

Juvenile salmon with high standard metabolic rates have higher energy costs but can process meals faster

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Basal or standard metabolic rate (SMR) has been found to exhibit substantial intraspecific variation in a range of taxa, but the consequences of this variation are little understood. Here we explore how SMR is related to the energy cost of processing food, known as apparent specific dynamic action or the heat increment of feeding. Using juvenile Atlantic salmon *Salmo salar*, we show that fishes with a higher SMR had a higher peak and a greater total energy expenditure when digesting a given size of meal. However, the duration over which their metabolism was elevated after consuming the meal was shorter. The greater energy costs they incur for processing food may be related to their assimilation efficiency. These relationships are likely to have implications for feeding strategies and growth rates, since individuals with a higher SMR have higher routine costs of living but recover more quickly following feeding and so may have a greater potential for processing food.

Keywords: metabolic rate; energetics; fish; digestion; growth

1. INTRODUCTION

All animals have a ‘baseline’ level of metabolic rate (MR), termed the basal MR (BMR) in homeotherms and standard MR (SMR) in poikilotherms, and defined as the level of energy consumption when inactive, not assimilating a meal and not paying off any oxygen debt associated with previous anaerobic activity (McNab 1988; Hulbert & Else 2000; Frappell & Butler 2004). It is well established that this MR (hereafter referred to as SMR) varies substantially among species (Blaxter 1989), tending to be the highest in those animals that have the most active lifestyles (White & Seymour 2004). However, there can also be a substantial (up to fivefold) variation in SMR within species, even under controlled conditions (Metcalfe *et al.* 1995; Steyermark *et al.* 2005). SMR represents a large component of the energy budget, for example, comprising up to 80 per cent in homeotherms and 90 per cent in free-living teleost fishes (Diana 1983; Speakman *et al.* 2003; Secor 2009). Therefore, it is important to understand the functional relevance of the wide intraspecific variation in this parameter.

Based on the variation among and within species, it has been hypothesized that SMR may relate to the cost of maintaining a scope for activity that is adapted to the lifestyles of the species (Hammond & Diamond 1997; Meerlo *et al.* 1997; Speakman *et al.* 2003). The scope for activity is the difference between standard and maximum MR (Fry 1947, 1971). A high-performance capacity could be expected to require a large mass of aerobically active tissues, such as the heart and lungs, which are relatively expensive to maintain (Steyermark *et al.* 2005) and would

lead to high basal costs. Such a relationship is observed when comparing interspecific trends in lifestyles, such as that illustrated in fishes by the relatively sessile pike (*Esox lucius* Armstrong *et al.* 1992) and flatfish (Duthie 1982) compared with the more active salmonids (Brett 1965) and tunas (Dewar & Graham 1994; Clarke & Seymour 2006; Blank *et al.* 2007).

The relationship between MR and lifestyle might also be invoked to explain intraspecific variation in SMR. Juvenile salmonid fishes have been a particularly useful subject for exploring individual variation in metabolism, because it has been possible to relate SMR to behavioural traits and therefore lifestyle within a species (Metcalfe *et al.* 1995; McCarthy 2000). SMR correlates with dominance status, which is reflected in the ability of fish to access high-value food patches (Metcalfe *et al.* 1989; Gotceitas & Godin 1992). Dominant individuals with high SMR tend to exhibit active aggressive behaviours, whereas subordinate fish are more passive, more cryptic and feed in more marginal areas (Höglund *et al.* 2000; Höjesjö *et al.* 2005). Therefore, a higher SMR in the more dominant salmon is consistent with a link between SMR and the scope for activity. However, in direct tests of this possibility, Cutts *et al.* (2002) found that juvenile Atlantic salmon (*Salmo salar* L.) with a higher SMR actually had a lower scope for activity.

An alternative possibility is that SMR relates to variations in capacity for processing food. Dominance, and hence SMR, is linked to food intake and growth of salmonids in habitats where spatial distributions of food patch qualities are predictable and can be defended, such as pools in rivers (Nakano 1995). The mechanical and chemical processes that accompany ingestion, digestion and assimilation of food result in an elevation in MR,

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termed the heat increment of feeding or apparent specific dynamic action (SDA; Beamish 1974). SDA increases rapidly to a peak or plateau after the ingestion of food, and then decreases more slowly as digestion of the meal proceeds (Jobling 1981). The costs of protein synthesis comprise a substantial component of SDA (Carter *et al.* 2001), and hence it relates directly to the rate of protein accretion and somatic growth. The faster digestion of food and accretion of tissues would result in a more rapid pronounced peak in SDA. Moreover, a reduction in the duration of SDA would enable a hastened capacity for further processing of subsequent meals with more rapid re-feeding and a greater throughput of food.

It is well established that the height and magnitude of SDA relate directly to the meal size (Jobling & Davies 1980; Secor & Diamond 1997; Zaidan & Beaupre 2003; Secor 2009), but there is no information on whether SDA for a given meal varies within species as a function of individual traits such as SMR. Here we explore this area, in particular testing the hypothesis that SMR is directly related to the speed and size of the SDA response. By measuring changes in the rate of oxygen consumption by Atlantic salmon of differing SMR, which consumed standard meal sizes, we show for the first time that there are strong links between SMR and the profile of energy expenditure during SDA, indicating the existence of intraspecific variation in food-processing strategies.

2. MATERIAL AND METHODS

The experiments were carried out on underyearling Atlantic salmon parr derived from wild parents; these were reared at the Fisheries Research Services Almondbank field station, Perthshire, and transferred to University of Glasgow in early August 2006 where they were held in a circular tank (1 m²) at 13.5°C in aerated, recirculated, copper-free water under an ambient seasonal photoperiod. They were fed to satiation on defrosted bloodworms (*Chironomid* larvae) once a day. While in the holding tank, the fish had access to shelters in the form of large stones and lengths of semicircular cut piping (approx. 120 mm in diameter). They were allowed to settle in the holding tank for one month before the first respirometry experiments took place. At the start of each round of experiments, four fish were selected at random, weighed and measured. They were then placed without food in individual respirometer chambers, maintained under subdued light at the same temperature of 13.5°C (± 0.5) throughout the whole experimental period, and allowed to settle for 2 days before the commencement of the first respirometry measurements (volume including pump, chamber and tubes was asymptotically equal to 1.6 l). Each of the separate respirometer chambers contained a clear Perspex shelter, since fish have a higher resting rate of metabolism when denied access to any shelter (Millidine *et al.* 2006). The chambers were kept in dim light to further reduce stress and activity levels; the water flow through the chambers was insufficient to prompt swimming, and therefore the fish remained resting on the substrate (water flow rate was 0.28 l s⁻¹). The apparatus was similar to that described in Millidine *et al.* (2006), and allowed measurements of oxygen consumption rates to be made using intermittent flow respirometry. All measurements were adjusted for temperature and barometric pressure using the table taken from Lewis (2006).

To measure SDA, it was first necessary to record the resting level of metabolism of the fish in a post-absorptive and quiescent state (which we define as their SMR, being the lowest level of metabolism that the fish is likely to reach on a regular basis). This was carried out between 08.00 and 09.00, 2 days after the fish had been placed in the respirometers. Measurements of oxygen consumption rates by fish were taken by closing the respirometer valves, thus preventing any water exchange, for a period of 10 min. After this time, the system was reopened to allow the water within the respirometer to be completely flushed with air-saturated water. Regular observations were made on the fish to ensure that they were inactive. Flow rate through the chamber did not significantly change during flushing and at no point did oxygen concentrations drop below 90 per cent saturation.

Food, in the form of defrosted bloodworms, was then given to the fish inside the respirometers. Two of the four fish were each given a single meal of bloodworms weighing 0.15 per cent (wet weight) of their body mass while the other two were each given a meal weighing 0.30 per cent of body mass. These chosen meal sizes were relatively small in comparison with their total daily intake, which is commonly offered in a single meal in studies of SDA (Secor 2009). However, they more closely simulate food intake in Atlantic salmon parr experiencing competition for feeding patches and irregular supply of food in natural conditions. The bloodworms were individually introduced to the respirometer chambers via the water inlet valve when the system was fully open. They were usually eaten immediately, and as soon as all the bloodworms had been consumed, the system was closed for a period of 5 min and the rate of oxygen consumption was measured. The system was then reopened, and when the water within the respirometer was completely flushed with air-saturated water (approx. 3 min), the system was again closed for a further 5 min to obtain another reading. This process was continued for approximately the first 2 hours until the peak in oxygen consumption rate had passed. After this point, oxygen consumption rates were recorded every half an hour, extending to every hour over the last 2 hours of the SDA response when the decline in oxygen consumption rate was minimal (less than 10% change). Once the rate of oxygen consumption of all fish had dropped to the initial rate (prior to the introduction of food), they were removed and replaced with another four fish of known weights. This procedure was then repeated until all fish had been tested. Any fish that either refused to eat or became active while within the respirometer was removed and replaced. The oxygen consumption of the fish was calculated from the rate of decline of oxygen in the closed respirometer and expressed as mg O₂ kg⁻¹ h⁻¹.

Over a five-week period, a total of 26 fish provided useable data (i.e. they consumed the correct amount of bloodworm introduced into the respirometer and were inactive throughout the feeding day). There was no significant difference between the mean weights of fish used in the two meal groups (0.15% body weight meal: mean = 6.42 g \pm 2.55 s.d., range 3.37–11.34 g, $n=12$; 0.30% meal: mean = 7.36 g \pm 1.78, range 3.99–11.37 g, $n=14$; independent samples t -test, $t_{24}=1.14$, $p=0.27$).

A range of parameters quantifying SDA was then calculated from the response of each fish: peak SDA (defined as the maximum postprandial MR—SMR); time taken to reach peak SDA; duration of the SDA response (i.e. time until the rate of oxygen consumption had returned to the preprandial level); and the magnitude of SDA

Table 1. The effects of meal size on the measured parameters of SDA in juvenile Atlantic salmon. (Data are presented as means \pm s.d.)

meal size (% of body weight)	no. of fish	SMR (mg O ₂ kg ⁻¹ h ⁻¹)	peak rate of O ₂ consumption (mg O ₂ kg ⁻¹ h ⁻¹) above resting level	time to reach peak (min)	duration of SDA effect (min)	magnitude of SDA (mg O ₂ kg ⁻¹)	increase in SDA above SMR (%)
0.15	12	179.06 \pm 57.81	92.91 \pm 23.47	35.08 \pm 7.35	199.08 \pm 51.58	871.95 \pm 200.22	56.0 \pm 8.61
0.30	14	179.21 \pm 48.06	131.34 \pm 41.56	50.42 \pm 14.06	447.71 \pm 57.57	1940 \pm 551.11	77.5 \pm 30.09
independent samples <i>t</i> -test		<i>t</i> ₂₄ = 0.007, <i>p</i> = 0.994	<i>t</i> ₂₄ = 2.39, <i>p</i> = 0.024	<i>t</i> ₂₄ = 3.42, <i>p</i> = 0.002	<i>t</i> ₂₄ = 11.56, <i>p</i> < 0.001	<i>t</i> ₂₄ = 6.75, <i>p</i> < 0.001	<i>t</i> ₂₄ = 2.39, <i>p</i> = 0.025

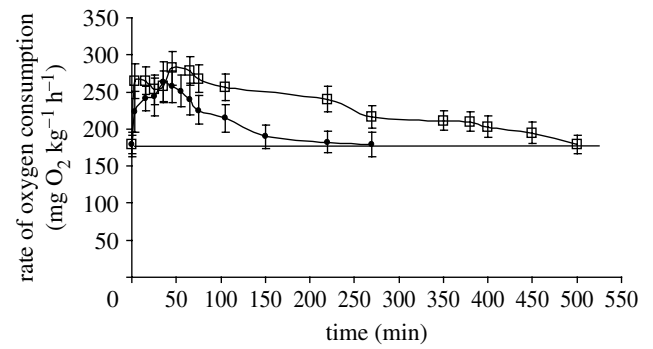


Figure 1. The general shape of the SDA response for fish eating different meal sizes (circles, 0.15% of fish body mass; squares, 0.30% of body mass). Symbols show the mean \pm s.d. based on data from 12 and 14 fish consuming meals at 0.15 and 0.30% of body mass, respectively. The horizontal line indicates the average SMR of the fish.

(defined as the overall oxygen consumption due to digestion, and equivalent to the area under the curve of SDA against time, calculated using MATLAB v. 6 to plot each SDA response). The corresponding data from all 26 fish were then analysed using general linear models in which these different measures of SDA were used as the dependent variables in successive analyses, with SMR, body weight, water temperature at the time of testing (which varied very slightly between trials) and relative size of meal as candidate-independent variables. Each fish consumed a single test meal and thus contributed one data point to the analyses.

3. RESULTS

The rate of oxygen consumption increased to a peak shortly after feeding and then gradually declined to the pre-feeding level over a period of 2.5–9.5 hours. As expected, the duration of this SDA response, the size of the peak SDA, the time to reach that peak and the overall magnitude of SDA were all significantly greater in fish consuming the larger meal (table 1). Figure 1 illustrates the general pattern of postprandial oxygen consumption rates for the two meal sizes. These effects of meal size were not confounded by SMR, since mean SMR did not differ between fish in the two meal size treatments (table 1).

However, many of the dimensions of apparent SDA were significantly related to inter-individual variation in SMR (table 2). As SMR increased, both the peak SDA and the overall magnitude of SDA increased for a given meal size, whereas the duration of the SDA response decreased (figure 2). By contrast, SMR did not influence the time that elapsed from when a meal was ingested until the peak SDA was reached (table 2; figure 2). The magnitude of SDA was influenced by a significant interaction between SMR and meal size ($F_{5,25} = 8.02$, $p = 0.01$), and therefore separate analyses were run to establish the effect of the independent variables (SMR, temperature and weight) for the two meal sizes. In both cases, the magnitude of the SDA response increased with SMR (at a faster rate at the larger meal size; figure 2d), while temperature and body weight had no effect (table 2).

4. DISCUSSION

The magnitude and among-individual range in SMR were similar to those of individuals recorded from the same stock of fish over long time periods (Millidine *et al.* 2008);

Table 2. Significance levels and coefficients of linear models relating the observed SDA responses from 26 juvenile salmon to meal size and SMR. (Separate analyses were run using (a) peak SDA, (b) time to reach peak SDA after food consumption, (c) duration of SDA effect, and (d) magnitude of SDA as the dependent variable for (i) 0.15% of body weight and (ii) 0.30% body weight; significant predictor variables are listed with their unstandardized regression coefficients (body weight and temperature were not significant and were removed from the model in all cases).)

dependent variable	significant independent variables	coefficient	significance, <i>p</i>
(a) peak SDA (mg O ₂ kg ⁻¹ h ⁻¹)	meal size (% body weight)	196.31	0.002
	SMR (mg O ₂ kg ⁻¹ h ⁻¹)	0.32	<0.001
	constant	7.60	0.599
(b) time to reach peak SDA (mins)	meal size (% body weight)	92.83	0.002
	constant	21.43	0.005
(c) duration of SDA (mins)	meal size (% body weight)	1525.74	<0.001
	SMR (mg O ₂ kg ⁻¹ h ⁻¹)	-0.61	0.009
	constant	90.67	0.062
(d) magnitude of SDA (mg O ₂ kg ⁻¹)	SMR (mg O ₂ kg ⁻¹ h ⁻¹)	2.428	0.006
	constant	443.78	0.007
(i) 0.15% body weight	SMR (mg O ₂ kg ⁻¹ h ⁻¹)	9.642	<0.001
(ii) 0.30% body weight	constant	212.49	0.534

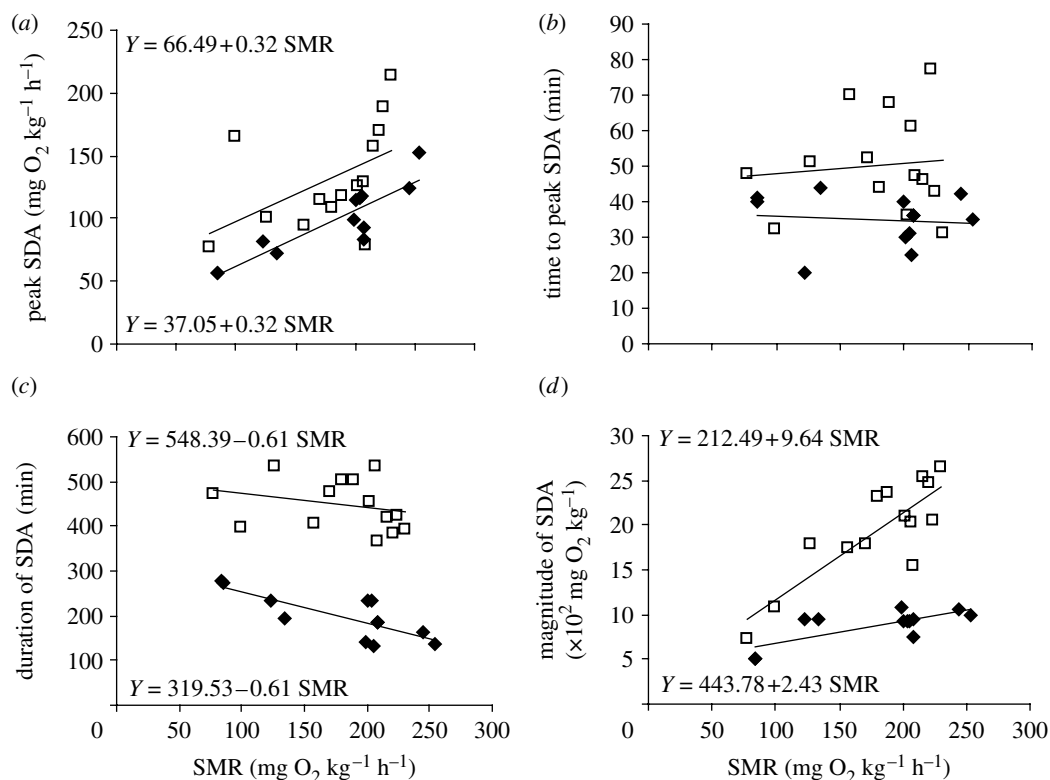


Figure 2. The effect of variation in individual SMR on (a) peak SDA, (b) time taken to reach peak SDA after ingesting a meal, (c) duration of SDA, and (d) magnitude of SDA. Squares and diamonds represent fish fed a single large or small meal (0.30 or 0.15% of body mass), respectively. See table 2 for statistical analyses. Individual relationships are shown between each SDA parameter and meal size where significant. Separate slopes are fitted in (d) where SMR interacts significantly with meal size.

previous work based on extensive observations has confirmed that activity is negligible in the study species given a suitable shelter in the respirometer (Millidine *et al.* 2006), hence justifying the description of SMR. The effect of meal size on subsequent oxygen consumption rates of salmon was similar to that often observed in other animals (Secor 2009): larger meals produced a higher peak elevation and magnitude of SDA; a longer time to reach the peak oxygen consumption; and a longer duration of SDA response. Such trends occur in various species of fishes (Beamish 1974; Jobling & Davies 1980; Boyce & Clarke 1997) and other poikilotherms including snakes

(Toledo *et al.* 2003; Zaidan & Beaupre 2003) and salamanders (Secor & Boehm 2006). More interesting were the differences in the relationship between SMR and SDA among individual salmon. A fish's SMR was related directly to the peak and the overall magnitude of its SDA response, and inversely to the recovery time. This finding suggests that the variation in SMR among fishes is linked to their food assimilation strategy.

What are the implications for variation in SDA patterns among fishes? Growth rate has been shown to correlate with the SDA peak in fishes (Jobling 1981) and SDA magnitude in starfish (Vahl 1984). A substantial

component of the SDA response in teleost fishes is due to the increased protein synthesis and turnover after feeding (Brown & Cameron 1991a,b; Lyndon et al. 1992; Carter & Houlihan 2001; Secor 2009). It is therefore likely that those individual salmon with a relatively high SDA and associated high SMR could experience an increase in growth potential, through extraction and assimilation of more nutrients from a given meal. This pattern would mirror among-species variation in the magnitude of SDA, which tends to be two to three times the SMR regardless of the magnitude of SMR (Secor 2009). An exception may be some of the tunas, which can have both a very high SMR and SDA in relation to SMR (Fitzgibbon et al. 2007).

As well as having a high peak and total SDA, individual salmon with a high SMR recovered rapidly to baseline levels of oxygen consumption following feeding. This phenomenon suggests that they process and assimilate meals rapidly. Such a link between SMR and the rate of processing food exists among species of snake (Secor & Diamond 1998), but has not previously been shown to apply within a species of animal.

Overall, the results of the present study suggest that a high SMR in salmon enables a high physiological potential for growth. In this respect, individuals with a relatively high SMR may be considered to be energy speculators, in the same sense as tunas (Fitzgibbon et al. 2007), having the potential to grow fast in favourable environments but at the cost of a high allocation of resources to routine metabolism. Those with lower SMR adopt a more conservative strategy that may be more resilient in adverse food environments due to low running costs but constrains performance as reflected in SDA. The large variation in SMR in Atlantic salmon may reflect the fact that individuals exhibit a diverse range of behavioural strategies to survive, from aggressive defence of space (Kalleberg 1958) to cryptic exploitation of marginal habitat (e.g. Höjesjö et al. 2005). This study provides the first evidence that intraspecific variation in metabolic costs incurred during digestion correlates with variation in basal metabolism; the way in which alternative metabolic, foraging, assimilation and growth strategies are linked and the trade-offs that underlie them are areas that are now open to much further research.

The experiments were authorized by licences from the UK Home Office and were approved by the University Ethics Committee.

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