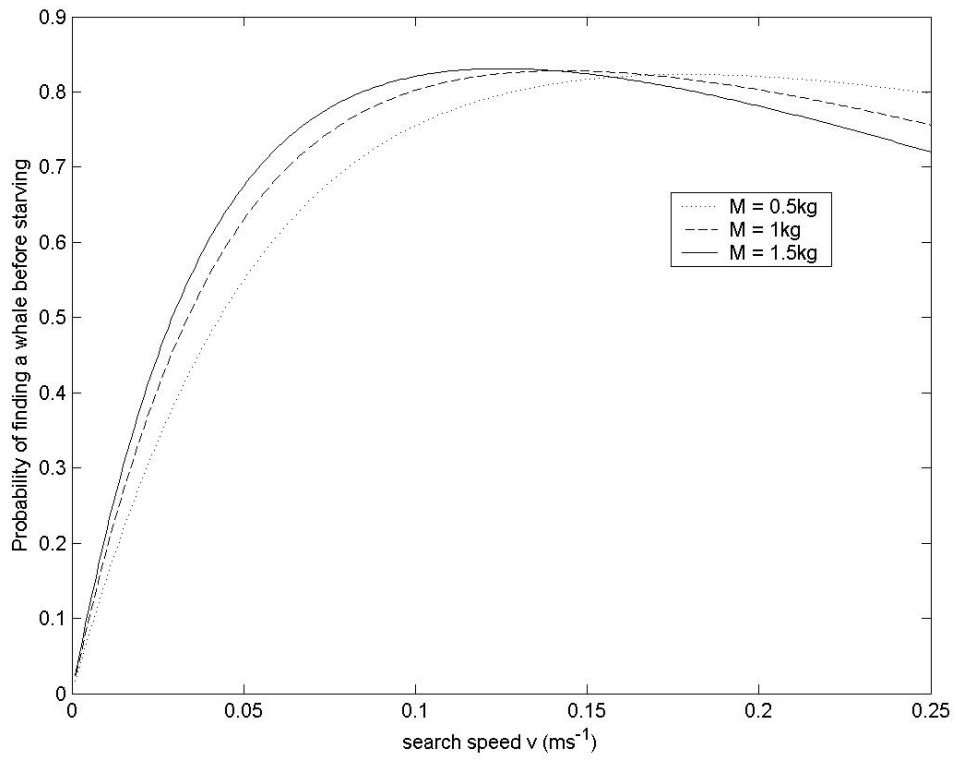
Figure 1:

Figure 2:

Figure 3: