The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions

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Summary. Respiratory, metabolic, and cardiovascular responses to swimming were examined in two species of pinniped, the harbor seal *(Phoca vitulina)* and the California sea lion *(Zalophus californianus)*.

1. Harbor seals remained submerged for 82–92% of the time at swimming speeds below $1.2 \text{ m} \cdot \text{s}^{-1}$. At higher speeds, including simulated speeds above $1.4 \text{ m} \cdot \text{s}^{-1}$, the percentage of time spent submerged decreased, and was inversely related to body weight. In contrast, the percentage of time spent submerged did not change with speed for sea lions swimming from $0.5 \text{ m} \cdot \text{s}^{-1}$ to $4.0 \text{ m} \cdot \text{s}^{-1}$.

2. During swimming, harbor seals showed a distinct breathhold bradycardia and ventilatory tachycardia that were independent of swimming speed. Average heart rate was 137 beats·min^{-1} when swimming on the water surface and 50 beats·min^{-1} when submerged. A bimodal pattern of heart rate also occurred in sea lions, but was not as pronounced as in the seals.

3. The weighted average heart rate (WAHR), calculated from measured heart rate and the percentage time spent on the water surface or submerged, increased linearly with swimming speed for both species. The graded increase in heart rate with exercise load is similar to the response observed for terrestrial mammals.

4. The rate of oxygen consumption increased exponentially with swimming speed in both seals and sea lions. The minimum cost of transport calculated from these rates ranged from 2.3 to $3.6 \text{ J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$, and was 2.5–4.0 times the level predicted for similarly-sized salmonids. Despite different modes of propulsion and physiological responses to swimming, these pinnipeds demonstrate similar transport costs.

Key words: Heart rate – Oxygen consumption – Harbor seal – Sea lion

Introduction

The swimming behavior of marine mammals often consists of prolonged periods of submergence that are briefly interrupted when the animal surfaces to breathe. This pattern of swimming represents a compromise between the respiratory demands of the animal and the hydrodynamic (Williams and Kooyman 1985), energetic (Williams 1989), and ecological (Fedak et al. 1988) factors that favor submergence. By keeping surface intervals brief these mammals increase swimming efficiency, but sacrifice the time permitted for ventilation and oxygen loading. Such a sacrifice could affect performance at high swimming speeds by reducing the availability of oxygen to working muscles when metabolic demands are greatest. To avoid this problem, marine mammals may decrease dive duration at higher swimming speeds and keep metabolism aerobic (Davis et al. 1991) or utilize pathways for oxygen uptake and delivery that differ from those of terrestrial animals.

In terrestrial mammals, elevated metabolic demands during exercise are met by increasing ventilation and heart rate. These responses are similar for different forms of exercise, including swimming. For example, minute ventilation and heart rate correlate positively with oxygen uptake, and therefore with work load in both running and swimming humans. Changes in the heart rate of human swimmers will depend on many factors, including training (Nielsen and Davies 1976), water temperature (Holmer and Bergh 1974), body temperature (Holmer 1972), and breath-holding (Butler and Woakes 1987). In contrast, the heart rate of marine mammals often undergoes a pronounced bradycardia and tachycardia that correspond to submerged and surface phases of swimming, respectively (Elsner 1969; Fedak 1986; Fedak et al. 1988).

It is difficult to distinguish between diving responses and exercise responses in swimming marine mammals.

The bradycardia that characteristically occurs during submergence results in regional vasoconstriction, reduced cardiac output, and possibly decreased organ metabolism (Elsner 1969; Elsner and Gooden 1983). Conversely, exercise in terrestrial animals is associated with tachycardia, as well as elevated metabolism and arterial vasodilation in the working muscles. In view of this, it appears that many physiological responses during submergence are in direct conflict with the needs of the active marine mammal.

To better understand the cardiovascular and metabolic responses of marine mammals to submerged swimming, we measured heart rate, surface and submerged intervals, and oxygen consumption over a wide range of work loads. Unlike previous studies, we examined the upper limits of performance by testing work loads that exceeded levels experienced at routine swimming speeds. Two species of pinniped were examined, the harbor seal *(Phoca vitulina)*, and the California sea lion *(Zalophus californianus)*. Results from this study demonstrate that the physiological responses to exercise and the strategies for oxygen loading during performance are different for the two species. Regardless of these differences, transport costs are similar for swimming harbor seals and sea lions.

Materials and methods

Animals. Four subadult harbor seals (average body weight = 24, 26, 34, and 44 kg) and three subadult sea lions (average body weight = 18, 21, and 25 kg) were used in the study. The animals were housed in saltwater pools and fed a diet of mackerel and herring supplemented with vitamins (Sea Tabs). Water temperatures in the holding pools ranged from 15.0 to 18.0 °C during the experimental period.

Experimental design. Heart rate, metabolic rate, and surface and submerged intervals were measured simultaneously as animals swam against a current in a water channel. Details of the water channel have been described by Davis et al. (1985). For the present experiments the channel was filled with fresh water at 15.0–18.0 °C.

Several weeks before the experiments, the animals were trained to swim in the flume for 30–60 min at water speeds up to 1.4 m · s⁻¹. Four to five practice sessions were required to obtain reproducible values (within 5%) for oxygen consumption at each speed. Each swimming session consisted of a 10–60-min rest period followed by three 30-min swimming periods of increasing work load. Resting measurements were taken before the swimming session while the animals floated in the water channel. Three work loads, expressed in terms of simulated swimming speed (see below), ranged from 0.5 to 3.2 m · s⁻¹ for the seals and from 0.5 to 4.1 m · s⁻¹ for the sea lions. The animals were permitted to rest for 20 min between each work load during which the oxygen analyzer and heart rate monitor were calibrated.

Increasing work load during swimming. Maximum water velocity in the water channel was 1.4 m · s⁻¹. Because both seals and sea lions can sustain swimming speeds greater than this (Williams and Kooyman 1985), two methods were used to increase the work load. First, body drag was increased by attaching two nylon drag cups (12 × 12 × 5 cm) to neoprene patches that were glued onto the animal's fur. These cups increased the frontal area, and hence the body drag and work load of the animal. The cups were positioned so as not to interfere with swimming movements. For sea lions, the cups were placed along the midline of the ventral surface at 40% and 60% of their body length. We positioned the cups between the

dorsal midline and axilla at approximately 30% of the body length of the seals.

Increased drag associated with the cups was determined by towing tests as described in Williams and Kooyman (1985). Briefly, seals and sea lions were trained to bite onto a neoprene mouthpiece while being towed passively through a 3.5-m deep water channel. The animals were towed in a gliding configuration at a depth of 1 m. Drag measurements were made for animals with and without drag cups towed at speeds over the range 0.9–3.8 m · s⁻¹. Drag forces were measured with a load cell (Western Scale, Inc.) that had been calibrated with a hand-held dynamometer (Weigh and Test Systems). Simulated swimming speed, the theoretical speed that an animal without drag cups would travel in order to match the drag of an animal with drag cups, was calculated from curves generated from the two types of towing data. The resulting equations were:

$$\log(V_{sim}) = \frac{0.80 + 1.92(V_w)}{2.17} \tag{1}$$

for harbor seals, and

$$\log(V_{sim}) = \frac{0.50 + 1.83\log(V_w)}{1.79} \tag{2}$$

for sea lions [presented in Feldkamp (1985)]. In these equations V_{sim} = simulated swimming speed (m · s⁻¹) and V_w = towing speed (m · s⁻¹) for animals with drag cups. Because stroke frequency at equivalent V_{sim} and $V_{without\ drag\ cups}$ were similar for the seals, we assumed that active drag associated with swimming movements was identical for both conditions. A similar verification could not be made for sea lions because of their complicated swimming kinematics (Feldkamp 1987a).

The second method for increasing work load during flume swimming followed the procedures of di Prampero et al. (1974). A line connected to a weight and pulley system was attached to animals swimming at 1.0 m · s⁻¹. Additional force was placed on the line by adding weights that ranged from 0.13 to 2.25 kg for the seals and from 0.13 to 4.00 kg for the sea lions. The weighted rope was attached to a loop that was epoxied on the back of the animal. A system of pulleys directed the line above the animal, but allowed the force to act horizontally to the direction of movement. The load was converted into a drag force (newtons) and added to the measured drag of the animal towed at 1.0 m·s⁻¹. The simulated swimming speed of tethered subjects was calculated by using this value to solve drag versus speed regressions of towed animals.

At comparable V_{sim}, these two methods resulted in identical levels of oxygen consumption for individual animals. Therefore, the physiological data for animals swimming with drag cups or with tethered loads were combined.

Heart rate. Electrocardiograms (ECG) were continuously recorded during rest and swimming using two cross-thorax surface electrodes. The electrodes (2.5-cm diameter copper disks) were placed on shaved skin in the axillary region at the level of the heart. ECG electroconductive gel spread on the skin improved the contact between the electrodes and the skin surface. Neoprene patches 10 cm in diameter glued to the surrounding fur insulated the electrode plates from the water. Plastic insulated wire leads from the electrodes trailed behind the animals and were connected to a Sanborn Heart Rate Monitor (Hewlett-Packard). Amplified signals were recorded at 2.5 cm·s⁻¹ on a strip chart recorder (Gould, Inc.).

Surface and submerged swimming intervals. An electronic switch that was activated by an observer when the animal submerged was used to assess the time spent swimming on the water surface or submerged. Signals from the switch were recorded simultaneously with ECG on the strip chart recorder.

Metabolic rate. Seals and sea lions were fasted overnight before swimming sessions in the flume. Oxygen consumption ($\dot{V}O_2$) was determined using an open-flow respirometry system. Details of the

system and its calibration have been discussed by Davis et al. (1985) for seals and Feldkamp (1987b) for sea lions. While in the water channel, the animals swam in a glass-panelled test section that was 2.5 m long and had a cross-sectional area of 1.1 m². A plywood cover restricted breathing in the test section to a $1.1 \times 0.6 \times 0.3$ m plexiglass dome. Ambient air was drawn into the dome at approximately $60\ l \cdot min^{-1}$. At this flow rate the content of O_2 in the dome always exceeded 20% during the experiments. Flow rate into the dome was monitored with a calibrated dry gas meter (American Meter Division). Both the vacuum pump and dry gas meter were calibrated at flow rates up to $100\ l \cdot min^{-1}$ with a Brooks Vol-U-Meter.

A portion of the outflow from the metabolic dome was dried (Drierite) and scrubbed of carbon dioxide (Baralyme) before entering an oxygen analyzer (Ametek S3-A, Inc.). Voltage output of the analyzer was monitored by a computer (Apple II+) that averaged $\%O_2$ over 1 min intervals. $\dot{V}O_2$ was calculated using equations of Withers (1977) and corrected to STPD. The entire respirometry system was calibrated with ambient air (20.94% O_2) and gases of known O_2 and N_2 content analyzed on a Scholander 0.5-c^3 gas analyzer (Scholander 1947). A N_2-dilution calibration, as presented in Fedak et al. (1981) and modified by Davis et al. (1985), was performed with and without water flowing in the flume. The theoretical and measured fraction of O_2 in the expired gas line agreed to within 0.01% at all water velocities tested.

Data analysis. The duration of surface and submerged periods, heart rate, and oxygen consumption were measured simultaneously for each animal during 1–7 sessions at each work load. Numerical values are presented as mean ± 1 SE. Statistical significance was tested by paired t-tests (Zar 1974). Linear and non-linear relationships were calculated by least squares procedures (Warme 1980). Swimming speeds greater than $1.4\ m \cdot s^{-1}$ represent simulated speed as calculated from cup drag or tethered load.

Heart rates were calculated by dividing the total number of beats by the surface or submerged period. ECG waveforms and fractions thereof were used according to recommendations by Chabot et al. (1989). Transition periods that occurred as heart rate changed between surface and submerged steady states were included in the submerged heart rate averages. Because these transition periods were brief (< 4.0 s), heart rates determined in this manner did not differ significantly (at $P < 0.001$) from analyses omitting the estimated transition periods.
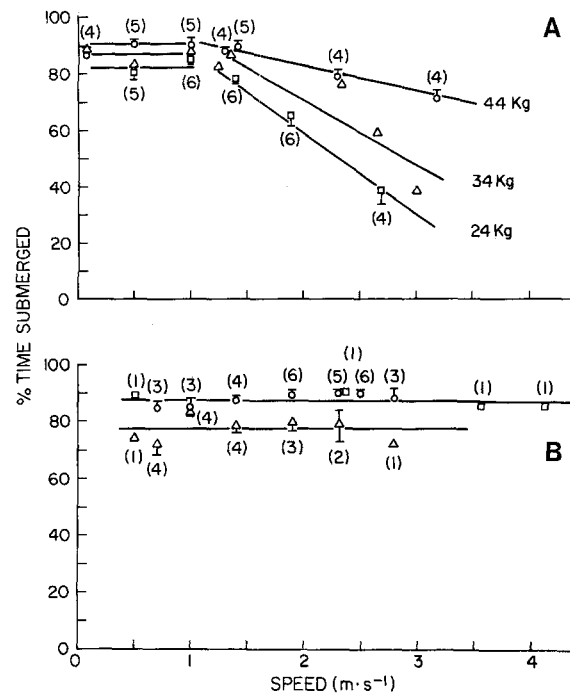
Results

Surface and submerged swimming intervals

Harbor seals remained submerged for 82–92% of the time while swimming at speeds less than $1.2\ m \cdot s^{-1}$ (Fig. 1a); at higher speeds the percent time submerged decreased. This relationship was inversely related to body weight for seals ranging from 24 to 44 kg. Least squares regressions describing the decrease in percent time submerged with speed are:

$$y = 118.2 - 29.18x \quad (r=0.99) \text{ for the 24-kg animal} \quad (3)$$
$$y = 116.3 - 22.81x \quad (r=0.90) \text{ for the 34-kg seal and} \quad (4)$$
$$y = 103.3 - 9.57x \quad (r=0.99) \text{ for the 44-kg seal} \quad (5)$$

where $y =$ % time submerged, and $x =$ swimming speeds above $1.2\ m \cdot s^{-1}$.

Submerged intervals also decreased as exercise load increased in the swimming harbor seals. At rest, mean submergence time was 61.3 ± 7.1 s. This decreased to 29.7 ± 5.5 s at $1.0\ m \cdot s^{-1}$ and 16.2 ± 4.5 s at $2.5\ m \cdot s^{-1}$.

Fig. 1. A Percent time submerged plotted in relation to swimming speed for three harbor seals. The results are divided into three weight classes that average 24 kg ($\square$), 34 kg ($\triangle$), and 44 kg ($\circ$). Each point represents the mean $\pm$ SE for (n) experimental sessions. For clarity only one direction for SE is illustrated. *Solid lines* denote the mean values at speeds below $1.0\ m \cdot s^{-1}$ and the least squares linear regression for higher speeds. **B** Percent time submerged plotted in relation to swimming speed for three California sea lions. The results are divided into two weight classes that average 18 kg ($\triangle$, $n=1$) and 21 kg ($\circ$, $\square$). Each point represents the mean ± 1 SE for (n) experimental sessions. For clarity only one direction for SE is illustrated. *Solid lines* denote the mean values for all speeds

In contrast, the percentage of time spent submerged for three sea lions did not change with swimming speed or follow the same body weight dependent relationships observed for seals (Fig. 1b). The average percentage was $77.9 \pm 1.6\%$ for an 18-kg sea lion and $88.3 \pm 0.7\%$ for two 21-kg animals. Based on the above weight relationships for seals, we would expect comparatively lower submergence time for the smaller sea lions. Instead, the sea lions remained submerged for a greater portion of the swimming period when compared to seals swimming faster than $1.2\ m \cdot s^{-1}$. However, the duration of each period of submergence was lower for the otariid. Submerged intervals were 5.8 ± 1.4 s for resting sea lions, 6.7 ± 0.5 s for animals swimming at $1.0\ m \cdot s^{-1}$, and 10.7 ± 0.6 s for animals swimming at $2.5\ m \cdot s^{-1}$.

Surface intervals for resting animals averaged 14.4 ± 2.1 s ($n=34$) for seals and 22.0 ± 7.1 s ($n=37$) for sea lions. The mean surface interval of swimming sea lions, 1.1 ± 0.01 s ($n=330$), did not vary with speed over the range $1.0–2.5\ m \cdot s^{-1}$. Only a single breath occurred during such short intervals at the surface. Surface intervals of swimming seals ranged from 3.6 ± 0.4 s ($n=87$) at $1.0\ m \cdot s^{-1}$ to 5.2 ± 0.5 s ($n=105$) at $2.5\ m \cdot s^{-1}$ and provided enough time for harbor seals to take several breaths.

Heart rate

The heart rate of seals and sea lions corresponded to changes in surface or submerged swimming (Fig. 2). Upon submerging, the interbeat interval of swimming seals gradually increased during a 1–4-s transition period. This was followed by a pronounced bradycardia for the remainder of the period of submergence. Immediately before surfacing, the interbeat interval decreased during a transition period that mirrored the pre-dive period. Because of the comparatively short surface intervals, transition periods for sea lions were less pronounced than observed for seals.

Heart rates of harbor seals showed a bimodal pattern that correlated with apneic and ventilatory periods rather than with swimming speed (Fig. 3a). Heart rate during submerged swimming was 63% lower than during surface swimming. Over the range 0.5–3.2 m · s^{-1} heart rate of the seals during surface or submerged swimming did not change significantly with speed. WAHRs were calculated from the equation:

$$\text{WAHR (beats·min}^{-1}) = T_{sub}(HR_{sub}) + T_{surface}(HR_{surface}) \quad (6)$$

where T = the fraction of time spent submerged or on the water surface (Fig. 1), and HR = heart rate measured during steady swimming.

WAHR increased linearly with swimming speed for the three seals:

$$\text{WAHR (beats·min}^{-1}) = 37.36 + 21.05 \text{ speed (m·s}^{-1}) \quad (7)$$
$(r = 0.80).$

Although a bimodal pattern of heart rate also occurred for sea lions, the average difference between the surface and submerged heart rate was only 15% (Fig. 3b). In contrast to seals, the heart rate of sea lions increased with swimming speed; the relationship is best described by the equations:

$$\text{heart rate (beats·min}^{-1}) = 78.79 + 14.86 \text{ speed (m·s}^{-1}) \quad (8)$$
$(r = 0.85)$

during submergence, and

$$\text{heart rate (beats·min}^{-1}) = 91.28 + 17.36 \text{ speed (m·s}^{-1}) \quad (9)$$
$(r = 0.90)$

during surface swimming. As seen in Fig. 3b, WAHR for the sea lion was similar to the animal's submerged heart rate, and reflected the percentage time submerged. WAHR in relation to swimming speed for sea lions is described by the equation:

$$\text{WAHR (beats·min}^{-1}) = 81.22 + 15.18 \text{ speed (m·s}^{-1}) \quad (10)$$
$(r = 0.89)$

Metabolic rate

Oxygen consumption increased exponentially with swimming speed for both seals and sea lions (Fig. 4). Regressions for these relationships followed those reported by Davis et al. (1985) for seals and by Feldkamp (1987b) for sea lions swimming at lower speeds. For the subadult harbor seals swimming over the range 0.5–3.4 m · s^{-1}, $\dot{V}O_2$ was best described by:

$$\dot{V}O_2 = 6.98 \ e^{0.49 \text{ speed}} \quad (r = 0.93) \quad (11)$$

where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and speed is in m · s^{-1}. The present study and Feldkamp (1987b) found
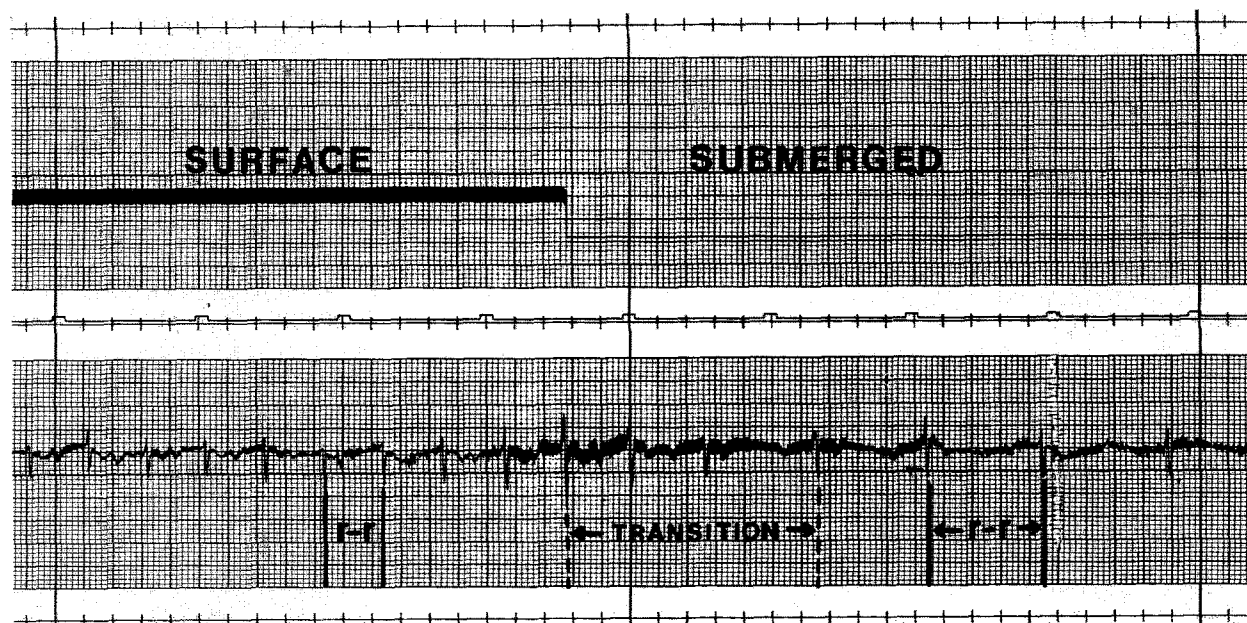
Fig. 2. Representative two-channel recording of behavior and ECG for swimming pinnipeds. The graph illustrates the recording for a harbor seal swimming in a flume at 1.0 m · s^{-1}. The upper portion of the trace represents the surface and submerged swimming activity, and the lower trace is the corresponding ECG. Note the changes in the interbeat (r–r) interval for surface swimming, a transition period, and submerged swimming
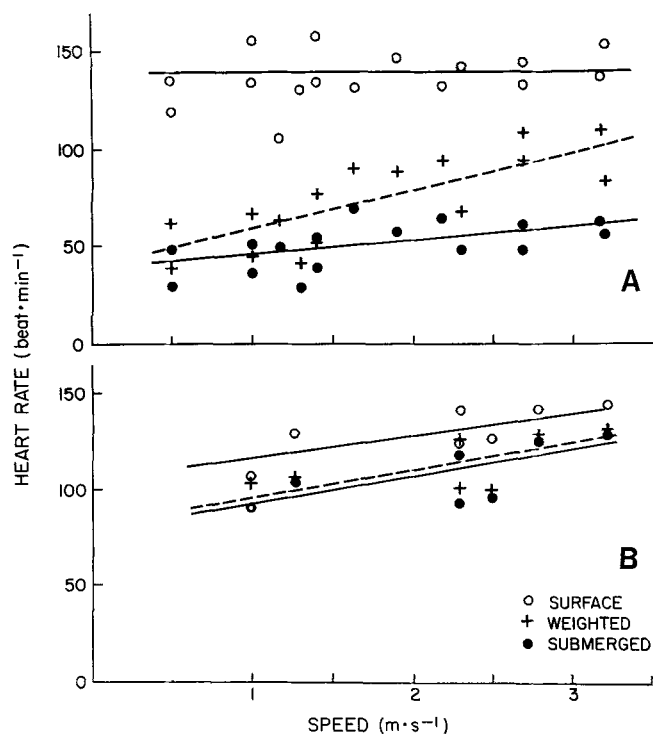
Fig. 3. A Heart rate in relation to swimming speed for three harbor seals (24, 26, 44 kg). Each point represents the average heart rate recorded in 5–7 different experimental sessions. WAHR (+) was calculated from the measured surface (o) and submerged (●) heart rates, and takes into account the percentage time surface or submerged. *Solid lines* denote the least squares linear regressions through the measured data points. The *dashed line* represents the linear regression for calculated values of WAHR. **B** Heart rate in relation to swimming speed for two California sea lions (18, 25 kg). Legend is the same as for **A**. For comparison the results for the sea lions are plotted identically to those for harbor seals. Note that the regressions for sea lions also include values for rest and swimming speeds up to 4.1 m · s⁻¹

a similar relationship for subadult sea lions swimming at 0.7–4.1 m · s⁻¹:

$$\dot{V}O_2 = 6.27 \; e^{0.48 \; speed} \quad (r = 0.90) \tag{12}$$

Discussion

Swimming physiology of pinnipeds

The metabolic demands of swimming in seals and sea lions are met by increases in oxygen consumption and average heart rate. In addition, the time available for pulmonary ventilation increases with swimming speed for seals. Although these responses may be masked by diving responses that are well developed in marine mammals, on closer inspection they are remarkably similar to those observed for terrestrial mammals. For example, a curvilinear increase in oxygen consumption with swimming speed has been demonstrated for humans (Holmer 1972; Nadel et al. 1974) and minks (Williams 1983), as well as seals and sea lions (Fig. 4). Increases in ventilation, whether brought about by changes in breathing
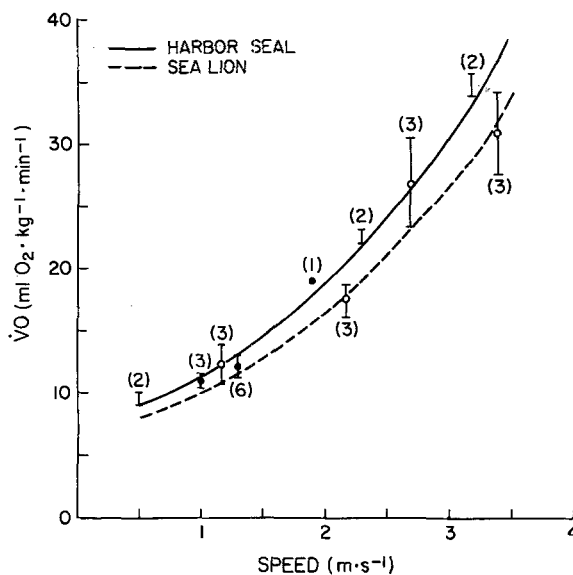
Fig. 4. Oxygen consumption in relation to swimming speed for two subadult harbor seals weighing 24 kg (●) and 34 kg (o). Points represent mean values ± 1 SE, except for n = 2 where the range is shown. Numbers in parentheses denote n. The *solid line* is the least squares exponential relationship through the data points. The *dashed line* denotes the relationship for three sea lions (BW = 22 kg) from this study and from Feldkamp (1987b)

frequency, duration of surface swimming, or tidal volume, occur during swimming in many species of terrestrial, aquatic, and semi-aquatic mammals.

Initially, it appears that the pinniped's cardiovascular response to exercise differs from that of other mammals. Heart rate typically increases as a function of exercise load in terrestrial mammals (Åstrand and Rodahl 1977). In comparison, the heart rate of swimming harbor seals was independent of work load and oscillated between approximately 50 beats · min⁻¹ when submerged and 137 beats · min⁻¹ when the animals were breathing on the water surface. The relationship between heart rate and work load for swimming sea lions seems to combine elements from the responses of both terrestrial mammals and harbor seals (Fig. 3). Although a bimodal pattern occurred in swimming sea lions, both surface and submerged heart rate increased with exercise load.

To calculate an average heart rate for pinnipeds, the percentage time spent on surface or submerged swimming must be taken into account. Based on these calculations, cardiovascular function responds predictably to work load. Figure 3 demonstrates that the WAHR of harbor seals and sea lions correlates positively with exercise load. Similar results have been reported for grey seals (Fedak et al. 1988). The WAHR of these pinnipeds also demonstrates a strong correlation with metabolic rate (Fig. 5; Fedak et al. 1988). Such correlations are consistent with the normal response for running mammals (Booyens and Hervey 1960) rather than with the inflexible bradycardia often associated with diving mammals.

The strong correlation between metabolic rate and heart rate (Fig. 5) allows us to examine the sustainable aerobic capabilities of swimming seals and sea lions.
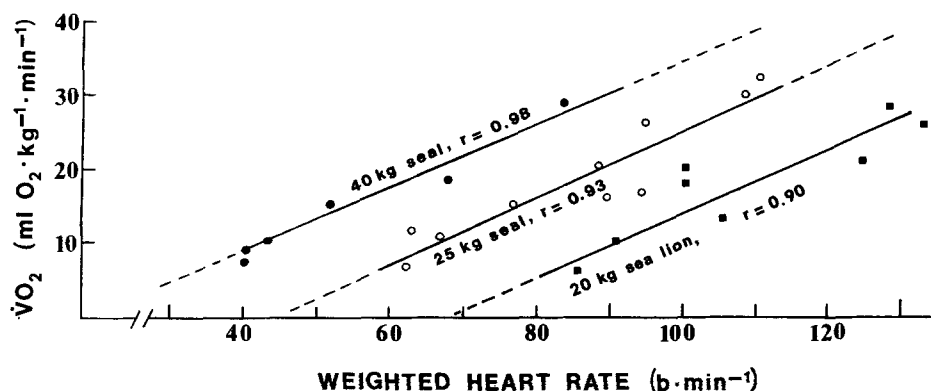
Fig. 5. Oxygen consumption in relation to weighted heart rate in seals (● BW = 40 kg, ○ BW = 25 kg) and a sea lion (■ = 20 kg). Least squares regressions were y = 0.45x − 19.42 (r = 0.93) for the larger seal, y = 0.44x − 8.42 (r = 0.99) for the smaller seal, and y = 0.45x − 30.95 (r = 0.90) for the sea lion. Metabolic rates for surface swimming (see text) were predicted from heart rate based on extrapolations of these regressions

WEIGHTED HEART RATE (b·min⁻¹)

Assuming that the relationship between heart rate and oxygen consumption remains linear over the experimental range (Fig. 5), then the predicted oxygen consumption for seals based on the measured maximum heart rate of 137 beats·min^{-1} is 52 ml O_2·kg^{-1}·min^{-1}. This predicted rate is 9 times greater than resting rates for a 23-kg seal (Davis et al. 1985), and approximates the aerobic scope of swimming seals pulling against a weighted line (Ponganis et al. 1990) or swimming in a flume while wearing drag cups (Davis et al. 1991). Similar calculations for sea lions result in a lower oxygen consumption (34 ml O_2·kg^{-1}·min^{-1}) and metabolic scope [5 times resting levels; Feldkamp (1985)]. If the aerobic scope of sea lions is actually comparable to that of seals, then these results suggest that we did not measure maximum heart rates in swimming sea lions. Possibly, the brevity of surface intervals for swimming sea lions does not permit the development of a maximum ventilatory tachycardia. Alternatively, as discussed below, these differences may reflect different strategies for oxygen loading in seals and sea lions.

In terrestrial mammals, the cardiovascular response to exercise includes a selective redistribution of blood towards the active skeletal muscles. Humans (Weibel 1984) and pigs (McKirnan et al. 1989) demonstrate a 6–18-fold increase in blood flow to the muscles of the active limbs during heavy exercise. Little change or a decrease in blood flow to the brain, kidneys, and gastrointestinal tract can occur in these subjects. Cardiac output may increase five-fold in humans performing heavy exercise, with up to 80% of the blood diverted to skeletal muscle; only 15–20% of the cardiac output is shunted to the same muscles during rest (Åstrand and Rodahl 1977).

In swimming seals and sea lions, the constant perfusion of skeletal muscles during submergence may not be as critical for supporting aerobic processes as it is in terrestrial mammals. This may explain in part the unusual patterns of heart rate (present study) and cardiac output (Ponganis et al. 1990) observed for swimming seals. Reserves of myoglobin-bound oxygen are three to four times larger in many marine mammals than in terrestrial mammals (Castellini 1981) and support aerobic metabolism during submergence (Scholander et al. 1942). In combination with blood and lung reserves, these intramuscular oxygen stores permit almost 6 min of aerobic

submergence in sea lions (Feldkamp 1985) and over 20 min of aerobic diving in large phocid seals (Kooyman 1981). The size of the oxygen store and the metabolic demands of the working muscle will limit the duration of support during submergence. During flume swimming, submergence intervals did not exceed 30 s for the seals and sea lions, and were therefore well below the predicted limit for aerobic metabolic support.

Oxygen loading during swimming

Despite the high energetic cost of surface swimming (Baudinette and Gill 1985; Williams 1989), seals and sea lions must surface long enough to replenish oxygen reserves that support aerobic metabolism during submergence. Both species remain submerged for approximately 80–90% of the time at slow swimming speeds. With increased metabolic demands at swimming speeds above 1.4 m·s^{-1}, the average time permitted for ventilation increases for harbor seals, but remains unchanged in sea lions (Fig. 1). These behavioral patterns probably reflect morphological and physiological differences between the pinnipeds. Cartilaginous reinforcement of the sea lion lung is similar to cetaceans and allows for high flow rates at low lung volumes during expiration (Drabek and Kooyman 1984). As a result, expiratory flow rates of sea lions are three times the level of humans, which shortens the time at the water surface required for the lung tidal volume exchange. Because only moderate reinforcement of the terminal airways are found in phocid seals (Denison and Kooyman 1973), the time required for oxygen loading during surface swimming may be longer than found for sea lions.

Increases in heart rate and ventilation that occur when phocid seals surface to breathe will also facilitate quick oxygen loading (Gallivan 1981; Hill et al. 1987; Fedak 1986). Harbor seals maintain comparatively high heart rates (present study) and minute ventilation (Gallivan 1981) when they surface. Consequently, the pathway for oxygen delivery is primed when the intake of oxygen is highest. The advantage of such a response becomes apparent when the natural history of the animal is considered. By rapidly exchanging O_2 and CO_2 while at the water surface, free-ranging seals can quickly replenish oxygen stores and maximize submergence time for foraging (Fedak et al. 1988).

The same arguments are applicable to free-ranging sea lions, yet the present study demonstrates that the cardiovascular and respiratory responses of sea lions are not as pronounced as those of seals. Such responses may not be necessary in the otariid, because mechanical adaptations permit rapid ventilation. To date, minute ventilation has not been measured for the swimming sea lion; therefore, more research is needed before we can directly compare oxygen loading in these two species.

Cost of transport during swimming

By remaining submerged, seals and sea lions avoid the high drag and elevated energetic costs of surface swimming. For example, the minimum cost of transport for surface swimming sea otters was $12.6 \, \text{J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$, 12 times the predicted value for a similarly sized salmonid fish (Williams 1989). Other swimming mammals including minks (Williams 1983), muskrats (Fish 1982), and humans (Homer 1972) demonstrate transport costs that approach 20 times predicted values. We found that the minimum cost of transport was $2.3 \, \text{J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$ for sea lions and $3.6 \, \text{J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$ for seals. These costs are only 2.5–4.0 times greater than predicted values for salmonid fish (from Brett 1964).

Although seals and sea lions use different means of propulsion (Feldkamp 1987a; Fish et al. 1988), the minimum cost of transport is similar for these two species. This similarity may be attributed in part to aerobic efficiency, the ratio of mechanical power output to metabolic power input (Table 1). Over the range $1.0-3.0 \, \text{m} \cdot \text{s}^{-1}$, the aerobic efficiency of a 21-kg sea lion increased with speed and was within 3% of the values for a 24-kg harbor seal.

In summary, the ability to maintain aerobic metabolism during submergence requires physiological adaptations that are usually associated with a diving response. For seals this includes a pronounced bradycardia during submergence, tachycardia during surface swimming, and

changes in ventilatory patterns. The diving response appears less pronounced in swimming sea lions. Nevertheless, these adaptations contribute toward a reduction in energetic costs during swimming in both harbor seals and sea lions.

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Table 1. Mechanical aerobic efficiency for a 24-kg harbor seal and a 21-kg sea lion. Total body drag was determined by towing the animals through a water channel as described in Williams and Kooyman (1985). Values for oxygen consumption are from this study and Feldkamp (1987b). Mechanical power output (W) was calculated from the product of towed drag (newtons) and water speed ($\text{m} \cdot \text{s}^{-1}$). $\dot{V}O_2$ was converted into metabolic power input (W) by assuming a caloric equivalent of $4.8 \, \text{kcal} \cdot 1 \, O_2^{-1}$ and a conversion factor of $1.163 \, \text{W} \cdot \text{kcal}^{-1} \cdot \text{h}^{-1}$. Aerobic efficiency is equal to the ratio of mechanical power output and metabolic power input

Speed ($\text{m} \cdot \text{s}^{-1}$)	Mechanical power output (W)		Metabolic power input (W)		% Aerobic efficiency	
	Seal	Sea lion	Seal	Sea lion	Seal	Sea lion
1.0	5.24	2.49	91.48	75.66	5.7	3.3
2.0	26.70	18.33	149.44	122.27	17.9	15.0
2.6	49.48	39.02	200.56	163.13	24.6	23.9
3.0	69.27	58.93	244.05	197.66	28.4	29.8

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