J Comp Physiol B (1990) 160:473–482

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

Cardiac output and stroke volume in swimming harbor seals

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Accepted July 23, 1990

Summary. Cardiac output was measured by the thermodilution method in three young harbor seals, at rest and while swimming up to the maximum effort for which they could be trained. Stroke volume was determined by counting heart rate simultaneously with determination of cardiac output. Cardiac outputs varied widely between surface breathing (7.8 ml · kg^{-1} · s^{-1}) and breath-holding while swimming under water (1.8 ml · kg^{-1} · s^{-1}). Stroke volume while at the surface was almost twice the volume while submerged. Surface cardiac output was always near maximal despite work effort, whereas submerged cardiac output gradually increased at higher work efforts. The cardiovascular performance of seals at the maximum MO_2 we could induce from them is equivalent to that of the domestic goat.

Key words: *Phoca vitulina* – Thermodilution – Percutaneous – Pulmonary artery – Breath-hold

Introduction

Cardiovascular function in an exercising animal can be best assessed by the measurements of cardiac output (CO) and the difference between arterial and mixed venous blood oxygen content. These measurements directly indicate the rate of oxygen transport and the amount of O_2 extracted in order to meet tissue metabolic needs. The cardiac output (CO) is determined by the heart rate (HR) and the stroke volume (SV). Due to the importance of these variables, much attention has been given to them in the course of exercise studies of humans and other terrestrial mammals that ventilate in a "conventional" way while exercising. In this context, conventional means breathing regularly and without interruption.

Few studies have addressed these cardiovascular variables in aquatic vertebrates during swimming exercise where respiration is unconventional. In this case, unconventional means interrupted breathing while the animal swims submerged. Interrupted breathing (breath-holding) is advantageous at high swim velocities to avoid the much greater drag induced by surface travel compared to submerged swimming (Williams and Kooyman 1985). This introduces the unusual situation into an exercise period in which the animal will breath-hold for short periods even when the oxygen needs are great. The nature of cardiovascular responses to this unusual respiratory regime has been reported only twice; in an exercise study in which heart rates were measured in gray seals swimming up to a level in which metabolic rate was five times the sleeping rate (Fedak 1986), and in the companion report to this one involving harbor seals and sea lions (Williams et al. 1991). These reports extend numerous studies of HR responses in mammals forcibly submerged while statically restrained, and a few studies of animals diving voluntarily in the wild or while captive in pools [see Butler and Jones (1982) and Kooyman (1989) for reviews]. In most of these studies, it is implied that HR is a good indicator of general cardiovascular responses. However, if HR is to be used as an indicator of CO, SV must be constant or the amount of change known.

Due to the difficulty of the measurements, estimates of CO and SV for aquatic animals are sparse. All six reports for diving mammals (Blix et al. 1976; Blix et al. 1983; Elsner et al. 1964; Murdaugh et al. 1966; Sinnett et al. 1978; Zapol et al. 1979) and the two for birds (Folkow et al. 1967; Jones and Holeton 1972) have examined only resting and forcibly submerged animals, with one exception in which a sea lion was trained to immerse its head in a bucket of water (Elsner et al. 1964).

In these studies there have been conflicting results in regard to SV. In mammals, three papers report that SV remains constant during forced and trained submersion

Abbreviations: *CO* Cardiac output; *HR* Heart rate; *SV* Stroke volume; MO_2 Metabolic rate; *FS* Forced submersion; *V* Velocity; C_{DF} Frontal drag coefficient; *CV* Cardiovascular

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while the three others report that it declines by as much as 50%. The two studies on birds are also not in accord. One reports a decline (Folkow et al. 1967) and the other an increase (Jones and Holeton 1972) of about 15% SV during submersion. These various papers are reviewed further in the discussion.

The purposes of this investigation were: 1) to determine control values for CO and SV during resting periods when it is normal for the seals to breathe arrythmically with short to extended apneic and eupneic intervals, 2) to measure the changes in CO and SV during graded levels of exercise when surfaced and submerged, 3) to compare the SV of both surface and submerged seals to previous studies, and 4) to compare the results with terrestrial mammals of similar body mass but different aerobic capacities.

Materials and methods

Three young harbor seals, *Phoca vitulina*, ranging in body mass from 28 to 39 kg were conditioned and trained to swim in the UCSD Hydraulics Laboratory 1 $m^2 \times 20$ m water channel. This system is described elsewhere (see below). All seals were hand-raised from newborns and were tame. They were kept in condition by being required to swim laps at 1–3.5 $m \cdot s^{-1}$ in an annular tank (Williams and Kooyman 1985). The conditioning was supplemented by regular exercise sessions in the water channel.

During an exercise experiment, water flow speed was 1.0 $m \cdot s^{-1}$ in the channel. To increase the seal's work level, weights were attached to a line connected to a strap epoxied to the aft third of the seal's back. A full data set was obtained on two of the seals, and only resting values on the other. Another complete CO data set was obtained on one seal (M) on another date; SV data were not obtained, however. For an effective experiment the seals had to swim with simple ascending and descending maneuvers. Those that rolled or looped were not satisfactory since they quickly tangled and kinked wires and catheters. The older the animal, the more likely that unsuitable behavior would develop. The exercise data sets presented represent three successful exercise experiments.

The oxygen consumption values were obtained as previously described (Davis et al. 1985). In brief, the seal swam in a test section covered with a plexiglas dome. Metabolic rate ($\dot{M}O_2$) was measured through an open system in which differences in inflow and outflow fractional oxygen content were measured with an AEI oxygen analyzer, and the $\dot{M}O_2$ calculated with an on-line Apple II computer. Differences from the earlier procedures were that calculations were done every 10 s rather than every minute and weights were attached and removed from the drag line to alter O_2 consumption. These weights ranged from 0.5 to 3.5 kg. Resting $\dot{M}O_2$ was measured with the same technique in the one seal (M) which rested under the dome with minimal activity.

Duration of the runs depended on the size of the load. Most were more than 5 min, but at the highest work effort the weight might be attached for a shorter period but no less than 3 min. This permitted the analysis to achieve a steady state before removal of the weight.

During these exercise periods flipper stroke frequency, submersion time, and surface duration were recorded. The two surface ECG electrodes mounted near the axillae were waterproofed by means of the glue which attached them to the body. Heart rates were obtained from a strip chart recorder, or hand-counted from an oscilloscope.

Cardiac outputs were determined by the thermodilution technique. General anesthesia with isoflurane similar to that previously described by Sinnett et al. (1981) was used in order to percutaneously insert an Edwards Swan-Ganz Paceport catheter into the superior vena cava. The advancement of the catheter to the pulmonary artery was assisted by fluoroscopy and proper placement was ascertained by the appearance of a diagnostic pressure waveform. To our knowledge, this is the first time such a placement has been done on seals without surgery. Anesthesia during this procedure, which included testing the catheter and preparing the external portion of the catheter for the exercise session, lasted about 3–4 h. Between 5 and 8 h were allowed for recovery before the seal was swum in the channel.

It was considered that the effects of isoflurane had resolved by the time of the CO studies. As during halothane anesthesia (Sinnett et al. 1981), CO was depressed during isoflurane anesthesia. Mean CO and SV for the seals were 2.15 $ml \cdot kg^{-1} \cdot s^{-1}$ and 1.3 $ml \cdot kg^{-1}$ ($n=15$) for all the animals at end tidal isoflurane concentrations of 0.70–1% (determined by Puritan Bennett Volatile Agent Analyzer). Emergence from anesthesia was accompanied by an increased CO. Apneic ventilatory and HR patterns returned gradually as the seals awakened and became more responsive.

Iced saline at about 3 °C was used as the injectate for resting CO. The injectate temperature for COs obtained from animals in the flume was at the flume water temperature of 15–20 °C (range of temperature values from different days) due to the 2-m length of catheter necessary for connection to the free swimming seal. The dilution curve from the 10-ml injectate was plotted by an Edwards Model 95820A CO computer, and the area under the curve was used to compute the CO. The catheters were factory calibrated and appropriate constants for different injectate temperatures were employed. Only those values for which normal thermodilution curves occurred were used in subsequent data analysis.

The injection system during exercise consisted of a 2-m length of high pressure tubing extending to a syringe and stopcock, which, in turn, were attached to a reservoir bag of injectate. The injectate was maintained for several hours at flume temperature in order to allow temperature equilibration. Thermistor cable connections were waterproofed with epoxy glue. The entire system was kept under water during the study so as to avoid temperature changes. This system (with injectate at flume temperature) was tested at COs of 2, 8, and 15 $l \cdot min^{-1}$ in the Edwards Laboratory; the percentage errors in CO determinations were within the 10% factory specifications at 2 and 8 $l \cdot min^{-1}$. There was a (+) 13% error at 15 $l \cdot min^{-1}$. Normal saline injectate was used because of simultaneous blood chemistry studies on these seals. It is realized that the calculations of the Edwards computer assume the specific gravity and specific heat of 5% dextrose in water, but substitution of saline results in only 2% difference in results. Consequently, no correction was made for this substitution.

SV was calculated from HRs obtained simultaneously with the CO measurement. At the end of the study the seal was restrained and the catheter was removed, and pressure was immediately applied manually for 10 min at the insertion site. Prophylactic cephalosporin antibiotic coverage was administered intravenously during the experiment, and p.o. for 5–7 days afterwards. No complications to the procedure were noted.

Surface and submerged times were measured with a stopwatch by timing the animals as they swam in the glass-walled flow channel. The $\dot{M}O_2$ was measured concurrently.

Results

Resting

Cardiac output while resting was obtained when the seals were out of water. This was after recovery from anesthesia but before the start of a swim period, and after removal from the swim channel shortly before conclusion of the experiments. The CO was obtained when the restrained seals were relaxed enough that the usual

Table 1A. Cardiac outputs for 3 young harbor seals while resting and breathing arrythmically. Values are mean ± standard deviation (sample size). Student's *t*-test showed significant difference at $P<0.01$ for individual CO of eupnea and apnea

Seal	Mass (kg)	Mean eupneic cardiac output ($ml \cdot kg^{-1} \cdot s^{-1}$)	Mean apneic cardiac output ($ml \cdot kg^{-1} \cdot s^{-1}$)	Scheffe procedure Significantly Different (0.05) * = apnea; + = eupnea			
				F	M	R_1	R_2
F	35	3.3±1.3 (14)	1.7±0.3 (4)				
M	31	4.1±1.3 (53)	–				
R_1	39	4.7±1.3 (14)	2.2±0.4 (30)	+			
R_2	34	5.4±1.3 (26)	3.1±0.5 (22)	+*	+	*	

Table 1B. Stroke volume measured simultaneously with the cardiac outputs. Statistical analyses are the same. Student's *t*-test showed significant differences at $P<0.05$ for individual SV of eupnea and apnea

	Mean eupneic stroke volume ($ml \cdot kg^{-1}$)	Mean apneic stroke volume ($ml \cdot kg^{-1}$)	F	M	R_1
F	2.5±0.45 (12)	2.0±0.29 (4)			
M	3.1±0.97 (53)	–			
R_1	3.0±0.75 (9)	1.8±0.31 (7)			

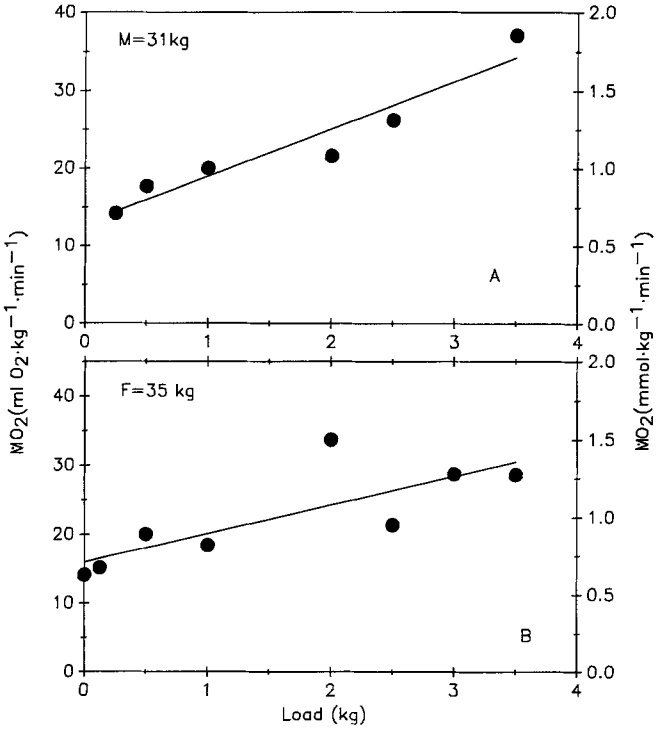

Fig. 1A, B. Oxygen consumption of seals M (**A**) and F (**B**) while swimming and pulling a load to increase swim effort. One mean standard error of estimate (SE) of MO_2 falls within the circles. Seal M mass was 31 kg; seal F mass was 35 kg. The regression equation for M and F are: MO_2 ($ml\ O_2 \cdot kg^{-1} \cdot min^{-1}$) = 12.9 + 6.1 load; MO_2 = 15.96 + 4.16 load, r^2 = 0.91 and 0.65, respectively. Note for and following figures the units of MO_2 in regression equations are expressed in $ml\ O_2 \cdot kg^{-1} \cdot min^{-1}$

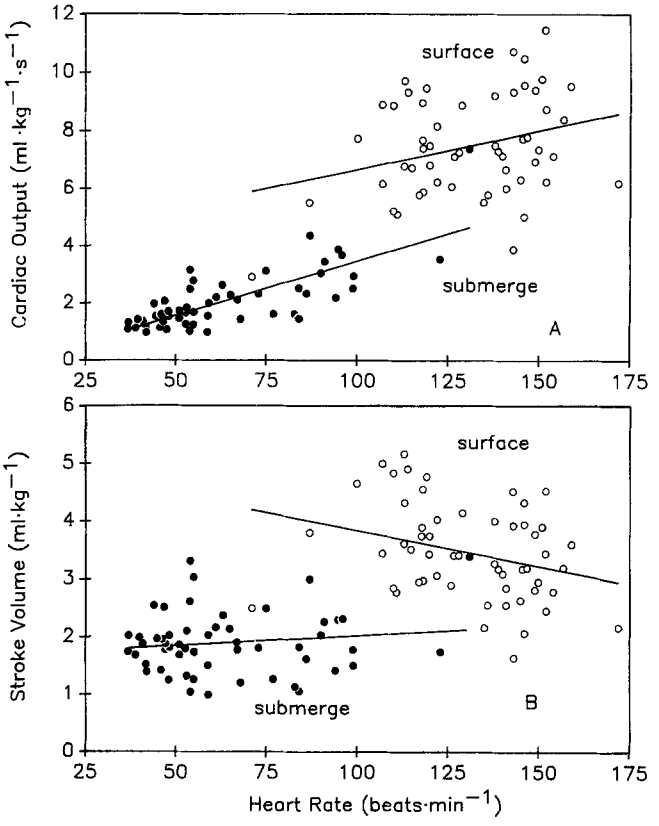

Fig. 2A, B. The relationship of cardiac output (**A**) and stroke volume (**B**) to heart rate during surface and submerged swimming. For cardiac output data, submerged and surface correlation coefficients are 0.77 and 0.30; for stroke volume data, 0.14 and −0.30

arrhythmic respiration prevailed. Seal M, however, never developed arrhythmic respirations while restrained. In addition, it should be noted that the resting CO observed on R at 34 kg were obtained 3 months later than that on the same animal at 39 kg. This weight loss was secondary to seasonal fluctuation, but contributes to elevated values for R at 34 kg.

The CO means for both eupnea and apnea were different among the three seals (one-way ANOVA, followed by Scheffe's procedures, Table 1). Eupneic COs were significantly greater than apneic COs in each seal (Student's *t*-test, $P<0.01$). Similar analysis showed that eupneic SV were also greater than apneic SV in the two seals in which data were available ($P<0.05$).

Work effort

The increase in MO_2 in relation to towed mass is expressed by the regression equations in Fig. 1. A comparison of seals M and F at 31 and 35 kg (body weight), respectively, shows the similarity in results between seals. The increase in MO_2 was rather linear with r^2 values for M and F equal to 0.91 and 0.65, respectively.

Resting MO_2 in M was 4.1 $ml\ O_2 \cdot g^{-1} \cdot min^{-1}$, yielding a 9-fold scope of MO_2 between rest and the maximal exercise values attained.

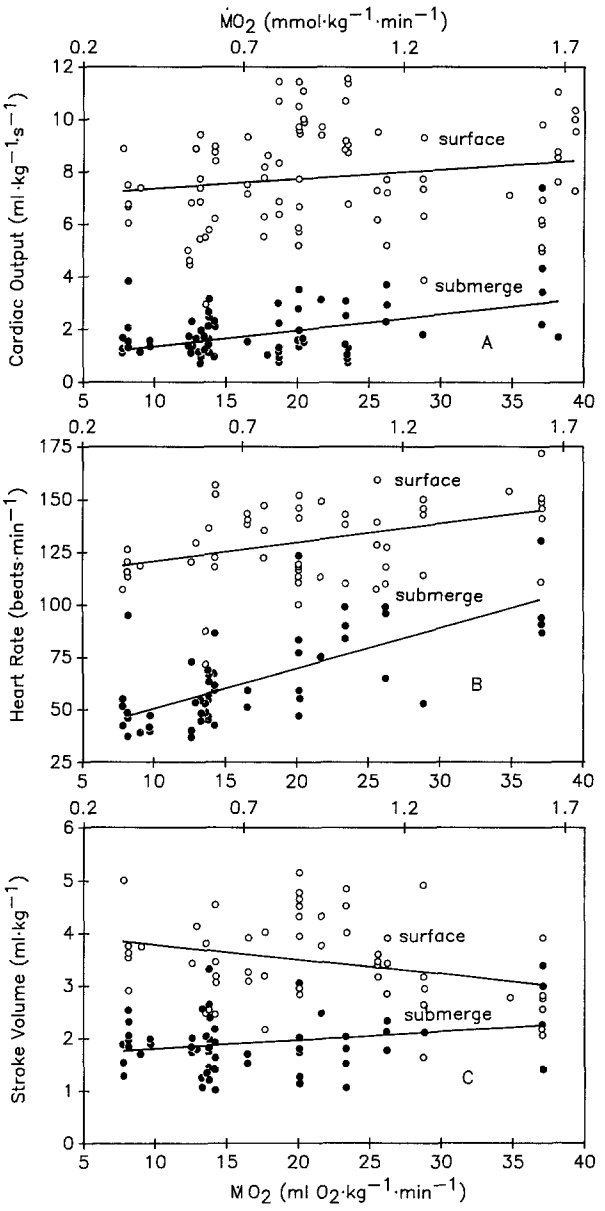

Fig. 3A–C. The relationship of cardiac output (**A**), heart rate (**B**), and stroke volume (**c**) to oxygen consumption for all exercise sessions ($n=3$ for cardiac output, $n=2$ for heart rate and stroke volume). The r^2 values for surface and submerged CO data were 0.03 and 0.19; for SV data, 0.09 and 0.06; for HR data, 0.16 and 0.48. Regression equations for data with $r^2>0.1$ are: CO (sub)$=0.74+0.06$ ($\dot{M}O_2$); HR (srf)$=111+0.92$ ($\dot{M}O_2$); HR (sub)$=31+1.9$ ($\dot{M}O_2$)

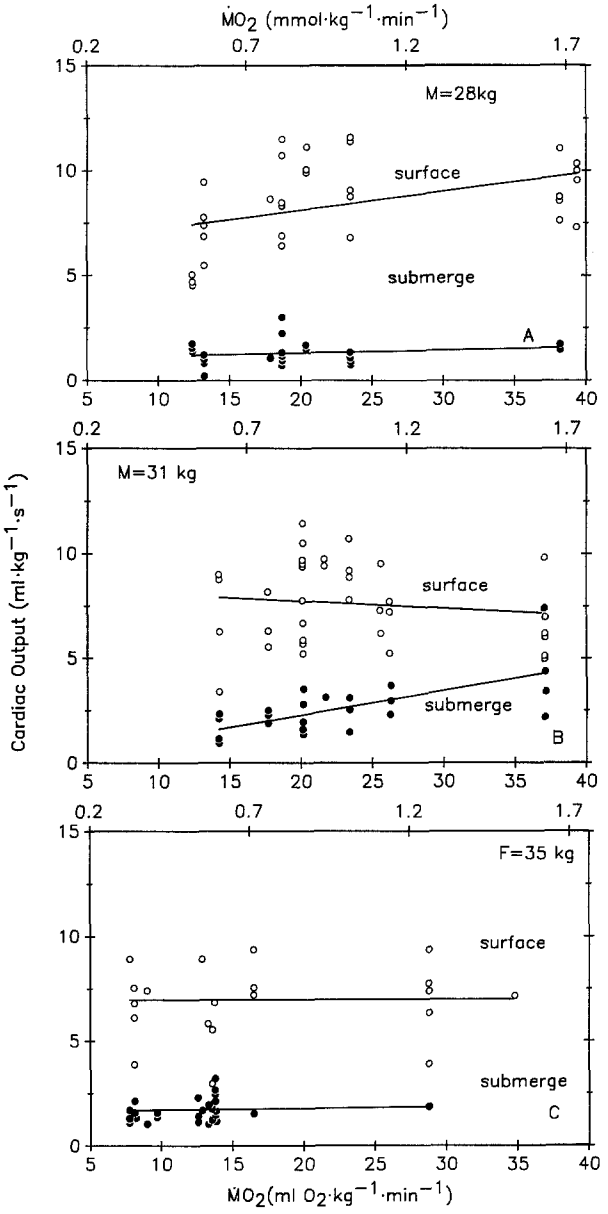

Fig. 4A–C. The relationship of cardiac output to oxygen consumption while swimming in seals M and F. Surface and submerged r^2 for M (28 kg)$=0.19$ and 0.05, respectively M (31 kg)$=0.06$ and 0.42, and F$=0.0006$ and 0.002, respectively. The regression equation for M (28 kg) is CO (srf)$=6.23+0.093$ $\dot{M}O_2$, and M (31 kg) is CO (sub)$=-0.089+0.12$ $\dot{M}O_2$

Surface and submerged cardiovascular responses

Heart rates, CO, and SV varied dramatically between surface and submerged states, as shown in Fig. 2. Despite variability and changes with workload, mean surface CO (7.8 ml · kg^{-1} · s^{-1}) and SV (3.5 ml · kg^{-1}) were significantly different ($P<0.001$, Student's t-test) from mean submerged CO (1.8 ml · kg^{-1} · s^{-1}) and SV (1.9 ml · kg^{-1}).

The correlation coefficient of submerged CO and HR was highly significant ($P<0.01$) at 0.77; the surface correlation was weak (0.30) but still significantly different from 0 ($P<0.05$). Surface stroke volume similarly correlated weakly with heart rate (-0.30, $P<0.05$), but submerged SV showed no correlation with heart rate (0.14, $P>0.05$).

Work and cardiovascular response

Review of the combined cardiac output data from three exercise sessions revealed no relationship of surface cardiac output and $\dot{M}O_2$ (Fig. 3A). Submerged cardiac output, however, increased slightly with workload, although the regression showed much variability

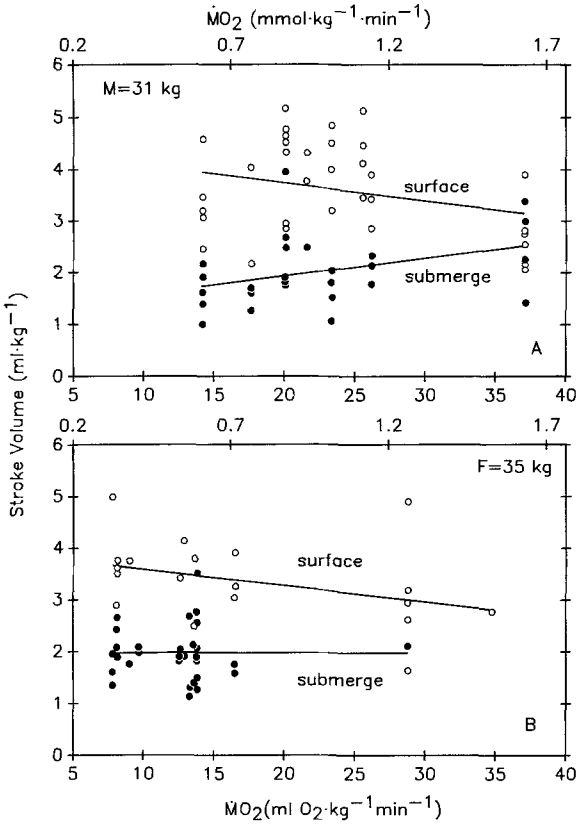

Fig. 5A, B. The relationship of stroke volume to oxygen consumption in harbor seals M (**A**) and F (**B**). Surface and submerged r^2 values for M = 0.11 and 0.22 and for F = 0.15 and 0.001, respectively. The regression equations for M are SV (srf) = 4.39–0.04 (MO_2); SV (sub) = 1.02 + 0.04 (MO_2); for F, SV (srf) = 3.91–0.03 (MO_2)

($r^2 = 0.19$). Heart rate was successfully recorded during two sessions, and, as MO_2 increased, submerged HR increased more significantly than surface HR (Fig. 3B). Again, however, variability was considerable (surface $r^2 = 0.16$, submerged $r^2 = 0.48$). The regression of submerged SV to MO_2 showed no relationship (Fig. 3C); although surface SV slightly decreased with MO_2, the regression was again highly variable ($r^2 = 0.09$).

Individual regression analyses of the cardiac output and stroke volume data are given in Figs. 4 and 5. In two of the seals (F and M–28 kg), submerged cardiac output was independent of workload, while in M–31 kg it increased primarily due to high values at the highest workload. Surface cardiac output, in this seal (M–31) also decreased with workload, again primarily due to relatively low values at the highest workloads. In contrast, in the other two seals, surface CO remained constant or slightly increased with workload. Stroke volume analysis in M–31 was similar to that for its CO; the submerged and surface data appear to merge at higher workloads, primarily due to similar values at the highest workload. In F, submerged SV did not change with workload. Surface SV appears to decrease as work effort increases in F; the slope, however, is not significantly different from 0 ($P > 0.05$).

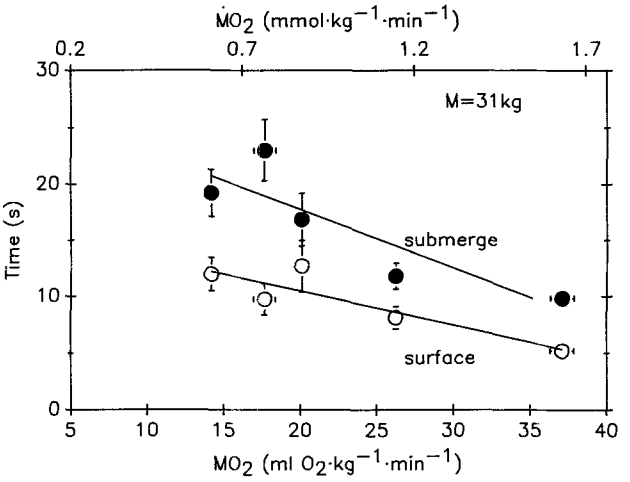

Fig. 6. The relationship of mean surface and submerged time in seconds for seal M. These are mean values because the sample sizes are too large for a scatter plot. Up and down N from left to right are for up: 32, 27, 29, 33, 37, and for down: 61, 26, 30, 32, 36. The N for MO_2 in increasing order are: 129, 60, 65, 92, 17. The SE falls within the circle of those that show no brackets. The regression equations are: time (sub) = 28.0–0.52 (MO_2), $r^2 = 0.76$; time (srf) = 16.5–0.30 (MO_2), $r^2 = 0.79$

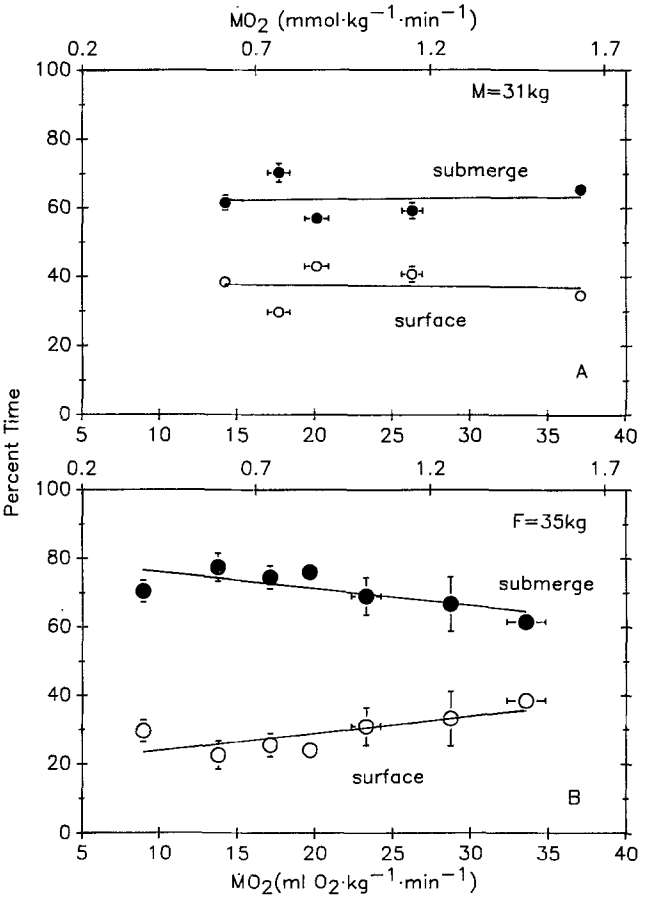

Fig. 7A, B. The relationship of surface and submerged time as a percent of total time to oxygen consumption in swimming harbor seals M (**A**) and F (**B**). The SE is the same as Fig. 4. The surface and submerged r^2 for M are 0.004. The regression equations for F are: srf% time = 18.9 + 0.50 (MO_2), $r^2 = 0.56$; sub% time = 80.9–0.49 (MO_2), $r^2 = 0.56$

Surface and submerged times

As MO_2 increased, M decreased both surface and submersion times (Fig. 6), so that mean submersion time was close to 10 s at the highest swim effort. In seal F, submerged time was 75% total time at low workload, decreasing to 60% at higher levels; in M, the percent submerged time was constant at about 60% (Fig. 7A, B).

Discussion

Exercise data collection

Requirements for accurate thermodilution CO determinations include proper catheter position, adequate mixing of injectate, and steady state conditions (Ganz and Swan 1972; Levett and Reploggle 1979; Stevens et al. 1985; Wessel et al. 1971). During exercise sessions, catheter placement was confirmed by examination of pressure tracings from the pulmonary artery and right atrial catheter ports. In the seals for which data are presented, examination of pulmonary artery temperature did not reveal any temperature changes either secondary to rapid ventilation or to different temperatures of returning venous blood. In addition, sham CO determinations were made with no injection in order to confirm a 0 value and a constant baseline temperature. Random checks of pulmonary artery temperature did not reveal significant large fluctuations in body temperature ($m = 37.6$ °C, $SD = 0.30$; $n = 19$ on 3 different animals) during the exercise sessions. During initial ventilations at the surface during exercise, or during the first breath after a long resting apnea, occasional large COs and SVs were calculated. Catheter placement was confirmed in many such instances and thermodilution curves appeared normal. These values were even obtained with the use of iced injectate at rest, and were reproducible by timing the injection properly in anticipation of the end of apnea. Such apparent errors could be due to lack of steady state at this point (Ganz and Swan 1972; Stevens et al. 1985; Wessell et al. 1971). On the other hand, post caval sphincter relaxation, a large increase in venous return, and distention of the pericardial venous plexus may contribute to such values. Consequently, we attempted to make eupneic and surface CO determinations in the middle of the breathing cycle, and apneic or submersion CO determinations in the middle of the breath-hold. In addition, the cardiac output computer calculation had to be completed prior to or very close to the start of the next breathing phase. It is thus thought that the requirements for accurate thermodilution CO measurements were achieved even though a continuous steady state at each work level did not exist during the rapidly fluctuating surface and submergence conditions.

We feel that the manufacturer's verification of computation constants and flow calculations and the use of only smooth washin-washout thermodilution curves provided accurate cardiac output determinations. At very low heart rates as seen in forced submersions (Sinnett 1977) thermodilution curves become prolonged and irregular; this problem was not observed in our data, probably because the lowest heart rates were in the range 40–50 beats · min^{-1}, much higher than during forced submersions. The accuracy of these thermodilution determinations is thus approximately 10%, similar to that reported by the manufacturer and in clinical studies (Levett and Reploggle 1979; Stevens et al. 1985).

The seals' swimming behavior at the highest workloads may still have affected our results. As shown in Fig. 6 and 7, both surface and submersion times decreased with workload. This was especially significant in M–31 kg, with mean submersion times of only 10 s at the highest workload. This limited the number of data points at this workload, since data was collected only when the animal was actively swimming, and either entirely submerged or surfaced for the cardiac output calculation. Despite these efforts, the surface and submerged data appear to merge in this animal. This may reflect a mixture of surface and submerged responses due to the seal's rapid surfacing and submergence pattern.

The surface exercise data (HR, CO, SV) are much more varied than the submerged data. This greater variability is at least partly secondary to the phase of the respiratory cycle during which the CO injectate was made. The seals swam at or just below the surface with frequent intermittent breaths during the surface period, and it was impossible to always inject at the same point in the respiratory cycle, or to expect the seal always to have the same breathing pattern after the injection. Such variation in results has been documented in clinical studies (Stevens et al. 1985).

The heart rate response to increased work effort, although only measured during a short interval of surface or submerged period, is similar to that found in the more detailed studies of Williams et al. (1991) and Fedak et al. (1986, 1988). Accordingly, this response will not be considered further. As shown in Fig. 2 and discussed above, cardiac output did correlate with heart rate.

Comparison to other aquatic vertebrates

Previous measurements of CO and SV in aquatic animals are sparse for restrained animals, and there are none for free and active animals. This may seem unusual considering the importance of CO as a direct measure of cardiovascular performance, but it is not surprising given the difficulty of the procedure. The following discussion briefly reviews previous studies and the bases for published discrepancies in CO and SV results in diving animals. The review is important in order to judge what has caused a discrepancy in the measurement of SV which, in turn, influences the interpretation of the many HR reports published on forced submersion and diving.

The most detailed study was that of Sinnett et al. (1978) in which he measured CO and SV in young harbor seals (average mass 45 kg). The method of measurement was similar to this report except minor surgery was required to expose the internal jugular for catheterization,

and the animals were restrained and static for all measurements. The mean resting CO during spontaneous breathing was 12 l · min^{-1} or 4.4 ml · kg^{-1} · s^{-1} compared to the highest average of this study for R_2 of 5.4 ml · kg^{-1} · s^{-1} and the lowest of 3.3 ml · kg^{-1} · s^{-1} for F (Table 1). During surface swimming, the highest average CO during breathing was 8.4 ml · kg^{-1} · s^{-1} for M (28 kg). The average CO during forced submersion (FS) was 0.7 ml · kg^{-1} · s^{-1} (Sinnett et al. 1978) compared to means of 1.2–2.7 ml · kg^{-1} · s^{-1} in animals swimming submerged (Fig. 4a, b, c).

The SV of seals restrained and dry just before FS was 2.8 ml · kg^{-1} (Sinnett et al. 1978). In the present study, resting animals out of the water had an average eupneic SV of 2.5 to 3.1 ml · kg^{-1} (Table 1). The apneic and eupneic stroke volume in each resting seal were significantly different (Student's *t*-test). During swimming and breathing the SV was about 3.5 ml · kg^{-1} (Fig. 5a, b). During FS the SV fell to about 67% of the presubmersion level (Sinnett et al. 1978). During swimming the submerged SV was 50–70% of the breathing SV, except possibly at the highest swim effort where the two values may be a mixed analysis of the breath-hold and ventilation (Fig. 5a, b). The possibility of a mixed analysis of surface and submerged cardiovascular responses during short submergence times at high workloads is reinforced by multiple past observations of increased HR during dives just prior to surfacing (Murdaugh et al. 1961; Fedak 1986; Fedak et al. 1988; Hill et al. 1987; Williams et al. 1991).

Working on slightly smaller seals (15–27 kg) of the same species, Murdaugh et al. (1966) obtained 43 measurements of CO. The seals were restrained, and the dilution rate of indocyanine green was measured after injection into a peripheral vein. The pre and post FS CO of 5.2 l · min^{-1} and 8.3 l · min^{-1}, respectively, were approximately the same as those of Sinnett et al. (1978) and of this report. The SV from 4 seals ranged from 4 to 40 ml; however, it was reported that SV was constant over the range of CO measured.

Three other studies on seals have reported CO and SV measurements. Zapol et al. (1979) estimated CO and SV measurements by thermodilution (1 seal) and by radioactive microsphere dilution (4 seals) in adult Weddell seals of approximately 300–400 kg body mass. The mean CO values were 1.6 ml · kg^{-1} · s^{-1} while resting and 0.2 ml · kg^{-1} · s^{-1} when forcibly submerged. The SV during FS declined by 53% from 1.8 ml · kg^{-1} to 0.85 ml · kg^{-1}. In contrast, one value from a six-month-old gray seal of unreported body mass was stated to have a constant SV during ventilation and FS (Blix et al. 1976). However, in a later paper Blix et al. (1983), using radioactive microsphere techniques, noted that after 5 min of FS the SV had declined by 43% from the predive level in young spotted seals and gray seals of about 30–40 kg body mass. Resting CO and SV were again similar to those found in this study.

The last study to report is that conducted on a distinctly different diving mammal, a 30-kg sea lion trained to immerse its head in a bucket. By estimating CO from a surgically implanted Doppler flowmeter cuff attached to the pulmonary artery, it was concluded that SV was constant during head immersions of about 1/2 min (Elsner et al. 1964).

During the forced phocid submersions reported above, cardiac output was always less than in the submerged swimming data of our study. This is explained by the greater decrease in HR and SV in those studies. The mechanism for SV reduction probably involves decreased venous return and cardiac filling (Harrison and Tomlinson, 1956; Elsner et al. 1971) and possibly a decreased ejection fraction secondary to a decreased cardiac inotropic state (Kjekshus et al. 1982; Elsner et al. 1985).

In concluding this brief discussion of other reports on CO and SV, in some cases there are few data to support conclusions of either reduced or constant SV during FS. All studies involved restrained or static animals. However, three studies, including two using similar procedures (Sinnett et al. 1978; Zapol et al. 1979; Blix et al. 1983), agree with our observations that SV declines during breath-holding.

Metabolic rate work effort, and equivalent swim velocities

In two prior studies, percent submersion time decreased as $\dot{M}O_2$ increased (Fedak 1986; Williams et al. 1991). Theoretically, as $\dot{M}O_{2\,max}$ is approached, one might expect submersions to disappear. This pattern, however, was not observed even though seals were encumbered with significant loads. Rather, both surface and submersion durations decreased with the percentage time submerged remaining almost constant (Fig. 7). The periods at the surface or submerged did become progressively shorter (Fig. 6) with frequent interrupted breaths on the surface. In addition, at the highest workload, the seals eventually resorted to diving to the back grate of the test section and resting under water rather than incurring the much greater drag (Williams and Kooyman 1985) and work at the surface. It may be that the additional encumbrances placed on our seals caused them to avoid the surface more than those animals used in the studies of Fedak et al. (1986) and Williams and Kooyman (1985), in which the animals were much less encumbered. Indeed in Williams' study, drag cups were used which inflated when the animal submerged and collapsed at the surface, thus causing some decrease in drag. It should be noted also that when swimming at maximal effort, the seals used all appendages; not only was there rapid sculling with the hind flippers, but "foreflipper drive" was in action with ipsilateral stroking from forward to aft of the foreflipper as the hind flipper thrusts laterally. Under normal circumstances, this sort of swimming is seen only during short bursts of acceleration.

For a perspective on how much effort was involved in the flume experiments, some swim velocities that would induce comparable drag are calculated. The drag equation is:

$$D = 1/2\ pAV^2C_{D_F}$$

where p is density of the water, A is frontal area of the seal, V = velocity and C_{D_F} is the frontal drag coefficient.

Rearranging:

$$V = \frac{2D}{pFC_{D_F}}$$

We assume a freshwater density of 1000 kg · m^{-3}, a frontal area (F) of 0.069 m^2, C_{D_F} of 0.038 at 1.8 m · s^{-1} (Williams and Kooyman 1985) and the maximum load of 3 kg or 29.4 N. The velocity calculated in this way is 4.7 m · s^{-1}. This is a maximum because the C_{D_F} used was for an animal gliding in calm water. It was assumed also that the induced load is the major part of the total drag and the drag due to turbulent flow in the flume and the motion of swimming are a small part of the total. If, on the other hand, we use a C_{D_F} from a towed animal at 1.2 m · s^{-1} and following a turbulent wake, then $C_{D_F} = 0.14$ and velocity is calculated to be about 2.5 m · s^{-1}. Similarly, if we match the force of the drag load to that determined for a 33-kg seal towed at known velocities (Williams and Kooyman 1985), the estimate of speed is 2.5–3.0 m · s^{-1}. At this point drag force is rising so rapidly that it is unlikely the seal could swim at much higher speeds for any duration other than for a short burst.

Since we were able to collect exercise data on only two seals which were rehabilitated after they beached themselves, the maximal $\dot{M}O_2$ values attained by these seals should not be considered the $\dot{M}O_{2\,max}$ (also expressed as $\dot{V}O_2$) for the species. The metabolic scope, as measured in M, however, was nine-fold. This is typical of many terrestrial mammals (Taylor et al. 1981) but certainly less than such elite, aerobic athletes as dogs and horses (Taylor et al. 1987). It is similar to that observed in other harbor seals by Davis et al. (1991), and, as far as we are aware, this is the highest metabolic scope observed in a marine mammal.

Comparison of cardiovascular (CV) performance to other exercising animals

Recently, Taylor et al. (1987) measured CV capacities and responses to graded exercise up to maximum O_2 consumption in "elite" and "normal" athletic mammals. These were the domestic dog and goat, respectively. They utilized the Fick principle with sampling catheters in the pulmonary artery and aorta, in order to measure CO. This study was ideal for comparison with the present investigation because the animals were of similar mass of about 30 kg.

The seal's CO during surface ventilation was always near maximum; therefore, this value (about 8 ml · kg^{-1} · s^{-1}) is considered the maximum CO of these seals. It is approximately 90% the CO of the "normal" goat and 60% that of the "elite" dog while exercising at their $\dot{M}O_{2\,max}$ (Taylor et al. 1987). The highest $\dot{M}O_2$ in this study (0.60 ml O_2 · kg^{-1} · s^{-1}) is 63% $\dot{M}O_{2\,max}$ of the goat, and only 26% that of the dog.

On the basis of these $\dot{M}O_2$ and CO comparisons, the seal should be considered, at best, a "normal", athletic mammal in terms of cardiovascular variables and probable maximum $\dot{M}O_2$. A comparison of SV data indicates some interesting modifications in seals. The SV during ventilation (2.5–3.6 ml · kg^{-1}) is 1.2–1.8 times that of the resting dog or goat. However, during apnea the seal SV is similar to these mammals. Again this property indicates that the seal CV system functions at a "normally" adjusted metabolic need when the animal is breath-holding and is near maximum when breathing. Presumably, this modification is an adaptation to shorten the O_2 loading and CO_2 unloading time and hence the surface time. Rather than considering the seal to have a decreased CO and SV during submersion, it is more appropriate to consider it to have an increased CO and SV during ventilation. This model seems appropriate in the seal while at rest and during a low level of exercise. In the extreme cases, the metabolic demands of the swim muscles must be considerable and a low CO in this circumstance begs for another explanation. There are no data to explain this phenomenon of low CO during heavy exercise, but a model has been described in detail where such a low CO would result in low muscle circulation and greater utilization of in situ muscle O_2 stores (Kooyman 1985; Fedak 1988). During an extended dive, pulsatile flow to the most active muscles would replenish the depleted O_2 stores from the circulating supply. However, in the short breath-holds of this study, blood flow to muscle may be restricted for the entire submersion and muscle O_2 restored during ventilation. The decreased duration of submergence periods at high workloads may be a reflection of a higher muscle metabolic rate and more rapid reduction of myoglobin oxygen stores.

The increase in SV of up to 50% in the dog at a high level of exercise, and that in the seal during respiration, probably have different causes. The running dog has much muscle pumping which would increase venous return and presumably enhance heart preload. In the seal a high venous volume may be poised to fill the atrium at anytime, and the post-caval sphincter restriction of venous flow probably declines during ventilation facilitating cardiac filling. When submerged, an active caval sphincter and decreased myocardial inotropic state (Elsner et al. 1971; Elsner et al. 1985) would induce a low SV.

Stress

The reduced CO, SV, and HR observed during submerged swimming resemble, qualitatively, the response of the heart to FS, and it might be argued that seals swimming under these conditions are not diving voluntarily and much of the CV response is due to fright. This is a reasonable assumption for an untrained animal because the water pumps make considerable noise, and the seal must be concerned about being swept down the current, especially with heavy loads and having to struggle to reach the breathing dome. However, all seals used in this study had much previous experience swimming under these conditions before the COs were done. Consequently, they were familiar with the challenge of remaining under the dome, and except for the highest loads this appeared to be an easy task for them. Furthermore, the

HR responses in this study were similar to those observed in free diving harbor seals (Murdaugh et al. 1961; Jones et al. 1973; Fedak et al. 1988) and to those of gray seals in another laboratory study (Fedak 1986). Similar bradycardias have also been recorded in free-diving Weddell seals (Kooyman and Campbell 1972; Hill et al. 1987).

Conclusions

In conclusion, CO and SVs have been determined in swimming seals at different work loads. CO and SV are elevated maximally during surface ventilation at all exercise levels. Although slightly increased at the highest workloads, both are depressed during submerged swimming. As workload increases, the duration of submergence decreases. When equivalent swim velocities are calculated by drag equations on the basis of the load pulled by the seal, these seals were close to maximal effort at the highest $M\dot{O}_2$s measured. A nine-fold metabolic scope was measured in one seal. The maximal COs observed during ventilation and the $M\dot{O}_2$s achieved with the highest workloads in this study would classify seals as "normal," athletic animals according to the description of Taylor et al. (1987). The CO responses, ventilatory patterns, and swimming characteristics of seals appear to minimize time at the surface, where increased drag is encountered. Finally, the changes in CO and SV in this study demonstrate that HR alone is not a reliable indicator of CO during diving.

Acknowledgements. This work was supported by USPHS HL 17731,NIHHL 41736-1 and NSF DEB 82-08668. Sharp Memorial Hospital donated monitoring and anesthesia equipment; Anaquest donated the isoflurane. We are grateful to E. Burkhart and J. Velasquez for technical assistance on instrumentation, and anesthesia assistance from W. Woods and J. Waldman. We would also like to thank C. Lieber and C. Phillips of Edwards Laboratories for verification of catheter calibration constants. Sea World of San Diego made available to us animals from their rehabilitation program. All procedures were performed at the Seaweed Canyon animal facility, and we appreciated the help of the staff. J. Powell and his staff provided the technical means to conduct this work at the Hydraulics Laboratory of Scripps Institution. L. Lessard assisted in training and collection of data for the stroke frequency to velocity analysis. Finally, P. Thorson provided general assistance, and numerous student assistants and volunteers helped in various aspects of the study.

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