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# Predicting metabolic rate from heart rate in juvenile Steller sea lions *Eumetopias jubatus*

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## Summary

**The validity of using heart rate to estimate energy expenditure in free-ranging Steller sea lions *Eumetopias jubatus* was investigated by establishing whether there is a relationship between heart rate ($f_H$) and oxygen consumption rate ($\dot{V}_{O_2}$) in captive sea lions while swimming and resting. Four trained Steller sea lions (2 males and 2 females; mass 87.4–194.4 kg; age 16 months–3 years) were each equipped with a datalogger and two dorsal subcutaneous electrodes to record electrocardiograms from which $f_H$ was calculated. $\dot{V}_{O_2}$ (measured using open-circuit respirometry) was simultaneously recorded while the previously fasted animals were at rest within an enclosed dry metabolic chamber or while they swam in an enclosed swim mill against water currents of various speeds (0–1.5 m s$^{-1}$). The mean regression equation describing the relationship between $f_H$ (beats min$^{-1}$) and $\dot{V}_{O_2}$ (ml h$^{-1}$ kg$^{-0.60}$) for all four animals was $\dot{V}_{O_2}$=(71.3$f_H$±4.3)–(1138.5±369.6) (means ± S.E.M.) ($r^2$=0.69, $P$<0.01). The relationship demonstrated between $f_H$ and $\dot{V}_{O_2}$ while fasting suggests that heart rate can potentially be used to monitor energy consumption in free-ranging Steller sea lions. However, a short-term feeding experiment revealed no significant increase in heart rate following a 6 kg or 12 kg meal to match the observed increase in rate of oxygen consumption. This suggests that heart rate may not accurately reflect energy consumption during digestion events. Additional research should be conducted to further elucidate how the relationship between heart rate and oxygen consumption is affected by such factors as digestive state, stress and age.**

Key words: heart rate, energy expenditure, Steller sea lion, *Eumetopias jubatus*, oxygen consumption, metabolic rate.

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## Introduction

Knowing how much energy an individual requires is fundamental to resolving a number of questions about marine mammals. These include determining how they have solved complex bioenergetic problems to successfully exploit their environment, and whether or not they compete with fisheries for prey (Markussen and Oritsland, 1991; Olesiuk, 1993; Rosen and Trites, 1997; Stenson et al., 1997; Trites et al., 1997; Boyd et al., 1999). Unfortunately, determining energy expenditure of free-ranging individuals is difficult. Measuring doubly labelled water (DLW) turnover rates and recording heart rate are two common techniques that have been used.

The DLW method suffers from two major limitations. The first is that it provides only a mean estimate of metabolism over the entire period between blood samplings. The second limitation is that there is a finite time over which the measurement can be made, due to the biological half-life of the chemical agents. In large vertebrates, this period is usually 5–10 days, after which the animals must be recaptured for blood sampling. Many assumptions, estimates and logistics needed to use DLW also compromise the applicability of this technique (see Costa, 1987; Speakman, 1993).

Recording heart rate is a technique for estimating energy expenditure that offers the possibility of monitoring metabolism for a year or longer, with a fine time resolution of hours or minutes that can be related to specific activities (Butler, 1993; Bevan et al., 1995b; Woakes et al., 1995; Andrews, 1998). When coupled with dive profiles from time–depth recorders, for example, heart rate may be used to estimate the energy expenditure of specific dives. Several comparative studies have shown that this technique is as robust as using the DLW method (Nolet et al., 1992; Bevan et al., 1994, 1995a; Boyd et al., 1995).

The heart rate method is based on Fick's relationship of oxygen consumption ($\dot{V}_{O_2}$) and heart rate ($f_H$) (Fick, 1870):

$$\dot{V}_{O_2} = Ca_{O_2} - C\bar{v}_{O_2} \times V_S \times f_H \,, \qquad (1)$$

where $V_S$ is stroke volume of the heart, and $Ca_{O_2}$–$C\bar{v}_{O_2}$ is the difference in oxygen concentration between arterial and mixed venous blood, respectively (also referred to as tissue oxygen extraction). Heart rate is a good indicator of $\dot{V}_{O_2}$ if $Ca_{O_2}–C\bar{v}_{O_2}$ and $V_S$ remain constant or change in proportion to changes in heart rate (Bevan et al., 1992; Butler, 1993). The relationship between stroke volume and oxygen extraction with heart rate, however, differs among and within both terrestrial species (horses, steers, dogs, goats, calves and rats) and aquatic species (seals and sea lions), and with activity (Horstman et al., 1974; Gleeson and Baldwin, 1981; Taylor et al., 1987; Jones et al., 1989; Ponganis et al., 1990; Butler, 1993).

Several studies have found close correlations between $f_H$ and $\dot{V}_{O_2}$ when animals are exercising in a steady state. However, diving animals present a unique problem. Dives may include a significant amount of anaerobic metabolism, and single dives may not be considered a steady state, given the inherent intermittency of gas exchange and large changes in heart rate that occur upon surfacing and submerging (Fedak et al., 1988; Butler, 1993). However, average heart rate and oxygen consumed may be correlated over complete dive cycles (surface plus dive time) (Fedak, 1986).

Significant correlations between $f_H$ and $\dot{V}_{O_2}$ have been found using average dive cycles in captive diving gray seals *Halichoerus grypus*, California sea lions *Zalophus californianus*, harbour seals *Phoca vitulina* and bottlenose dolphins *Tursiops truncatus* (Williams et al., 1991, 1993; Butler et al., 1992; Boyd et al., 1995; Hurley, 1996). While it is probable that the general pattern holds true for Steller sea lions, there is no reason to expect the predictive relationship to be identical between the diverse species or between life stages already studied, given differences in phylogeny, body mass, diving behaviour, and foraging patterns. Resulting differences can reveal much about the physiological adaptations of these species and the development of physiological processes in Steller sea lions. Therefore the specific relationship between $f_H$ and $\dot{V}_{O_2}$ must be determined for this species, particularly before it can be applied to animals in the wild.

Our objective was to test the feasibility of using heart rate to monitor metabolic rate in Steller sea lions using captive, juvenile animals. Alaskan Steller sea lion populations have declined to less than 20% of their peak mid-1970s abundance (Trites and Larkin, 1996). Changes in the animals' energy budget due to changes in their prey base have been considered a potential reason for the decline (Alverson, 1992; Merrick et al., 1997; Rosen and Trites, 2000). Testing this hypothesis by measuring the energy expenditures of free-ranging Steller sea lions using DLW is difficult, however, given the problem of recapturing an aquatic mammal in a set time interval. The heart rate method permits data to be collected with a finer time resolution, allowing the metabolic cost of specific activities to be estimated. Additionally, long-term data can be recorded and retrieved from dataloggers, avoiding restrictive time constraints for animal recapture.

We tested whether a relationship exists between heart rate and postabsorptive oxygen consumption in each of four captive Steller sea lions. Data were collected while each animal rested in a dry metabolic chamber or while swimming, diving or resting within a swim mill. The results were evaluated in terms of the future potential of using the heart rate technique to monitor energy expenditure of free-ranging Steller sea lions.

Additionally, we wanted to investigate how feeding may change the $f_H/\dot{V}_{O_2}$ regression. To our knowledge, no studies have examined this potential factor. Instead, the $f_H/\dot{V}_{O_2}$ relationship has been determined for subjects fasted prior to any experiments (thus, excluding food effects completely) (Butler, 1993; Boyd et al., 1995) or after the subjects had the opportunity to ingest a meal (excluding comparison between data with and without food) (Williams et al., 1991; Li et al., 1993; McCrory et al., 1997). Only one study on bottlenose dolphins (Williams et al., 1993) and one on Antarctic fur seals (Boyd et al., 1999) have determined the $f_H/\dot{V}_{O_2}$ relationship over a period that was likely to have involved some feeding. Close relationships between $f_H$ and $\dot{V}_{O_2}$ were reported in these studies, but whether or not feeding changed the relationship was not tested. We performed a preliminary investigation into the accuracy of estimating energy expenditure from heart rate over periods of time that encompassed feeding by comparing the regressions of a single sea lion when fed and when fasted.

## Materials and methods

### *Animals*

Data were collected from four juvenile Steller sea lions *Eumetopias jubatus* Schreber 1776, two males and two females. They were housed at the Vancouver Aquarium Marine Science Centre (Vancouver, British Columbia, Canada) in outdoor enclosures with access to large pools of filtered seawater and haulout space. All animals were weighed every morning and followed a daily husbandry protocol consisting of scheduled feedings and training for research purposes. The study began in October 1998 when all animals were about 16 months old, and was completed in May 2000 when the animals were almost 3 years old. Over the duration of the experiment, the mass of Male 1 increased by 50% while the masses of the other animals changed less than 5% over the study period (Table 1).

### *Experimental apparatus*

#### *Monitoring heart rate*

Two dorsal electrodes were attached to each sea lion while under anaesthesia in areas that gave the cleanest electrocardiogram (ECG) signal – either one above each scapula, or one above a scapula and the other above the pelvis

Table 1. *Range of mass during data collection, experimental period and number of trials for each animal*

| Animal | Mass range (kg) | Time range for data collection | Number of trials |
|---|---|---|---|
| Male 1 (M97TI) | 102.2–152.8 | October 1998–August 1999 | 49 |
| Male 2 (M97KO) | 188.0–194.4 | April–May 2000 | 64 |
| Female 1 (F97HA) | 87.4–90.4 | March–September 1999 | 71 |
| Female 2 (F97SI) | 111.2–115.4 | June–December 1999 | 53 |

on opposing sides. Four previous styles of electrodes were tested before the final, most appropriate design, was applied (see McPhee, 2001, Appendix 2). These final electrodes consisted of two basic parts: (1) 12 cm of 28-gauge bioelectric cable inserted subcutaneously and (2) an external base of epoxy resin containing a female underwater connector soldered to the subcutaneous cable, and underlaid with a portion of neoprene that was glued with fast-setting cyanoacrylate to the fur of the animals.

The ECG was sampled and recorded at 100 Hz by a datalogger housed in the pocket of a nylon and neoprene harness worn by the sea lion.

### *Monitoring oxygen consumption*

Open circuit respirometry measured the oxygen consumption of each animal during dry and swimming trials as described by Rosen and Trites (1997, 2002). For dry trials, the sea lions entered a sealed opaque metabolic chamber through which air was drawn at a constant rate of 153 l $\text{min}^{-1}$. From a desiccated subsample of expired air, an S-3 A/I solid oxide cell analyzer (Ametek Inc., Pittsburgh, PA, USA) determined oxygen concentration while an AR-60 infrared gas analyzer (Anarad Inc., Santa Barbara, CA, USA) determined carbon dioxide concentration. A Sable Systems (Henderson, Nevada, USA) Data Acquisition System calculated average concentrations from 200 subsamples of expired air every second. The system was base-lined to known ambient air concentrations before and after each trial and periodically calibrated with gases of known concentrations. The amount of oxygen consumed during a trial was calculated from the difference in oxygen concentration between airflow into and out of the chamber, with flow corrected to STPD. Air temperature within the chamber varied between 2°C and 25°C (see McPhee, 2001, Appendix 1). A video camera and lighting within the chamber allowed activity to be monitored.

For swimming trials, the animals entered a seawater-filled swim mill (active space = 3.2 m length × 1.8 m width × 1.0 m depth). The sea lions could only surface to breathe under a transparent Plexiglas dome at one end of the swim mill. Air was drawn through the dome at a rate of 142 l $\text{min}^{-1}$. The system was base-lined to known ambient air concentrations at the beginning of a swimming session and after every following hour. Oxygen concentrations were determined as above for the dry trials using carbon dioxide concentrations to mathematically remove their affect on oxygen readings (equation 3b in Withers, 1977).

To promote a range of oxygen consumption and heart rates from the animals, the water current speed within the swim mill was altered. Previous experience had shown that swimming activity increased with increasing water speed. However, swim speed was not always equivalent to water current speed. When there was current, the animals often swam in a circular pattern toward the back of the swim mill, where they would briefly rest before swimming against the current to return to the dome to breathe. Occasionally, they would rest motionless on the bottom or beneath the dome. For these trials the water speed within the flume was set at 0.0, 0.9, 1.1 and 1.3 m $\text{s}^{-1}$. Male 1 was also tested at 1.5 m $\text{s}^{-1}$. Water temperature varied between 2°C to 11°C for Male 1, but remained between 9°C and 11°C for the other three animals.

### *Protocol for fasting trials*

For each data-collecting period, the sea lions wore their harnesses with the datalogger in the pocket. The free end of each of the two wires from the datalogger ended in a specialized male connector (Underwater Systems, Stanton, California, USA) to match the female connector of each electrode. Once the wires were attached to the electrodes, the logger began to record ECG. The animals were usually fasted for the previous 12–24 h. However, they were occasionally fed a small amount of herring (up to 200 g) prior to a session of heart rate trials to ensure cooperation. The animals were then enclosed in either the swim mill or the metabolic chamber, during which time their ECG and oxygen consumption rates were monitored simultaneously.

A swimming session was divided into a series of 18 min trials. Each trial consisted of a 10 min period to allow the animal to reach a physiological steady state at the set water current speed and to allow air to equilibrate within the enclosed system. This was followed by an 8 min period of $\dot{V}_{O_2}$ data collection, which was sufficient to derive a stable reading of $\dot{V}_{O_2}$, and was the minimum length of time that the animals were trained to remain reasonably calm. During each trial, the animals swam in the swim mill at one of the randomly preselected water current speeds. At the completion of the trial, the water current would remain the same or would be switched to a new speed and another 18 min trial would begin. There was no water current during the first trial in a series. If an animal appeared to become agitated while swimming against a certain water speed, the next trial was run without a current. A swim session continued for a maximum of 6 h, depending on the animals' cooperation, yielding a maximum of 18 trials in a day's session. Occasionally, at the end of a session, the animals would be directed to remain as motionless as possible with their heads above water in the respirometry dome (denoted as a 'hold') so that resting values in the mill could be obtained. No holds were obtained from Male 2.

A dry session for resting values comprised a 15 min equilibration period once the animal was enclosed in the metabolic chamber, followed by a 15 min $\dot{V}_{O_2}$ data collection period. Only one dry trial was run in a day. Dry trials were obtained from only Male 1 and Female 1, as Male 2 and Female 2 would not enter the chamber.

### *Protocol for feeding sessions*

Data were collected after feeding events from Male 1 in the swim mill. The equipment and protocols were the same as for the fasting trials with the following exceptions. The sea lion entered the swim mill 32–73 min after having ingested a bulk amount of either 6 or 12 kg of herring. This typically represented a half or full daily ration, and was equivalent to the intake predicted for wild Steller sea lions (Winship et al., 2002). Each swimming session was 3 h and consisted of monitoring the animal's heart rate and oxygen consumption rate while swimming in the swim mill without any applied current. After an initial 10 min air-equilibration phase, each session was split into successive trials lasting 5 min each. When one 5 min trial ended, another began immediately following it until 3 h had passed since the first trial. Three swimming sessions preceded by 6 kg feedings were performed on three separate days in close succession, followed by another three sessions after 12 kg feedings.

## *Analysis*

### *Heart rate*

After the initial equilibration periods, mean heart rate was calculated over the following 5 min in the swim mill and the following 15 min in the dry chamber. The mean heart rate during the first 5 min of a hold was also calculated. These intervals were chosen based on stabilization of the heart rates or as the most representative of the heart rates during a trial.

The recorded electrocardiogram was downloaded from the datalogger to a desktop computer after each session. Mean heart rate in beats $\text{min}^{-1}$ over the required interval was derived from interbeat intervals on the ECG.

### *Oxygen consumption*

Mean rate of oxygen consumption was calculated from differences between incurrent and excurrent oxygen concentration and measured flow rates corrected to STPD. There was variation in the body mass of individuals over the course of the experiments, as well as substantial differences between individuals (Table 1). Therefore, the potential effect of body mass on the relationship between heart rate and oxygen consumption had to be considered.

Past studies have attempted to 'correct' for changes in mass by expressing oxygen consumption rates on a mass-specific basis ($\dot{V}_{O_2}\,M^{-1}$). However, there is no physiological or empirical basis for assuming such a conversion (Packard and Boardman, 1988; Hayes, 2001). We decided to empirically derive an appropriate exponent by calculating a multiple factor power relationship. This allowed us to compensate for differences in body mass without making any *a priori* assumptions of what the correction factor should be.

The analysis was performed on all of the pooled fasting data from all animals. It was inappropriate to perform analyses on each animal as changes in individual body mass were much smaller than differences between individuals (Table 1), and the source of the mass changes (i.e. metabolically active tissues or inactive blubber) was unknown.

The data were log-transformed so that a linear multiple regression analysis could be generated using Systat software (Systat, Inc., Richmond, California, USA). This transformation was based on the relationship that:

$$\dot{V}_{O_2} = a \times f_H{}^{b} \times M^{c} \qquad (2)$$

or

$$\log(\dot{V}_{O_2}) = \log(a) + \beta \times \log(f_H) + c \times \log(M)\ . \qquad (3)$$

where a, b and c are coefficients. Exploratory analysis of our pooled data revealed that the coefficient values were a=19.41, b=1.245 ($t_{234}$=17.3, $P$<0.0001) and c=0.597 ($t_{234}$=12.9, $P$<0.0001). Thus we chose to express oxygen consumption in the more familiar 'mass-corrected' form with the exponent of mass $M$ rounded to 0.6:

$$\dot{V}_{O_2}/M^{0.6} = a \times f_H{}^{b}\ . \qquad (4)$$

Mass-specific oxygen consumption was calculated by dividing total oxygen consumption per hour by body mass measured for each sea lion at the time of data collection.

As many previous studies have assumed a linear relationship between $f_H$ and $O_2$, we then produced general linear regressions for each individual as well as the pooled data based on the derived exponent for body mass that followed the general form:

$$\dot{V}_{O_2} \times M^{-0.6} = a + b(f_H)\ . \qquad (5)$$

In addition, to aid comparison with results of other published studies, we derived a linear model from the pooled data using the general mass-specific equation:

$$\dot{V}_{O_2} \times M^{-1.0} = a + b(f_H)\ . \qquad (6)$$

### $f_H/\dot{V}_{O_2}$ *relationships*

For each animal, a simple linear regression between $f_H$ and the corresponding $\dot{V}_{O_2}$ values calculated from the swim and dry trials was run using Systat software. The data points used were the mean $f_H$ and $\dot{V}_{O_2}$ values from each 8 min analysis period of the swim trials or from each 15 min dry trial. Since a mean 2.8 min delay was incurred between the time the air was drawn from the respirometry dome to when it reached the oxygen analyzer, $\dot{V}_{O_2}$ data were shifted ahead by 2.8 min to temporally synchronize oxygen consumption with heart rate. The resulting regression was then plotted with $f_H$ on the abscissa and $\dot{V}_{O_2}$ on the ordinate axis. Probability levels of $P$<0.05 were considered significant. Analysis of covariance (with heart rate as the covariate) was used to compare the resulting regressions from each animal. Residuals (calculated as the vertical distance of the recorded $\dot{V}_{O_2}$ from the estimated $\dot{V}_{O_2}$ of the regression line) were plotted in the order of data collection and fit with lowess-smoothed curves for each animal to detect any temporal trends in the data.

To determine a mean regression, all four data sets were pooled and fitted with a mixed linear procedure (PROC MIXED, SAS). Data from each animal were treated as a repeated-measures set, as were data collected within any single day within an animal. Because timing of data collection was imbalanced within each animal (time intervals between successive data points were not equivalent), a compound symmetry covariance structure was considered. This analysis was performed using both forms of the 'mass-corrected' oxygen consumption data (i.e. $M^{-0.6}$ and $M^{-1.0}$).

### *Comparison of fasted and fed data*

The regression obtained during the feeding trials for Male 1 was compared with the regression obtained from the same

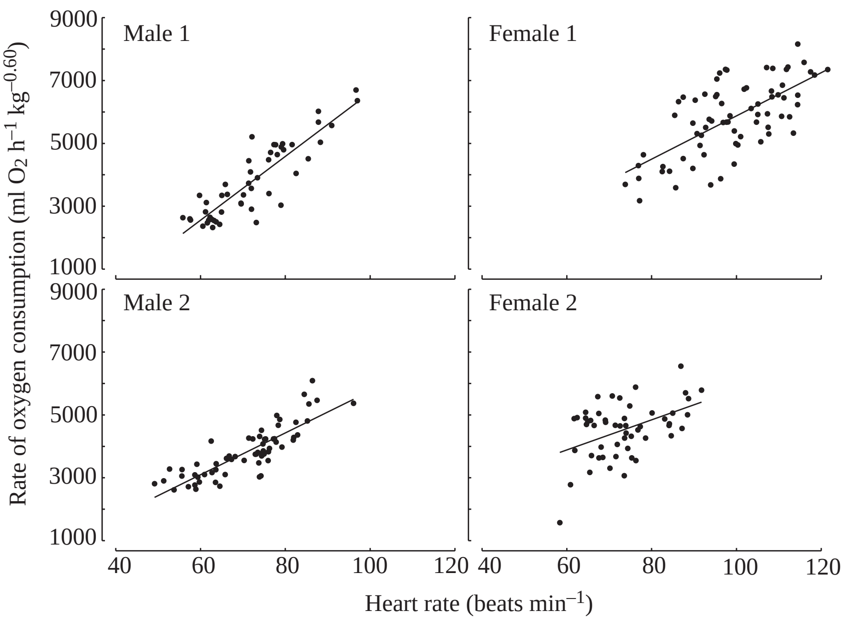

Fig. 1. The relationship between heart rate (beats min$^{-1}$) and rate of oxygen consumption (ml $O_2$ h$^{-1}$ kg$^{-0.60}$) in each of the four sub-adult Steller sea lions, plotted with the corresponding least-squares fitted linear regression (see Table 2). Each regression was fitted to all types of data available in an animal's set: swim and dry trials, and holds. See text for details.

individual during the fasting trials. For each of the six feeding sessions, a time series using mean heart rate from each 5 min trial and a second using mean oxygen consumption rate was constructed to investigate behaviour of the variables as digestion progressed after feeding.

## Results

### *Data collection*

Data collection spanned 14 months between October 1998 and May 2000 (Table 1). Initially, data were collected infrequently due to the short attachment time of surface electrodes. With revised training and trial protocols, and improved electrode style, the number of trials completed daily and monthly increased. The data collected from the sea lions showed that $\dot{V}_{O_2}$ increased between 2.3 and 4.2 times while $f_H$ only increased between 1.6 and 2.0 times.

### *Relationship between fasted heart rate and oxygen consumption*

Plotting mean heart rate (beats min$^{-1}$) and the corresponding mean rate of oxygen consumption (ml $O_2$ h$^{-1}$ kg$^{-0.60}$) from each trial showed a linear relationship between the two variables for each animal (Fig. 1). Slopes varied between 47.7 and 101.5 ml $O_2$ beat$^{-1}$ kg$^{-0.60}$, with intercepts between 1028.0 and –3536.6 ml $O_2$ h$^{-1}$ kg$^{-0.60}$, and $r^2$ values between 0.21 and 0.78 (Table 2).

Comparing the slopes of the four regressions (Fig. 1) revealed that only those of Male 2 and Female 1 were statistically similar ($P$>0.10). All regression intercepts were significantly different among animals ($P$<0.01).

Smoothing the residuals (arranged by order of data collection) showed that the regressions poorly described the data collected from the females at the beginning and end of the study (Fig. 2). Possible explanations include some unknown change in equipment during collection or a physiological change in the animal (resulting in a change in the heart rate and oxygen consumption relationship). A similar but slighter trend was evident for Male 1, while residuals from Male 2 were evenly distributed about a mean of zero (Fig. 2).

A mean regression for all four Steller sea lions could be determined by calculating the mean slope and intercept of the four linear regressions (Table 2, Fig. 3A). However, a better method was to pool the four data sets and fit the resulting set with a mixed linear model, treating all data from an animal (and from a day within an animal) as a repeated-measures set with a compound symmetrical covariance structure. The mean regression relating oxygen consumption rate (in ml $O_2$ h$^{-1}$ kg$^{-0.60}$) to heart rate resulting from

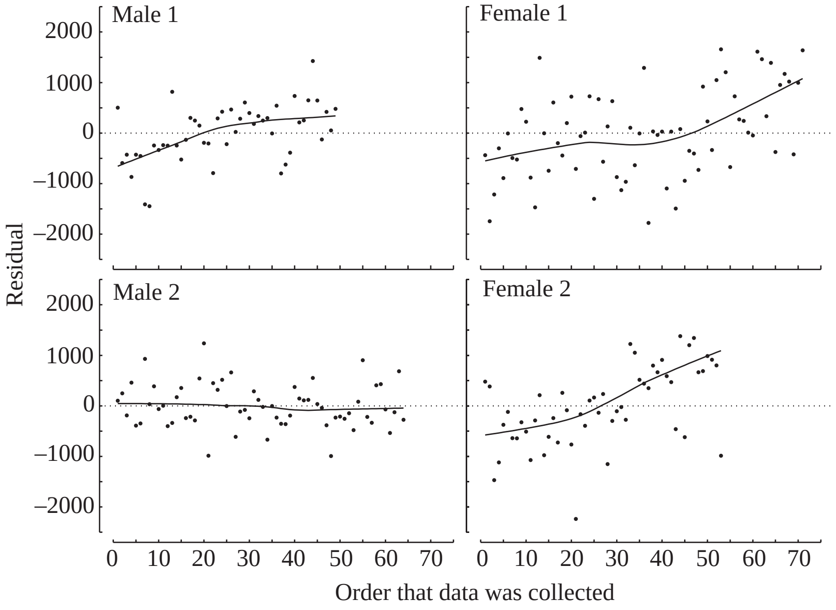

Fig. 2. Residuals ($y$-axis) in chronological order of data collection ($x$-axis) for each of the four sub-adult Steller sea lions. Lowess-smoothed curves have been fitted to the data.

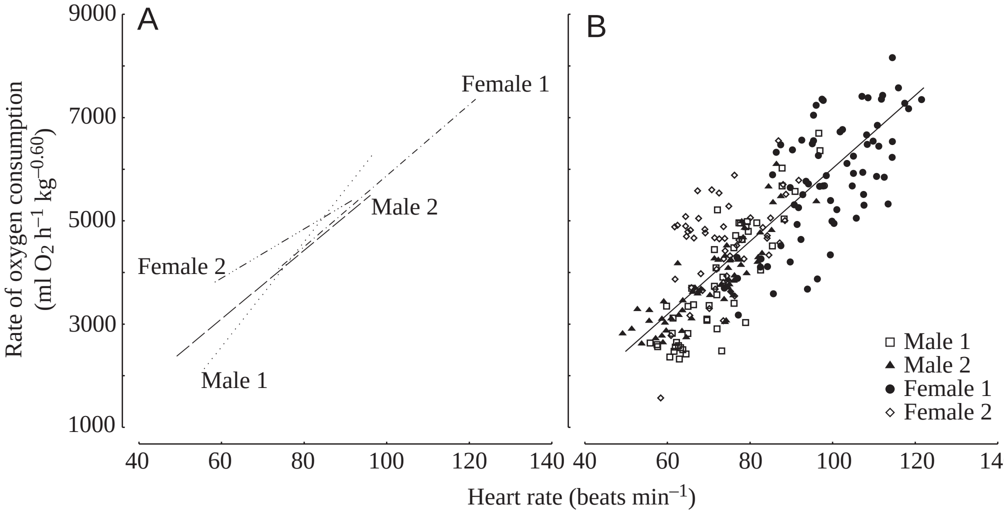

Fig. 3. (A) Linear regressions (from Fig. 1) for all four sea lions and (B) the mean regression [$\dot{V}_{O_2}$=(71.3$f_{\rm H}$±4.3)–(1138.5±369.6), $r^2$=0.69] shown with all sea lion data.

Table 2. *Slopes, intercepts, and* r$^2$ *values of the four individual Steller sea lion regression lines shown in Fig. 1*

| Animal | Slope | Intercept | *N* | $r^2$ |
|---|---|---|---|---|
| Male 1 | 101.5±7.9 | –3536.6±575.6 | 49 | 0.78 |
| Male 2 | 66.4±5.4 | –884.0±386.9 | 64 | 0.71 |
| Female 1 | 68.8±9.1 | –1002.6±910.0 | 71 | 0.45 |
| Female 2 | 47.7±13.0 | 1028.0±964.3 | 53 | 0.21 |

Values are means ± S.E.M.

The equations describe the relationship between rates of oxygen consumption (ml O$_2$ h$^{-1}$ kg$^{-0.60}$) to heart rate (beats min$^{-1}$).

this analysis (Fig. 3B) was $\dot{V}_{O_2}$=(71.3$f_{\rm H}$±4.3)–(1138.5±369.6) (means ± S.E.M.) ($r^2$=0.69, $P$<0.01). To aid comparisons to some previously published studies, the analysis was rerun with the rate of oxygen consumption in ml O$_2$ h$^{-1}$ kg$^{-1.0}$, yielding $\dot{V}_{O_2}$=(0.19$f_{\rm H}$±0.01)–(4.12±1.3) ($r^2$=0.69, $P$<0.01).

### *Effect of feeding on heart rate*

Rate of oxygen consumption significantly increased over time following ingestion of all 6 and 12 kg meals (Fig. 4). However, heart rate was more variable and increased slightly in only one of the six trials (a 12 kg feeding). Heart rate either declined or showed no significant change as $\dot{V}_{O_2}$ rose in all feeding trials (Fig. 4, Table 3).

When the 12 kg feeding trial data were considered alone, $\dot{V}_{O_2}$ changes were independent of $f_{\rm H}$ ($P$=0.13), while the 6 kg trials had only a weak linear $f_{\rm H}$/$\dot{V}_{O_2}$ relationship [$\dot{V}_{O_2}$=(32.65$f_{\rm H}$±5.04)+(1855.77±391.41); $r^2$=0.28, $P$<0.01].

When all feeding data was considered, the relationship between $f_{\rm H}$ and $\dot{V}_{O_2}$ was weak (Fig. 5; $r^2$=0.20, $P$<0.01) compared to when the animal was fasting ($r^2$=0.69, $P$<0.01). These two regressions (i.e. fasting trials only and feeding trials only) were significantly different ($P$<0.05), indicating that digestion of food alters the $f_{\rm H}$/$\dot{V}_{O_2}$ relationship derived for fasted animals.

## Discussion

As shown for a number of other species (Fedak, 1986; Williams et al., 1991; Butler et al., 1992; Williams et al., 1993;

Table 3. *Regression parameters describing the linear change in rate of oxygen consumption over time for Male 1 following bulk feeding*

| Date (2000) | Ingested food (kg) | $f_{\rm H}$ (beats min$^{-1}$) | | | $\dot{V}_{O_2}$ (ml O$_2$ h$^{-1}$ kg$^{-0.60}$) | | |
|---|---|---|---|---|---|---|---|
| | | Regression | $r^2$ | $P$ | Regression | $r^2$ | $P$ |
| May 4 | 6 | $f_{\rm H}$=0.02$t$+65.30 | 0.07 | 0.11 | $\dot{V}_{O_2}$=8.06$t$+2921.92 | 0.71 | **<0.001** |
| May 11 | 6 | $f_{\rm H}$=0.02$t$+80.49 | 0.06 | 0.15 | $\dot{V}_{O_2}$=5.40$t$+3850.13 | 0.82 | **<0.001** |
| May 12 | 6 | $f_{\rm H}$=–0.02$t$+82.33 | 0.16 | **0.016** | $\dot{V}_{O_2}$=4.11$t$+3758.60 | 0.70 | **<0.001** |
| May 23 | 12 | $f_{\rm H}$=–0.05$t$+86.55 | 0.40 | **<0.001** | $\dot{V}_{O_2}$=5.22$t$+3848.17 | 0.73 | **<0.001** |
| May 26 | 12 | $f_{\rm H}$=–0.04$t$+87.20 | 0.40 | **<0.001** | $\dot{V}_{O_2}$=1.89$t$+4295.72 | 0.25 | **<0.001** |
| June 3 | 12 | $f_{\rm H}$=0.04$t$+78.09 | 0.35 | **<0.001** | $\dot{V}_{O_2}$=6.88$t$+3738.11 | 0.82 | **<0.001** |

$f_{\rm H}$, heart rate; $\dot{V}_{O_2}$, rate of oxygen consumption.

Significant differences at the $P$<0.01 level are shown in bold.

The regression coefficient $t$ is time (in s).

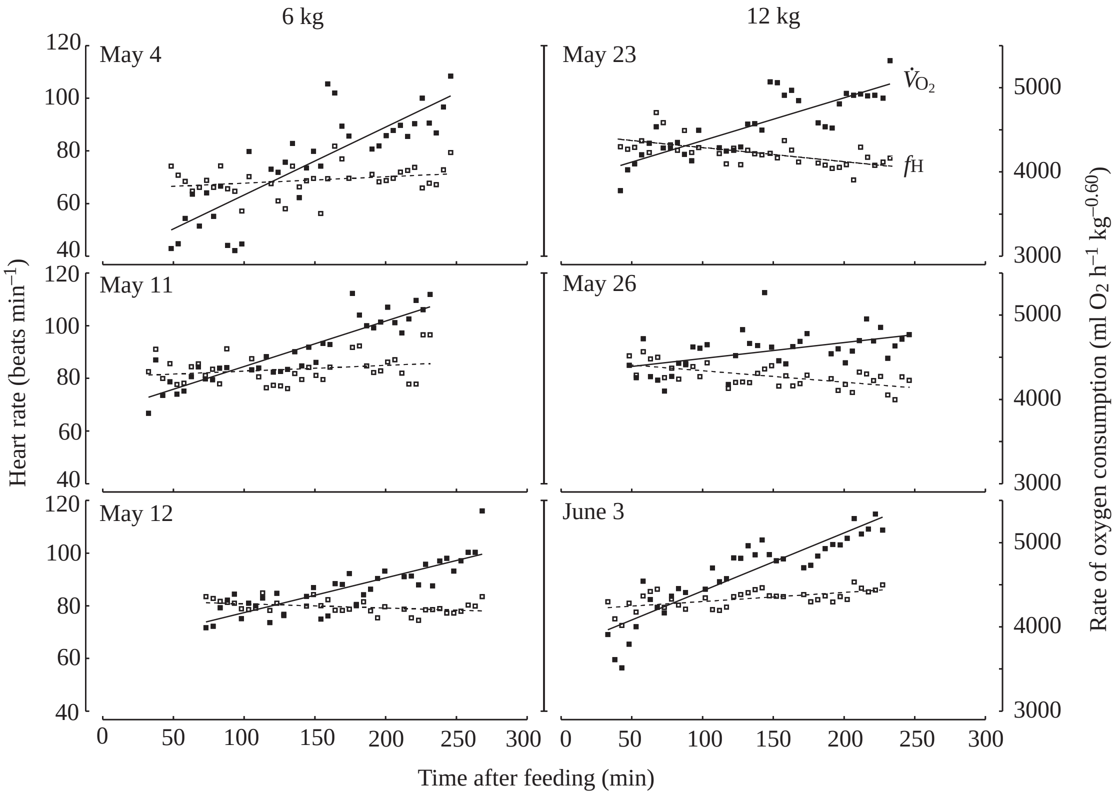

Fig. 4. Time series of heart rate (beats min$^{-1}$) (open squares, broken lines) and rate of oxygen consumption (ml O$_2$ h$^{-1}$ kg$^{-0.60}$) (filled squares, solid lines) in a male Steller sea lion after 6 and 12 kg feedings. See text and Table 3 for regression parameters.

Hurley, 1996; Froget et al., 2001), there was a significant correlation between heart rate and metabolism in fasted Steller sea lions. However, there was considerable variability within the data for the two females and the regressions for the four individuals were not all statistically similar. Therefore, the degree to which the mean regression we calculated for the four animals can be applied to wild individuals is unclear.

### *Factors affecting the* $f_H/\dot{V}_{O_2}$ *relationship*

A number of factors might explain the variability in the measurements of heart rate and oxygen consumption within and between individual animals (Fig. 1). They include possible changes or differences in stress level, fitness and other physiological parameters of the study animals.

Considerable data on humans, dogs and rhesus monkeys have shown that psychological stress brought on by threatening stimuli can lead to heart rate variations that do not always correspond positively with variations in metabolism (Johnson and Gessaman, 1973; Obrist et al., 1974; Stromme et al., 1978; Langer et al., 1979, 1985). Stress (through the release of epinephrine to beta-adrenoreceptors) can cause the heart rate to increase beyond levels that can be predicted from measured oxygen uptake (Blix et al., 1974; Stromme et al., 1978; Turner and Carroll, 1985; Wilhelm and Roth, 1998).

Physical fitness, which increases the functional capacity of the cardiovascular system, may also affect the $f_H/\dot{V}_{O_2}$ relationship. As fitness improves, the heart enlarges, ventricular stretching is enhanced, and blood volume increases, resulting in an increased stroke volume, allowing reduction in the heart rate for a given oxygen consumption relative to that

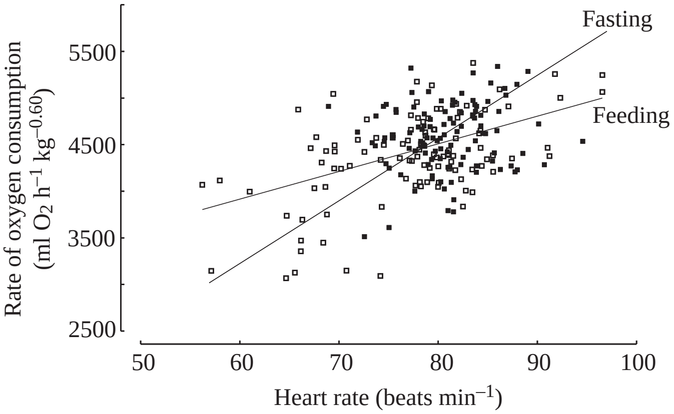

Fig. 5. Relationship between postprandial heart rate (beats min$^{-1}$) and rate of oxygen consumption (ml O$_2$ h$^{-1}$ kg$^{-0.60}$) as determined in a male Steller sea lion after a bulk feed of 6 kg (open squares) or 12 kg (filled squares). Data points, consisting of mean $f_H$ and $\dot{V}_{O_2}$ values at 5 min intervals, were collected between 30 min and 4 h after feeding. The regression equation for the pooled feeding data is $\dot{V}_{O_2}$=(29.7$f_H$±4.0)+(2136.6±320.5), $r^2$=0.20, $P$<0.01. The fasting regression line ($\dot{V}_{O_2}$=(71.3$f_H$–4.3)–(1138.5–369.6), $r^2$=0.69, $P$=<0.01) is shown for comparison.

of more sedentary individuals (Swaine et al., 1992; Plowman and Smith, 1997; Mtinangi and Hainsworth, 1999).

Other factors for consideration are potential ontogenic changes, including mass fluctuations and changes in the allometry of the circulatory system. The potential of these changes to contribute to the variability in the $f_H/\dot{V}_{O_2}$ relationship is of concern given the extended period over which some of the data were collected. Unfortunately, published studies specifically discussing the effects of ontogenic factors on the $f_H/\dot{V}_{O_2}$ relationship were not found. This includes a dearth of data on developmental changes in the allometry of the heart, lungs or other components of the circulatory system that would theoretically alter the $f_H/\dot{V}_{O_2}$ relationship.

Changes in body mass might also alter the $f_H/\dot{V}_{O_2}$ relationship, particularly if these are due to changes in percentage of lipid mass. Unfortunately, whether fat-free or absolute body mass is the primary predictor of resting metabolic rate is the subject of considerable debate (Cunningham, 1991; Ferraro and Ravussin, 1992), and changes in total body mass do not always reflect changes in either lipid or lean tissue mass in pinnipeds. In the present study, the strongest regression was obtained from the individual that had the greatest changes in body mass (Male 1). However, changes in body mass may still have to be taken into account when applying the heart-rate method over extended periods.

It is not clear to what extent the above factors may have affected the $f_H/\dot{V}_{O_2}$ relationship of our study animals. The negative to positive trend in the regression residuals (plotted in the order of data collection) of the female Steller sea lions showed initially high heart rates for a given oxygen consumption. This suggests either a decrease in stress, an increase in fitness, or a decrease in body condition as our study progressed (Fig. 2). We ruled out seasonal changes as a factor, given that the bulk of the data were collected within a short time frame (a month or less) and the overall residual trends did not change when the data were separated into various time blocks. Despite a 50% mass increase over the study period and data collection spanning nearly a year, the regression of $\dot{V}_{O_2}$ on $f_H$ for Male 1 showed a high $r^2$ value and only a slight trend in the regression residuals. The lack of a trend and high $r^2$ in the regression on data from Male 2 suggests no effect of stress, fitness, changing body composition or mass changes (which were insignificant as in the females) over time. Data were collected in a week, thus no seasonal effects were assumed. However, with several factors potentially affecting the $f_H/\dot{V}_{O_2}$ relationship, it is possible that concurrent contrary effects would result in a constant $f_H/\dot{V}_{O_2}$ relationship by chance in Male 2.

### *Stroke volume and oxygen extraction*

As per Fick's original equation (Fick, 1870), the heart rate method assumes that stroke volume and arterio–venous oxygen extraction remain constant or vary in a predictable, systematic manner in order to reliably estimate $\dot{V}_{O_2}$ from heart rate measurements.

The $r^2$ values from the regressions of $\dot{V}_{O_2}$ on $f_H$ suggest that $f_H$ explains 71–78% of the variation in measured $\dot{V}_{O_2}$ for the males, and 21–45% of the increase in the females (Table 2). However, a closer examination of the data in Fig. 1 reveals that $\dot{V}_{O_2}$ increased approximately 2.5–4.0 times while $f_H$ only doubled across the ranges recorded in the four sea lions. This suggests that the heart rate data can physiologically explain only 38–87% of the increase in $\dot{V}_{O_2}$. A systematically increasing stroke volume and/or tissue oxygen extraction might explain the remaining increase in $\dot{V}_{O_2}$ if heart rate is truly linearly related to $\dot{V}_{O_2}$, which may or may not be true in Steller sea lions.

Ideally, stroke volume and tissue oxygen extraction should be measured as they have been in other mammals. In horses, steers, goats, calves and some dogs, mass-specific stroke volume remains constant over a range of exercise (Horstman et al., 1974; Taylor et al., 1987; Jones et al., 1989). Oxygen extraction, however, increased with exercise in a systematic curvilinear manner. In rats and some dogs, both stroke volume and extraction increased in a linear fashion with exercise (Gleeson and Baldwin, 1981; Horstman et al., 1974). Similar changes in Steller sea lions (i.e. a systematically increasing stroke volume and/or extraction) would help explain the remainder of the increase in $\dot{V}_{O_2}$.

Data from other diving pinnipeds is scarce and contradictory. Over a range of workloads, harbour seals showed a slightly decreasing stroke volume while surface-swimming. However, while swimming submerged, the seals showed a constant stroke volume that was about half that observed during surface-swimming (Ponganis et al., 1990); oxygen extraction was not reported. California sea lions, on the other hand, have been shown to maintain a constant stroke volume over a continuous period of short submergence and surface-swimming events, regardless of workload (Ponganis et al., 1991). Stroke-volume changes in Steller sea lions are probably similar to those reported for California sea lions, since swimming in our study involved short dive and surface events and the species are evolutionarily related.

If it is true that stroke volume remains constant, extraction might be responsible for the observed increase in $\dot{V}_{O_2}$ that is not explained by $f_H$. However, without recorded values, this is purely speculative. We would expect over the course of a dive that the arterio–venous oxygen difference would change; thus, oxygen extraction per heart beat might change. However, such a change may not be evident during a swim trial that includes only very short dives. In the wild, Steller sea lions dive an average of 4–6 min during foraging bouts and so the validity of applying a swim-mill regression to free-ranging animals is uncertain.

### *Steller sea lion regressions and data collection*

A degree of variability in data collection is normal and does not mean that the heart rate method is inadequate, especially relative to other available techniques. It may have been possible to reduce some of the variation in the Steller sea lion data set by experimentally collecting all data within 24 h. This has been done previously in some captive marine bird and mammal studies, where significant $f_H/\dot{V}_{O_2}$ relationships were obtained with minimal variation ($r^2$ values were above 0.70) (see Williams et al., 1991; Butler et al., 1992; Bevan et al., 1994, 1995a,b). Although prompt data collection on captive animals would be likely to reduce variation due to development, fitness levels and stress, the application of the regressions to wild Steller sea lions living in the open ocean will probably be done over several days or months. Wild Steller sea lions would experience such changes in physiological parameters throughout a monitoring period. Thus, it is probably more meaningful to calibrate regressions on captive animals over an extended time period, as we have done, rather than in a single day.

### *Comparison with other methods and species*

Studies on other species such as California sea lions (Butler et al., 1992; Boyd et al., 1995), barnacle geese (Nolet et al., 1992), gentoo penguins (Bevan et al., 1995b) and black-browed albatrosses (Bevan et al., 1994) have concluded that heart rate is a good indicator of metabolism, despite significant differences between slopes and intercepts of individual regressions. These studies compared predicted to observed oxygen consumption and found that heart rate could predict oxygen consumption with an error less than or equivalent to that predicted by use of doubly labelled water. In captive swimming California sea lions, doubly labelled water turnover overestimated metabolic rate by as much as 36.4% on average (range –10% to 86%), while heart rate overestimated by an average of only 2.7% (range –28% to +23%) (Boyd et al., 1995). However, both techniques were considered valid. Thus, although regressions in our study differed among individuals, heart rate may still yield a better estimate of oxygen consumption relative to the doubly labelled water technique. However, validation experiments to determine the mean regression's ability to accurately estimate metabolism are still needed before it can be applied with confidence to estimate the mean metabolism of groups of Steller sea lions in the field.

The mean $f_H/\dot{V}_{O_2}$ regression, $\dot{V}_{O_2}=(71.3f_H\pm4.3)-(1138.5\pm369.6)$, determined from the four Steller sea lions in our study had a reasonably tight fit to the data ($r^2=0.69$) (Fig. 3A). Re-running the mixed linear models to determine a mean regression with oxygen consumption measured in ml $O_2$ min$^{-1}$ kg$^{-1}$ for comparison with other marine mammal studies resulted in the equation $\dot{V}_{O_2}=(0.19f_H\pm0.01)-(4.12\pm1.3)$. This regression is different from that of other marine mammal species, although it is most similar to other otariids, and suggests that regressions of $f_H$ and $\dot{V}_{O_2}$ may be species-specific (Fig. 6). As expected from their larger body mass, males generally consumed less $O_2$ kg$^{-0.60}$ of mass than the females (Fig. 3A), indicating that there may even be separate regressions for the sexes, an idea suggested by Hurley (1996) with California sea lions that should be explored further.

### *The effect of feeding*

As seen in previous experiments, oxygen consumption of the sea lion continued to rise over all 3 h feeding runs regardless of meal size, indicative of the heat increment of feeding (Blaxter, 1989; Rosen and Trites, 1997). However, heart rate increased in only one 12 kg feeding run, and either remained unchanged or decreased over time during the other 6 and 12 kg feeding trials (Fig. 4, Table 3).

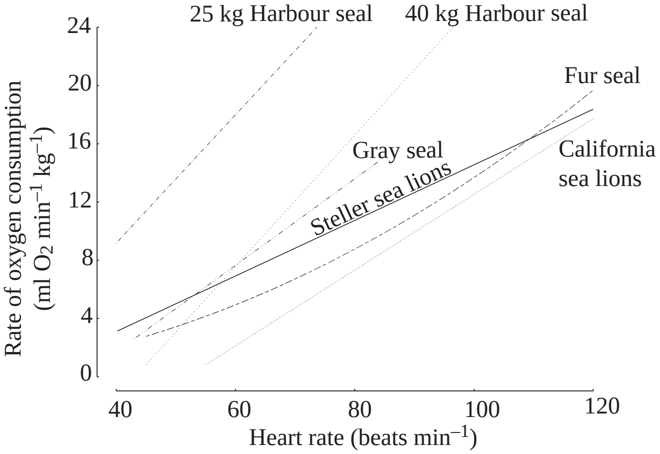

Fig. 6. The relationship between heart rate (beats min$^{-1}$) and rate of oxygen consumption (ml $O_2$ h$^{-1}$ kg$^{-1}$) in Steller sea lions [$\dot{V}_{O_2}=(0.19f_H\pm0.02)-(4.12\pm1.68)$, $r^2=0.69$] shown, for comparison, with that determined in other pinniped species (Fedak, 1986; Williams et al., 1991; Butler et al., 1992; Boyd et al., 1995, 1999).

Unlike many human studies where the haemodynamic response to feeding may continue for hours, haemodynamic variables in other mammals (dogs, calves and pigs) return to baseline values at the end of feeding (Fronek and Stahlgren, 1968; Houpt et al., 1983; Kelbaek et al., 1989). In those studies where cardiac output increased with postprandial metabolism, there was also considerable conflicting data on whether increased stroke volume or heart rate was the major contributor (Kelbaek et al., 1989; Waaler et al., 1991; Muller et al., 1992; Sidery and MacDonald, 1994). In young lambs, oxygen extraction appeared to be responsible for the increase in $\dot{V}_{O_2}$. Additional potential haemodynamic responses included increased oxygen extraction (Grant et al., 1997) and the redirection of blood flow from other vascular beds in the body to the digestive organs (Yi et al., 1990).

Regressing oxygen consumption on heart rate with data collected after 12 kg feedings failed to produce a significant relationship. Data from the 6 kg feedings provided only a weak relationship. Regressing $\dot{V}_{O_2}$ onto $f_H$ from all feeding trials (both 6 and 12 kg) yielded a poor relationship that was significantly different from the fasting regression (Fig. 5). The above findings indicate that digestion alters the $f_H/\dot{V}_{O_2}$ relationship when compared to a fasting condition. Curiously, increases in rates of oxygen consumption induced in king penguins through increased thermal challenges also failed to induce comparable changes in heart rate (Froget et al., 2001).

We were unable to properly explain the effect of feeding on the relationship between $f_H$ and $\dot{V}_{O_2}$ with our limited data. Our results are included here only to draw attention to the possibility that feeding may alter the relationship. Further study examining temporal effects with a larger sample size and longer trials is needed. Consideration should also be given to studying feeding while swimming at various speeds to further elucidate the behavior of the feeding regression at the higher levels of oxygen consumption and heart rate that are experienced in the wild.

### *Captivity* versus *free-ranging environment*

The assumption that the $f_H/\dot{V}_{O_2}$ relationship determined from captive animals is similar to that existing in free-ranging animals warrants discussion. Accurately calibrating a relationship in free-ranging animals undergoing completely natural, undisturbed behaviour is currently difficult, if not impossible. We do not know to what extent our results were affected by the confining nature of the swim mill and metabolic chamber. The dive intervals of the animals in our study were too short to result in a perceptible bradycardia. Therefore, it is difficult to speculate how this and other aspects of the dive response (e.g. vasoconstriction) would affect the relationship between $\dot{V}_{O_2}$ and $f_H$. An obvious next step would be to collect similar data from animals swimming in a much larger pool equipped for direct respirometry, or swimming beneath a respirometry hood alongside a boat in the open ocean. Both approaches offer reduced confinement and may yield more natural behaviour.

To simulate field conditions more closely, food intake could be varied and live fish could be introduced. Regressions determined from such data could then be used to estimate metabolism from heart rate in free-ranging animals with more confidence.

In conclusion, our study provides important basic information on an otariid species that could be useful in comparative studies. However, our results raise a number of questions regarding the potential effects of gender, season, age class, digestive state, stress and body condition on the $f_H/\dot{V}_{O_2}$ relationship that necessitate more detailed examination. Using regressions determined from captive animals to predict metabolic rate from heart rate in free-ranging animals should therefore be approached with caution.

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