# Comparison of Fasting and Postfeeding Metabolic Rates in a Sedentary Shark, *Cephaloscyllium ventriosum*

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We measured the standard and postfeeding metabolic rates of a sedentary shark, the swellshark, *Cephaloscyllium ventriosum* (Scyliorhinidae). The average standard metabolic rate (SMR) of juvenile swellsharks (0.14–0.23 kg) was 44.3 ± 6.4 mg $O_2$ kg$^{-1}$ h$^{-1}$. Metabolic rate increased and reached a maximum approximately 9 h post-feeding. The maximum postfeeding metabolic rate averaged 2.3 times SMR, and the entire duration of the response was approximately 12 h. The overall pattern and magnitude of the postfeeding response is similar to those previously reported for the small-spotted catshark (*Scyliorhinus canicula*; Scyliorhinidae) and for many teleosts. The return to a prefeeding metabolic rate appears to be much more rapid in the swellshark than in the small-spotted catshark.

W HEN physiological ecologists attempt to understand how an organism survives in its natural environment, they often attempt to estimate the amount of energy the organism ingests and expends and will do so by constructing an energy budget for the organism. The construction of an energy budget requires determining metabolic expenditure; however, metabolism is influenced by many factors including body size, temperature, activity, and phylogeny. One component of an energy budget that researchers often measure is the organism's basal rate of metabolism, or for ectotherms, the standard metabolic rate (SMR). This is the minimum energy expenditure necessary to keep an organism alive at a given temperature, or the rate of metabolism of an organism at rest, in a postabsorptive state, and during its inactive period of the day (*sensu* Krogh, 1914). Measuring SMR of fishes historically has proven to be a challenge because many fish swim constantly or actively maintain a certain position or posture within the water column, therefore incurring an added metabolic expenditure. Thus, SMR for many fish species cannot be measured directly.

Researchers have resorted to several different methods for determining SMR in fishes. A common approach is to measure "routine metabolic rate," defined as standard metabolism plus "normal spontaneous activity" (Beamish, 1964). By regressing routine metabolic rate against speed of locomotion, the y-intercept can be used to estimate SMR when swimming speed is zero (i.e., no activity; for example Bushnell et al., 1989; Carlson et al., 1999). Alternatively, normal spontaneous activity may be eliminated by restraining or anesthetizing the fish during metabolic measurement (for example, Piiper and Schuman, 1967; Hughes and Umezawa, 1968; see Appendix 1). Notable problems with

such approaches include the following: (1) There is no generally accepted definition of normal spontaneous activity; (2) There are few data that support the assumption that the change in metabolic rate across the transition from sedentary to active behaviors is linear; (3) Continuously active fish may never achieve a SMR (as traditionally defined), and with the last method; (4) No attempt has been made to account for the potential effects of restraint or anesthesia, which may artificially elevate or reduce metabolic rate.

Metabolic rate typically becomes further elevated following the ingestion of a meal because of physiological activities associated with digestion (Jobling, 1981). The total metabolic expenditure reslting from these activities is commonly referred to as specific dynamic action (SDA). SDA is another component of an organism's energy budget; therefore, its quantification is valuable in evaluating energy intake and usage. However, measuring SDA in active fish species is subject to the same problems that confound measurements of SMR.

In this study, we circumvent these experimental problems in measureing SMR and SDA in fish by measuring fasting and postfeeding metabolic rates in the diurnally inactive swellshark, *Cephaloscyllium ventriosum* (Garman). This member of the catshark family (Scyliorhinae) is active for only short periods at night. During the remainder of the day, it rests on the seafloor or in cracks and crevices in rocky reefs (Nelson and Johnson, 1970). This shark is also amenable to a captive environment and will lie stationary in a tank for up to 12 h at a time (pers. obs.). The prolonged bouts of inactivity characteristic of this shark allow measurements of SMR and SDA to be obtained without the confounding

influence of added metabolism resulting from swimming.

The goals of this study were to quantify the standard and postfeeding metabolic rates of swellsharks under voluntary resting conditions and to determine the extent to which these sharks elevate their metabolism during the processing of a meal. The experimental conditions used in our study actually meet the assumptions of SMR measurement (the organisms is at rest during its inactive period and in a postabsorptive state); thus, our measurements of both SMR and SDA should provide useful new information for determining energy budgets in fishes in general. As a first attempt at determining the utility of measuring metabolic rate in such species, we compare our findings with those from other metabolic studies of sharks and teleosts.

## MATERIALS AND METHODS

We measured fasting and postfeeding metabolic rates from four juvenile swellsharks, *C. ventriosum* (0.14–0.23 kg mass). Sharks were housed in a common tank containing filtered seawater (34 ppt), experienced a 12:12 day:night cycle, and were maintained on a diet of mackerel (*Scomber japonicus*) and squid (*Loligo* sp.). We fasted sharks for a minimum of seven days prior to measuring SMR. Each shark was subsequently placed into a respirometry tank and allowed to acclimate, undisturbed, for a minimum of 12 h prior to measurements.

We used a closed-system recirculating flow-tank style respirometer described in Sepulveda and Dickson (2000) and Donley and Dickson (2000) to measure metabolic rate. The tank has a holding area of 45 cm × 13.5 cm × 13.5 cm through which seawater was continuously circulated at approximately 5 cm $s^{-1}$ (about 1 liter $s^{-1}$). Water passed through a biological filter, UV filter, and chiller prior to reentry into the holding area. Water temperature was maintained at 16 ± 1 C. Oxygen concentration (mg $liter^{-1}$) was measured using a YSI dissolved oxygen probe placed in the holding area and YSI dissolved oxygen meter connected to a strip-chart recorder. Metabolic rate was calculated from the chart trace as a change in oxygen concentration over time. Prior to each measurement the oxygen sensor was calibrated using a known concentration of oxygen.

From preliminary trials, we found that SMR estimates were best collected at approximately 1.5-h intervals during daylight hours when the sharks were normally sedentary. At least three repeatable measurements of SMR were collected for each shark and separated by at least 4 h.

Visual observations confirmed that activity during a metabolic trial was easily detected as large and extremely short-duration spikes in oxygen concentration on the chart tracings. These measurements were not used. When dissolved oxygen concentration in the flow-tank fell below 6.0 mg $O_2$ $liter^{-1}$ (or 65% $O_2$ saturation), additional oxygen was added to the system by pumping gaseous oxygen into the water.

To induce a postfeeding metabolic response (SDA), sharks were fed between 0600 and 0700 a ration of thawed Pacific mackerel (*S. japonicus*) weighing 5 ± 1% of the individuals shark's mass (at which point all sharks appeared satiated). After feeding, sharks readily settled back onto the base of the working section, and remained largely stationary for the duration of the data recording period. We recorded dissolved oxygen concentration, water temperature, and shark position at 1–1.5-h intervals until metabolic rates returned to prefeeding levels. From this data we identified (1) maximum postfeeding metabolic rate (peak $\dot{V}_{O_2}$), (2) the time from feeding to the time of maximum $\dot{V}_{O_2}$ ($t_{peak}$), (3) the time from feeding to the return to prefeeding metabolic rates (SDA duration), (4) the relative increase in metabolic rate from SMR to the postfeeding peak (peak $\dot{V}_{O_2}$/SMR = scope), and (5) the total energy expenditure during the period of elevated metabolic rate (SDA) expressed in kJ using an oxycalorific coefficient of 13.55 kJ $g^{-1}$ $O_2$ (Sims and Davies, 1994).

After each SMR or SDA experiment, the shark was removed, and the tank was resealed. Oxygen concentration was measured for a minimum of 1 h to determine the background depletion of dissolved oxygen caused by microorganisms in the water. The tank was then cleaned with a mild bleach solution, rinsed with fresh water several times, and refilled with filtered seawater to prevent the accumulation of metabolic wastes over time.

SMR and SDA were compared for individuals using paired *t*-test. Linear trends in the data with mass were investigated using regression analysis. Statistical analyses were performed using Systat and Statview statistical packages with significance levels of $P = 0.05$ adjusted using a modified Bonferroni correction (Rice, 1989). All means are presented ± 1 SE.

## RESULTS

Mean SMR of the four swellsharks averaged 7.9 ± 0.4 mg $O_2$ $h^{-1}$ (Table 1). As the sharks were similar in size, we did not detect a significant linear relationship between SMR and body

TABLE 1. SDA VARIABLES FOR THE FOUR SWELLSHARKS RANKED BY BODY WEIGHT (BW). Other terms in the table are defined in the Materials and Methods section. Values in boldface text are means ± SE.

| Mass (kg) | SMR (mg $O_2$ h$^{-1}$ ± SE) | Ration size (% BM) | Peak $\dot{V}_{O_2}$ (mg $O_2$ h$^{-1}$) | $t_{peak}$ (h) | Scope (× SMR) | SDA (kJ) |
|---|---|---|---|---|---|---|
| 0.14 | 8.7 ± 0.1 | 4.2 | 12.0 | 10.4 | 1.4 | 2.7 |
| 0.17 | 7.6 ± 0.3 | 5.9 | 17.7 | 9.0 | 2.3 | 3.1 |
| 0.20 | 8.5 ± 1.9 | 5.1 | 16.0 | 9.25 | 1.9 | 12.5 |
| 0.23 | 6.8 ± 1.7 | 5.2 | 24.8 | 9.0 | 3.6 | 10.3 |
| **0.19 ± 0.02** | **7.9 ± 0.4** | | **17.6 ± 2.7** | **9.4 ± 0.3** | **2.3 ± 0.5** | **7.2 ± 2.5** |

mass ($r^2 = 0.55$; $P = 0.26$). Thus, the calculation of mass-specific SMR data was not necessary to standardize the data to compare among individuals studied here. However, we calculated an average mass-specific SMR of 44.3 ± 6.4 mg $O_2$ kg$^{-1}$ h$^{-1}$ to facilitate comparisons with other studies.

Following feeding, oxygen consumption peaked at 17.6 ± 2.7 mg $O_2$ h$^{-1}$ (Table 1), or 93.7 ± 6.6 mg $O_2$ kg$^{-1}$ h$^{-1}$. The postfeeding oxygen consumption peak was significantly greater than SMR ($t = -3.06$, $P = 0.04$) by an average factor of 2.3 (Table 1, Scope). The peak was not significantly positively related to mass ($r^2 = 0.83$; $P = 0.09$), nor was scope ($r^2 = 0.65$; $P = 0.13$).

The postfeeding peak was reached approxi-



Fig. 1. Postfeeding metabolic rate curves for the first 15 h of measurement as indicated by oxygen consumption rate. Values are means for all four individuals and error bars are ± 1 SE.

mately 9 h after the feeding event (Fig. 1). An earlier peak can be seen in Figure 1; however, this was primarily because of a single individual who experienced two peaks in metabolic rate, one at 4 h and a second, larger peak at 9 h postfeeding. There was no detectable relationship between mass and the time at which the peak was reached ($r^2 = 0.54$; $P = 0.27$). Oxygen consumption declined to values not significantly greater than SMR within approximately 12 h of feeding ($t = 0.66$, $P = 0.56$).

DISCUSSION

A primary goal of this project was to compare SMR data for swellsharks with values published for other fish species that share similar taxonomic affinities or similar habits. As previously mentioned, the method of determining SMR varies widely among these studies (Appendix 1). Our measured SMR at l6 C for the swellshark is similar to that of the small-spotted catshark (*Scyliorhinus canicula*), another scyliorhinid, measured at 15 C using comparable technique (Appendix 1; see Sims and Davies, 1994). Our values seem slightly higher than the SMR values reported from previous studies of both restrained and anesthetized scyliorhinids measured at temperatures similar to ours (13–19 C; Appendix 1). However, our data do fall within the upper bounds of the ranges reported. Anesthetic techniques may have had a dampening effect on the metabolic rate data collected, and experiments are warranted to determine whether SMR is lower for these sharks simply because the animal is being artificially ventilated and no longer incurring a cost of ventilation during the experiment.

The SMR for the swellshark was generally lower than rates reported for more active carchariniforms, the order which contains the scyliorinids (Appendix 1). This difference may be a function of higher water temperatures during metabolic measurements (Appendix 1). Additionally, species with the highest SMR like the scalloped hammerhead (*Sphyrna lewini,* Lowe,
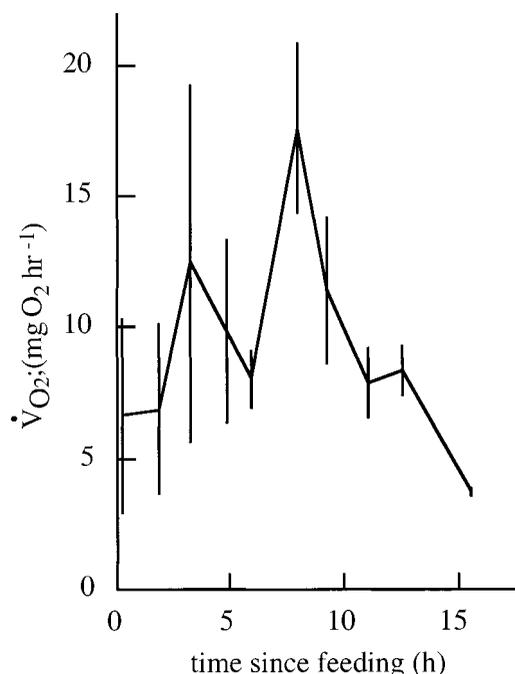
in press) and the blacknose shark (*Carcharinus acronotus,* Carlson et al., 1999) swim nearly continuously (Appendix 1). A higher SMR may simply be a reflection of the very active habits of these two species (see also Dickson et al., 1993). However, these data were also collected using indirect determinations of SMR. Problems outlined above cannot be refuted as a cause for the higher values in the other studies.

For elasmobranchs, variables related to specific dynamic action have previously been reported only for the small-spotted catshark. For this shark, a maximum increase of 2.8 ± 0.2 times SMR occurred within 4–10 h after ingesting a meal (Sims and Davies, 1994). This increase is similar to increases observed in the swellshark. In most teleosts examined to date (reviewed by Winberg, 1960; Jobling, 1981), oxygen consumption rates rise soon after feeding and also reach a peak rate that is about twice the prefeeding rate within about 12 h (Jobling, 1981). The SDA recorded for both shark species were also similar (data for the small-spotted catshark was expressed as %IE, or percent ingested energy, which was 6–13% compared with a rough approximation of 5–17% in the swellshark). In the small-spotted catshark, however, oxygen consumption dropped off less rapidly after peaking and returned to prefeeding rates within 24–96 h of feeding. The longer duration of the SDA response in small-spotted catsharks relative to the swellshark is somewhat surprising given that temperature, animal mass, and relative meal sizes in the two sets of experiments were similar, and the animals are closely related and share similar habitats (Compagno, 1984). It is possible that a difference was caused by the food used; Sims and Davies (1994) fed a ration of squid, whereas we used fish.

More complete information about both SMR and SDA in other shark species is clearly needed. Studies that measure SDA duration in other shark species will help to determine whether the relatively short duration of the swellshark or the longer duration reported for the small-spotted catshark is more typical of elasmobranchs or whether there is a great deal of variation in this variable present across species. Many of the larger shark species may feed more infrequently (see for example Goldman et al, 1996) and might show patterns similar to the extreme SDA activities observed in foraging lizards and snakes that naturally experience long bouts of fasting ($\geq 10\times$ SMR, see Secor and Diamond, 1995; Secor and Phillips, 1997). Future studies that measure true SMR, as well as metabolic variables during activity (such as digestion and swimming), will allow us to construct the first comprehensive energy budget for an elasmobranch.

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APPENDIX 1. COMPARATIVE DATA ON SMR FOR ELASMOBRANCHS BY PHYLOGENY AND HABIT.

| Species | T (C) | Mass (kg) | SMR (mg $O_2$ kg$^{-1}$·h$^{-1}$) | Determined by | Citation(s) |
|---|---|---|---|---|---|
| "Inactive" sharks of the family Scyliorhinidae; SMR determined using quiescent individuals: | | | | | |
| Swellshark (*C. ventriosum*) | 16 ± 1 | 0.14–0.23 | 44.3 | Respirometry of quiescent fish | This study |
| Small-spotted catshark (*S. canicula*) | 15 | 0.1–0.2 | ~63 | Respirometry of quiescent fish | (Sims and Davies, 1994) |
| Small-spotted catshark (*S. canicula*) | 15 | 0.59–0.80 | ~55 | Respirometry of quiescent fish | (Sims and Davies, 1994) |
| "Inactive" sharks of the family Scyliorhinidae; SMR determined by manipulative techniques: | | | | | |
| Spotted "dogfish" (*Scyliorhinus stellaris*) | 18 | 0.97–2.50 | 35 | Manipulated: cannulated & restrained | (Randall et al., 1976)[a] |
| Spotted "dogfish" (*S. stellaris*) | 15–19 | 0.24–3.90 | 40.2 (25–55) | Manipulated: tail cut, gill chambers | (Piiper and Schuman, 1967; see also Piiper et al., 1977)[a] |
| British "dogfish" (*s. canicula*) | 12–14 | 0.15–0.60 | 20–55 | Manipulated: rubber membrane between gill bars | (Hughes and Umezawa, 1968) |
| British "dogfish" (*S. canicula*) | 7, 12, 17 | 0.56–1.0 | 20.76, 27.9, 44.1 | Manipulated: cannulated, restrained | (Butler and Taylor, 1975) |
| "Very active" sharks of the order Carcariniformes (contains the Scyliorhinidae); SMR determined by "extrapolation" methods: | | | | | |
| Blacknose (*C. acronotus*) | 27–29 | 0.45–3.51 | 240 | Extrapolation of active rates | (Carlson et al., 1999) |
| Lemon shark (*Negaprion brevirostris*) | 22 | 0.8–1.3 | 95 | Extrapolation of active rates | (Bushnell et al., 1989; for additional data, see also Scharold and Gruber, 1991) |
| Leopard shark (*Triakis semifasciata*) | 16 | 2.2–5.8 | 68 | Extrapolation of active rates | (Scharold et al., 1989) |
| Scalloped hammerhead (*S. lewini*) | 26 | 0.51–0.93 | 189 | Extrapolation of active rates | (Lowe, in press; for *Sphyrna tiburo*, see also Parsons, 1990) |

[a] There are more such manipulation studies where SMR was determined during experiments with other primary objectives; all of which generally agree with the SMR given here.