DIVING AND SWIMMING PERFORMANCE OF WHITE WHALES, *DELPHINAPTERUS LEUCAS*: AN ASSESSMENT OF PLASMA LACTATE AND BLOOD GAS LEVELS AND RESPIRATORY RATES

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Summary

The white whale *Delphinapterus leucas* is an exceptional diver, yet we know little about the physiology that enables this species to make prolonged dives. We studied trained white whales with the specific goal of assessing their diving and swimming performance. Two adult whales performed dives to a test platform suspended at depths of 5–300 m. Behavior was monitored for 457 dives with durations of 2.2–13.3 min. Descent rates were generally less than $2 \, \mathrm{m \, s^{-1}}$ and ascent rates averaged $2.2–3 \, \mathrm{m \, s^{-1}}$. Post-dive plasma lactate concentration increased to as much as $3.4 \, \mathrm{mmol \, l^{-1}}$ (4–5 times the resting level) after dives of 11 min. Mixed venous $P_{\mathrm{O_2}}$ measured during voluntary breath-holds decreased from 79 to 20 mmHg within 10 min; however, maximum breath-hold duration was 17 min. Swimming performance was examined by training the whales to follow a boat at speeds of $1.4–4.2 \, \mathrm{m \, s^{-1}}$. Respiratory rates ranged from $1.6 \, \mathrm{breaths \, min^{-1}}$ at rest to $5.5 \, \mathrm{breaths \, min^{-1}}$ during exercise and decreased with increasing swim speed. Post-exercise plasma lactate level increased to $1.8 \, \mathrm{mmol \, l^{-1}}$ (2–3 times the resting level) following 10 min exercise sessions at swimming speeds of $2.5–2.8 \, \mathrm{m \, s^{-1}}$. The results of this study are consistent with the calculated aerobic dive limit (O_2 store/metabolic rate) of 9–10 min. In addition, white whales are not well adapted for high-speed swimming compared with other small cetaceans.

Key words: diving, swimming, lactate, blood gases, aerobic dive limit, white whale, *Delphinapterus leucas*.

Introduction

White whales *Delphinapterus leucas* are exceptional divers compared with other small odontocete whales. They routinely dive to depths exceeding 200 m (maximum 647 m, trained dive) and stay submerged for up to 18.3 min (average 12.9 min) (Martin *et al.* 1993; Ridgway *et al.* 1984). However, our understanding of the physiology enabling these dives is limited, a fact generally true for most cetaceans. A large blood volume, a high hemoglobin level and a high hematocrit give these whales a large blood oxygen-carrying capacity (Ridgway *et al.* 1984), which is a major adaptation to prolong submergence times (Hedrick and Duffield, 1991; Kooyman, 1989; Lenfant, 1969; Ridgway and Johnston, 1966). Despite the blood volume and hematological studies, no other physiological characteristics have been reported for diving white whales.

Although the acquisition of behavioral and physiological data from wild cetaceans is especially difficult, trained animals can provide unique opportunities to make physiological measurements (Fish, 1993; Lang, 1975; Lang and Norris, 1966; Ridgway *et al.* 1969, 1984; Ridgway and Howard, 1979; Shaffer *et al.* 1995; Williams *et al.* 1992, 1993*a*). In the present study, a similar approach was adopted. Trained white whales swimming freely in the open sea were used to examine exercise and dive performance.

Although white whales have a fusiform body shape, they are quite robust and probably adapted for agility rather than speed (Brodie, 1989). Observations of migrating whales in the Canadian high Arctic indicate that white whales travel at fairly modest speeds of $2–4 \, \mathrm{km \, h^{-1}}$ ($0.6–1.1 \, \mathrm{m \, s^{-1}}$) (Martin *et al.* 1993). This swimming speed is remarkably slow compared with that of other small cetaceans that have been observed traveling at speeds as fast as $32 \, \mathrm{km \, h^{-1}}$ ($8.9 \, \mathrm{m \, s^{-1}}$) (Lang, 1975; Ridgway and Johnston, 1966; Würsig and Würsig, 1979). For comparison, Williams *et al.* (1992) determined that $7.6 \, \mathrm{km \, h^{-1}}$ ($2.1 \, \mathrm{m \, s^{-1}}$) was an energetically economical speed for bottlenose dolphins, *Tursiops truncatus*, and that faster speeds could be achieved if the animals began wave-riding. At present, evaluations of swimming performance by unrestrained bottlenose dolphins provide the only experimental assessment of swimming cetaceans.

The primary goal of this study was to assess the aerobic diving capability of white whales by examining dive behavior,

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respiratory rate and the onset of lactic acid accumulation in the blood of whales performing voluntary dives. Subsequently, in a second experiment, measurements of blood gas levels, pH, hematocrit and the production of lactic acid were made during periods of apnea in non-exercising, sedentary whales. Lastly, the hypothesis that white whales are not adapted for high-speed travel at the surface was tested by observing changes in swimming behavior, respiratory patterns and lactic acid accumulation during exercise sessions in which the whales were trained to follow a moving boat. These experiments indicate that white whales are well adapted to repetitive deep diving, but are limited to slow surface swimming relative to other small cetaceans.

Materials and methods

The performance of trained white whales was assessed during swimming and diving trials. The whales were trained over a period of 2 years using standard operant conditioning techniques; however, both whales had previous open ocean diving experience in an earlier study (Ridgway *et al.* 1984). The sex, age, mass and morphometrics of the study animals are given in Table 1. The whales were fed 2–4 times per day on a diet of herring, mackerel, smelt and capelin supplemented with vitamins. Each whale was housed in a separate floating pen (12 m×12 m×6 m deep). Experimental sessions were conducted 1–2 km offshore from San Clemente Island, California, where the mean sea surface temperature during the trials was 20.2 ± 1.1 °C. Resting respiratory rates were measured while the animals were held in the holding pens.

Diving performance

During diving sessions, the whales made repetitive dives to a test platform that was suspended from a boat floating passively on the surface (Ridgway *et al.* 1997). The test platform was lowered to targeted depths of 5, 10, 50, 100, 200 and 300 m as determined by an echo sounder (model FCV-561, Furuno, Inc.) or time/depth recorder (Mk 3e, Wildlife Computers, Inc.). To monitor the whales' arrival and departure from the platform, lights and a video camera (Deep Sea Power and Light, Inc.) were attached to the suspension cable just above the platform. Descent and ascent rates were determined by timing the duration of the whale's travel between the

Table 1. *Sex, estimated age, body morphometrics, and fineness ratio of the white whales used in this study*

Animal	Age (years)	Mass (kg)	Length (cm)	Maximum diameter (cm)	FR
Male	20	907	443.0	74.5	5.9
Female	28	645	374.5	70.0	5.4

The mass of the male whale exceeded the range of the scale so a conservative estimate was used.

FR, fineness ratio (length/maximum diameter).

platform and the surface. On many trials, times and depths were verified using time/depth recorders (TDR) in removable fabric pouches attached to the whale's flippers. As whales swam directly to the platform, held their position and then swam directly to the surface, any time not in transit was spent stationing on the platform and varied from 2 to 10 min.

Each experimental session began with a 5–20 min boat follow to the dive site. The whales were given a brief rest period (3–5 min) and then signaled to dive to the submerged test platform. Once on the platform, the whale remained on station for 3–12 min before being given an acoustic signal to return to the boat. At the surface, the whale was rewarded with fish and given a post-dive surface interval (PDSI) of roughly half the previous dive time (DT). On five occasions, blood samples were obtained after a single dive or after the first dive in a series. All other experimental sessions consisted of 2–6 repetitive dives of varying duration but constant depth (Fig. 1) followed by sequential blood sampling 3–8 min after the last dive in a session. The whales' post-dive respiratory rate was determined by counting breaths during each PDSI. Generally, two sessions were conducted each day with 2–3 h between trials.

Although it would have been beneficial to have monitored blood chemistry before and after each dive, this was not possible. Such frequent blood sampling would have required indwelling catheters, which would be difficult to maintain on the flukes or peduncle of a freely swimming and diving cetacean. Without catheterization, the frequency of venipuncture would have been too great to maintain voluntary behavior patterns. Furthermore, this study was conducted in concert with a larger study that examined the hearing and echolocating ability of the whales at depth (Ridgway *et al.* 1997). Consequently, the number of dives in a bout, dive duration and dive depth were determined by the requirements of the psychoacoustics study.

Sedentary breath-hold capability

In a parallel study, the whales' breath-hold capabilities were determined by examining the physiological effects of apnea while minimizing the influence of physical activity. Each whale was trained to hold its breath voluntarily while resting on a submerged platform. Concurrently, the whale was positioned ventral side up to facilitate blood sampling from its flukes while keeping its blowhole submerged. Sequential blood samples were collected at 1–2 min intervals to monitor changes in P_{O_2}, P_{CO_2}, pH, hematocrit (Hct) and plasma lactate and glucose concentrations.

Swimming performance

Each whale was trained to maintain its swimming speed by following an inflatable boat travelling at 1.4–4.2 m s^{-1} for durations of 5–20 min. A global positioning system (GPS, Commander model, Magellan, Inc.) was used to monitor boat speed (held constant during each trial) and to provide GPS coordinates accurate to within ±10 m. The distance of the swimming effort was calculated from the initial and final GPS

coordinates using PLGRGRID software (Naval Research and Development laboratory, San Diego, CA, USA). Total travel time was recorded with a stopwatch, and observers determined mean respiratory rate by counting breaths during the timed exercise period. In addition, post-exercise blood samples were obtained following selected 10 min swimming trials.

Blood collection and analyses

Each whale was trained to present its flukes voluntarily for collection of blood samples. To obtain a sample, a 19 gauge butterfly catheter was placed in a vessel on the ventral side of the peduncle or the ventral surface of the flukes (Ridgway *et al.* 1984). Blood was collected into 10 ml sodium heparin vacutainers (Becton Dickinson), between 2 and 6 min post-exercise or 3–8 min post-dive, and stored on ice until centrifuged. All blood samples were assumed to be a mixture of venous and arterial blood. Samples were processed 30–90 min after collection by centrifugation at $1000\,g$ for 10 min at ambient temperatures. Plasma was frozen at $-80\,°C$ until analyzed within 2 weeks of collection. Values for total lactate and glucose concentrations were obtained and compared with those of baseline samples acquired during fasting, non-exercise periods. Lactate and glucose assays were performed on a YSI 2300 STAT lactate/glucose analyzer (Yellow Springs Instruments Co.) calibrated daily with lactate (range $0–15.0\,\text{mmol}\,l^{-1}$) and glucose (range $0–25.0\,\text{mmol}\,l^{-1}$) standards. The stability of lactate and glucose in stored samples was tested by analyzing a set of baseline samples on the day of collection, and then every subsequent week for 1 month, freezing the samples between assays. No significant changes were observed. Similarly, human plasma has been stored for up to 90 days at $-10\,°C$ with no significant change in total lactate concentration (Buono, 1986).

Samples collected for blood gas measurements were drawn into 3 ml heparinized syringes (A-line kits, Becton Dickinson) and measured with a portable blood gas analyzer (i-STAT thermal control model, Signal Devices, Inc.). This instrument required only three drops of whole blood, placed into special cartridges ($^{G}3^{+}$ i-STAT cartridges, Signal Devices, Inc.) to measure P_{O_2}, P_{CO_2} and pH. Because the cartridges contained calibrating buffers, instrument calibration was checked before each sample was analyzed, and blood gas levels and pH were determined within 90 s. This portable unit was tested simultaneously against a standard bench-top blood gas analyzer (158 pH/blood gas analyzer, Corning) using whole blood from a bottlenose dolphin and a northern elephant seal *Mirounga angustirostris*; no significant differences were observed in blood gas levels or pH.

Data analyses

Within each diving bout, the ratio of dive time (DT) to post-dive surface interval (PDSI) was calculated for each dive sequence in a series (Fig. 1). The mean of all the ratios (i.e. mean DT/PDSI) in a bout was then compared with blood chemistry and respiratory rate.
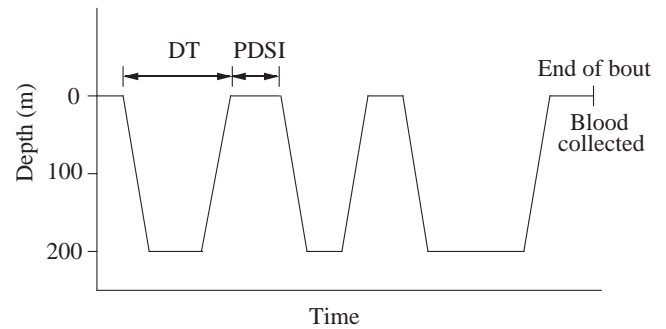

Fig. 1. Diving bout of white whales trained to dive to a stationary platform (i.e. bottom portion of dive). Dive time (DT) and post-dive surface interval (PDSI) were recorded for each sequence and their ratio (DT/PDSI) determined. The mean of all DT/PDSI ratios for the entire bout was determined and compared with changes in respiratory rate and blood chemistry.

Data analyses were performed using statistical software (Jandel Scientific, Inc.) with the probability of a type I error set at $P<0.05$. Means were compared using Student's *t*-tests, and regressions were performed using the method of least squares. Exponential functions were used to describe the relationships between swimming speed and depth because statistically they provided the best-fitting line and intuitively the rate of change should decrease as an animal reaches its maximum cost of transport speed (COT). All means are presented with $\pm\,1$ standard error (S.E.M.) unless designated otherwise.

Results

Diving performance

In total, 457 dives were recorded during this study. The female whale completed the deepest (maximum 300 m) and longest (maximum 13.3 min) dives, while the male only dived to a maximum platform depth of 128 m for a maximum dive time of 10.9 min (Table 2). After concluding this study, however, the male whale completed dives to a maximum platform depth of 300 m (Ridgway *et al.* 1997). Swimming speeds differed between the two whales on the descent portion of a dive, with the female swimming faster (Fig. 2A; Table 2). The ascent rates of the whales were indistinguishable over comparable depths and were therefore combined (Fig. 2B). Both relationships, descent rate *versus* depth (i.e. each whale) and combined ascent rate *versus* depth, were statistically significant at $P<0.05$.

The respiratory frequency of both whales increased concomitantly with increasing dive time ($P<0.05$ for both, $N=213$ and $N=97$ for the female and male whale, respectively). The maximum post-dive respiratory rate was as high as $9.6\,\text{breaths}\,\text{min}^{-1}$, which was six times the normal resting rate of $1.6\,\text{breaths}\,\text{min}^{-1}$.

Associated with the increase in respiratory rate were changes in plasma lactate and glucose concentrations. These changes in lactate concentration were affected by (1) the total dive time and (2) the duration of the PDSI in relation to the DT within

Table 2. *Summary statistics of dive durations, descent rates and ascent rates of all recorded dives completed by the white whales in this study*

Depth (m)	N	Dive duration (min)			Descent rate (m s^{-1})		Ascent rate (m s^{-1})	
		Mean	Mode	Maximum	Mean	Maximum	Mean	Maximum
Male								
5–49	104	5.2±2.2	5.2	10.3	0.83±0.28	1.70	1.20±0.56	2.32
50–99	18	4.5±2.6	2.2	8.7	1.32±0.28	1.82	2.03±0.32	2.38
100–128	64	7.5±1.7	8.2	10.9	1.19±0.24	1.67	2.19±0.26	2.64
Female								
5–49	93	5.6±2.4	4.6	10.7	0.73±0.28	1.67	0.84±0.33	1.92
50–99	10	2.9±1.4	4.0	4.6	1.65±0.15	1.87	2.22±0.20	2.53
100–199	125	6.8±2.2	7.8	13.3	1.95±0.29	2.67	2.68±0.29	3.62
200–300	43	8.2±2.1	7.9	11.4	2.15±0.29	3.18	3.02±0.51	4.34

Values are means ± S.D.

a bout of serial diving. Plasma lactate increased to 2–2.4 times resting concentration (0.7±0.2 mmol l^{-1}) following single dives with durations greater than 9 min ($P<0.05$, $t=-3.63$, $N=11$; Fig. 3A). Additionally, plasma lactate levels exhibited a significant increase for DT/PDSI ratios above 1.5, reaching levels as high as 4.5 times resting concentration ($P<0.05$, $N=19$, $r^2=0.591$; Fig. 3B). This implies that there is a threshold in lactate production for DT/PDSI ratios between 1.5 and 2 (Fig. 3B). Similarly, both whales exhibited post-dive hyperglycemia, although the response was highly variable and only weakly correlated with mean DT/PDSI for the female whale ($P<0.05$, $N=8$, $r=0.632$). The range of post-dive glucose concentrations for both animals was 5.4–8.0 mmol l^{-1} compared with baseline concentrations of 6.1–6.5 mmol l^{-1}.

Sedentary breath-hold capability

Each whale made three sedentary breath-hold dives with mean durations of 16.1±0.4 min (maximum 17.0 min) for the female and 14.8±1.5 min (maximum 16.5 min) for the male. The change in blood gas levels and pH were monitored during four of the six breath-hold trials; the responses for each whale were very similar, so the data were combined. The P_{O_2} of the blood measured in the first minute of the breath-hold averaged 63.5 mmHg (maximum 79 mmHg) (1 mmHg=0.1333 kPa), which decreased precipitously in the first 8 min to approximately 28 mmHg (Fig. 4). Beyond 10 min, P_{O_2} remained fairly constant at 20–23 mmHg until the breath-hold was terminated. These data were fitted with the quadratic equation: $P_{O_2}=0.212t^2-5.99t+64$ (where t is time in min, $P<0.05$, $N=35$, $r^2=0.8$). Conversely, P_{CO_2} increased linearly from 61 to 83 mmHg ($P<0.05$, $N=34$, $r^2=0.501$). The pH declined from 7.26 to 7.17 ($P<0.05$, $N=34$, $r^2=0.293$). Hematocrit (Hct) did not vary significantly with the duration of breath-hold for either whale (mean Hct was 53.1±0.3 % for the female and 52.1±0.5 % for the male). Each whale exhibited variable changes in plasma lactate concentration during the breath-hold trials. The male exhibited increases of 1.5–2 times the initial lactate concentration of 0.7–0.8 mmol l^{-1} or no

change (Fig. 5B), while the female displayed more variability between trials and only minor changes from initial concentrations within each trial (Fig. 5A). Although initial
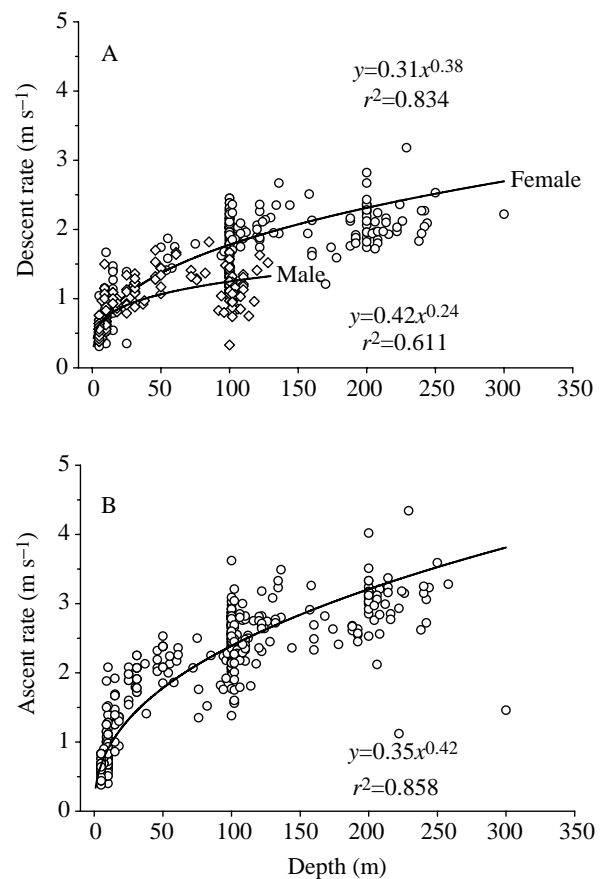

Fig. 2. Descent (A) and ascent (B) rates as a function of dive depth for white whales transiting between the surface and a stationary platform. Each point in A, (◇) male and (○) female, represents the overall descent rate of a single dive, where $N=182$ for the male and $N=271$ for the female whale. Data in B are the pooled ascent rates of both whales ($N=446$ dives).

A

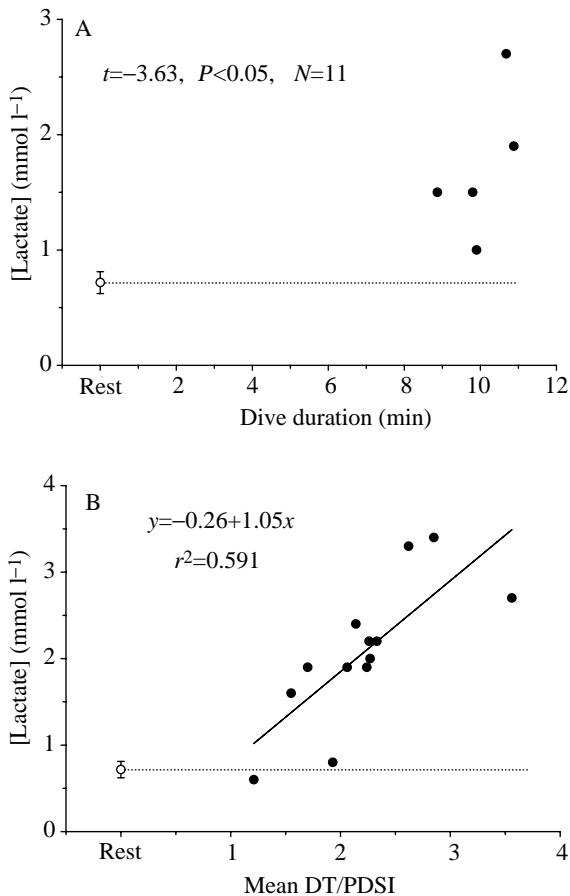$t=-3.63$, $P<0.05$, $N=11$

B

$y=-0.26+1.05x$

$r^2=0.591$

Fig. 3. Plasma lactate concentration as a function of dive duration for single dives (A) and serial diving (B) (i.e. mean DT/PDSI) in white whales. Blood samples collected at rest (○) were acquired during separate non-exercise periods and compared with post-dive blood samples (●). The dotted lines represent the mean resting lactate concentration (0.7 ± 0.1 mmol l^{-1}, mean ± s.e.m., $N=6$).

Fig. 4. Blood gas levels (P_{O_2} and P_{CO_2}) and pH measured during breath-holds of resting, sedentary white whales. These data were combined from two trials for each whale (four trials in total). Least-squares regressions were used to fit each line, and changes in all three relationships were statistically significant ($P<0.05$).

glucose concentration varied between trials (4.8–6.2 mmol l^{-1}), neither whale exhibited a significant change during the breath-hold period. Post-breath-hold respiratory rates were as high as 7 breaths min^{-1}, but the whales generally resumed rates below 2 breaths min^{-1} within 5–6 min.

Swimming performance

Together, the whales completed 207 boat-following trips during the study period. Swimming sessions for the male covered an average of 1375 ± 70 m and lasted 10.3 ± 0.4 min, while the female whale covered 1735 ± 51 m which required 12.0 ± 0.4 min. The whales' position relative to the boat shifted forwards at speeds below 2 m s^{-1} and slightly backwards at speeds greater than 2.5 m s^{-1}, with the majority of swimming occurring at a depth of 1–2 m below the surface. Speeds faster than 3.1 m s^{-1} resulted in a noticeable decrease in swimming effort by the female whale because a sizeable stern wake was created by the boat which enabled the whale to 'surf' behind it. This adjustment in swimming behavior appeared to be beneficial because stroke frequency declined noticeably,
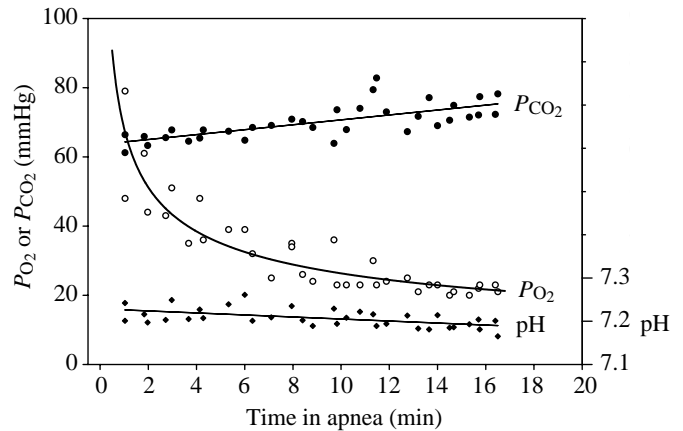
although the foam and spray created by the wake made it difficult to quantify. The male whale refused to follow the boat at speeds greater than 3.1 m s^{-1}.

Both respiratory rate and blood chemistry changed in relation to swimming speed at the water surface. Breathing rate increased to a maximum of 5.5 breaths min^{-1} when swimming speed reached 1.7–1.9 m s^{-1}. For trials conducted at swimming speeds greater than 1.9 m s^{-1}, mean respiratory rate decreased with subsequent increases in swimming speed (Fig. 6). Surprisingly, the lowest exercising respiratory rate (2.1 breaths min^{-1}, female) was observed during the fastest swimming trial (4.2 m s^{-1}). This low respiratory rate was probably due to a reduction in effort as a result of wake-riding, which was observed only in this animal at this speed.

Mean plasma lactate concentration for both whales increased from 0.7 ± 0.2 to 1.8 ± 0.6 mmol l^{-1} ($P<0.05$, $N=14$) after swimming at 2.5–2.8 m s^{-1} for 10 min. Glucose concentration decreased slightly in both whales, but this decrease was significant only for the male ($P<0.05$, $N=7$). The male's post-exercise glucose concentration decreased by 15 % of the resting concentration (6.1 mmol l^{-1}), while that of the female whale decreased by only 5 % below the resting concentration (6.5 mmol l^{-1}).

Discussion

Aerobic dive limits and diving performance of white whales

The aerobic component of diving metabolism is thought to be the major determinant of diving ability (Kooyman, 1989; Ponganis *et al.* 1993). Aerobic dives are constrained by the total oxygen stored in the muscle, blood and lung and by the rate at which it is utilized. The aerobic dive limit (ADL) is experimentally defined as the diving duration beyond which blood lactate levels increase above resting levels (Kooyman, 1985). Although, ADL has been estimated for many diving vertebrates (Kooyman, 1989; Boyd and Croxall, 1996), it has

been determined experimentally in only two species of pinniped. The ADL of Weddell seals, *Leptonychotes weddelli*, was measured as 18–20 min (Kooyman *et al.* 1980, 1983; Guppy *et al.* 1986) and that of the California sea lion *Zalophus californianus* was 2.3 min (Ponganis *et al.* 1997). In the present study, we determined an ADL of 9–10 min for white whales (Fig. 3A). These are the first empirically determined measurements of ADL for a cetacean.

The duration of dives that produced lactate can be compared with estimates of the white whales' ADL based on measurements of oxygen stores and estimates of metabolic rates. Calculated on a mass-specific basis, the oxygen store of a white whale is $51\,\mathrm{ml\,O_2\,kg^{-1}}$ (Table 3). This value is high compared with that of short-duration divers such as the bottlenose dolphin ($32.7\,\mathrm{ml\,O_2\,kg^{-1}}$; Williams *et al.* 1993*b*) and California sea lion ($38.1\,\mathrm{ml\,O_2\,kg^{-1}}$; Feldkamp *et al.* 1989), but intermediate to that of prolonged-duration divers such as harbor seals *Phoca vitulina* ($56.8\,\mathrm{ml\,O_2\,kg^{-1}}$; Davis *et al.* 1991) and Weddell seals ($86.2\,\mathrm{ml\,O_2\,kg^{-1}}$; Ponganis *et al.* 1993). Although metabolic rates were not directly measured, estimates were derived from the minimum COT of marine mammals (Williams, 1997). Since COT is the metabolic cost of locomotion per unit distance, it is possible to solve for metabolic rate on the basis of a range of travel speeds commonly used. Assuming that dives are performed at minimum COT speeds (Thompson *et al.* 1993), swimming metabolic rate (SwMR) would be $5.1\text{–}6.3\,\mathrm{ml\,O_2\,kg^{-1}\,min^{-1}}$ for white whales swimming at average speeds of $1.6\text{–}2.0\,\mathrm{m\,s^{-1}}$. This SwMR is approximately 3–4 times the predicted basal metabolic rate (BMR) of a 1000 kg animal (Kleiber, 1975) and

Table 3. *Estimated oxygen storage capacity of a white whale based on a body mass of 1000 kg (modified from Feldkamp* et al. *1989)*

| Lungs	
Total lung capacity (TLC): 75.9 l	Kooyman (1989)
Diving lung volume (75 % of TLC): 56.9 l	Goforth (1986)
Alveolar [O_2]: 15 %	Kooyman (1973)
Total lung O_2 available: 8.5 l or $8.5\,\mathrm{ml\,kg^{-1}}$	
Muscle	
Muscle mass (0.36×body mass): 360 kg	Goforth (1986)
Myoglobin [Mb]: $3.4\,\mathrm{g\,Mb\,100\,g^{-1}}$ muscle	Noren (1997)
O_2 combining capacity: $1.34\,\mathrm{ml\,O_2\,g^{-1}\,Mb}$	Kooyman (1989)
Total muscle O_2 available: 16.6 l or $16.6\,\mathrm{ml\,kg^{-1}}$	
Blood	
Volume ($127.5\,\mathrm{ml\,kg^{-1}}$): 127.5 l	Ridgway *et al.* (1984)
Arterial volume (0.33×total volume): 42.1 l	Lenfant *et al.* (1970)
Venous volume (0.67×total volume): 85.4 l	Lenfant *et al.* (1970)
Hemoglobin (Hb) content: $20.9\,\mathrm{g\,100\,ml^{-1}}$	Ridgway *et al.* (1984)
O_2 combining capacity: $1.34\,\mathrm{ml\,O_2\,g^{-1}\,Hb}$	Kooyman (1989)
Arterial stores (95–20 % saturation): 8.8 l	Kooyman (1989)
Venous stores (90–15 % saturation): 17.1 l	Kooyman (1989)
Total blood O_2 available: 25.9 l or $25.9\,\mathrm{ml\,kg^{-1}}$	
Combined O_2 stores available: 51.0 l or $51.0\,\mathrm{ml\,kg^{-1}}$	
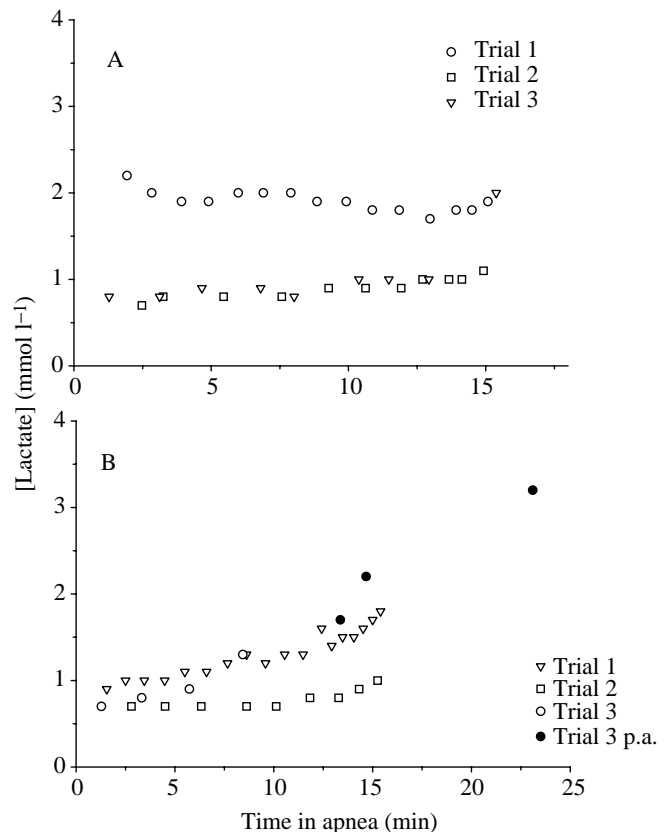
Fig. 5. Plasma lactate concentration as a function of time spent in apnea during sedentary breath-holds of white whales (A and B are female and male, respectively). In B, three post-breath-hold blood samples were collected following a 10.5 min period of apnea. p.a., post-apnea.

only slightly greater than the SwMRs of 1.3 times BMR for harbor seals or 2–3 times BMR for bottlenose dolphins swimming at minimum COT speeds (Davis *et al.* 1985; Williams *et al.* 1993*a*).

On the basis of the above estimates of oxygen stores and metabolic rate, we calculate a theoretical ADL of 8–10 min for white whales swimming continuously at speeds of $1.6\text{–}2.0\,\mathrm{m\,s^{-1}}$; a value remarkably consistent with the elevated lactate levels observed in dives longer than 9–10 min. It is interesting that both our blood lactate measurements and theoretical ADL are lower than the 8.7–18.3 min (mean 12.9 min) dives reported for white whales in the Arctic (Martin *et al.* 1993). Several factors could explain the discrepancy between our data and those of the Arctic animals. First, our whales made serial dives with significantly shorter surface intervals (3–5 min) than those measured for whales in the Arctic (mean 6.5 min; Martin *et al.* 1993). Second, our whales were not feeding or traveling as whales in the Arctic would. Instead, our whales swam directly to a platform, remained there and then returned to the surface. Third, the descent and ascent rates of our whales were considerably faster ($0.5\text{–}3.8\,\mathrm{m\,s^{-1}}$ descent rate and $0.5\text{–}4.3\,\mathrm{m\,s^{-1}}$ ascent rate; Fig. 2; Table 2) than those reported for whales diving in the high Arctic (1.4–2.2 and $1.2\text{–}1.8\,\mathrm{m\,s^{-1}}$, respectively; Martin *et*
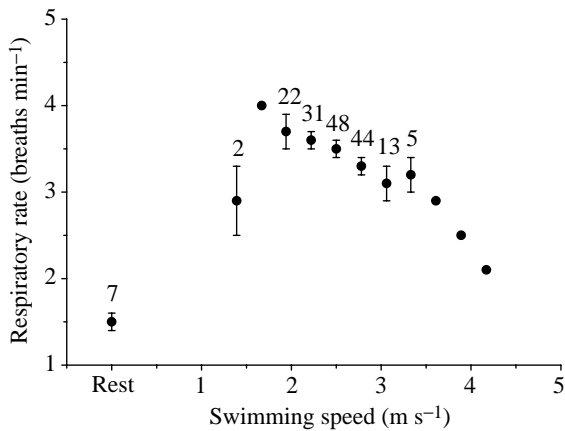
Fig. 6. Respiratory rate in relation to swimming speed for white whales trained to follow a moving boat. Boat speed was held constant for each trial, and the number of experimental sessions conducted at each speed is given except for single events. Each point represents a combined mean (± S.E.M.) for both whales.

al. 1993). Faster swimming speeds will increase O_2 consumption, leading to lower ADLs. Further, the white whales in the Arctic utilize a range of speeds (1.2–2.2 m s^{-1}; Martin *et al.* 1993) that may be adjusted to match the effort on a 'planned' dive (Kooyman, 1985), and they also probably use burst-and-glide locomotion. Video footage of entire diving sequences of a northern elephant seal and bottlenose dolphin reveal that burst-and-glide swimming is used extensively during diving (Williams *et al.* 1996). This mode of swimming could potentially reduce the animals' effort and thus prolong the duration of aerobic metabolism during a dive. Moreover, mean dive duration may not be completely representative of aerobic dives because a mean considers all dives and hence may be skewed in favor of long durations. Finally, if our data are representative, one would be left to conclude that white whales in the wild include some component of anaerobic metabolism during diving. A mixed strategy of both anaerobic and aerobic dives has been suggested for northern fur seals (Ponganis *et al.* 1992). Therefore, it is conceivable that white whales dive in a similar manner.

A value consistent with elevated lactate levels after 10 min comes from our measurements of blood gas and lactate concentrations during sedentary apneas (Figs 4, 5). For both animals, blood P_{O_2} decreased to minimum levels (20–23 mmHg) by 10 min. On the basis of the low initial pH levels, the samples probably consisted of mixed venous blood; however, the dramatic decline in blood P_{O_2} is indicative of declining blood oxygen stores. Furthermore, in at least one animal in which lactate level was measured following a 10.5 min apnea, the ADL was surpassed, as is evident from the increased lactate concentration (3.3 mmol l^{-1}, which was 2–3 times the resting value; Fig. 5B). Lastly, the maximum breath-hold durations achieved under voluntary conditions for both animals were 16.5–17.0 min, values that are remarkably similar to the maximum dive duration of 18.3 min reported for Arctic whales (Martin *et al.* 1993).

Serial dives with durations within the ADL do not generally have a significant effect on blood chemistry (Castellini *et al.* 1988). When mean DT/PDSI is low, i.e. when surface interval time is nearly equal to or greater than the preceding dive time, lactate that is produced could be completely metabolized before diving resumes. As the DT/PDSI ratio increases, a greater proportion of time is spent under water per surface interval. On a dive that surpasses the ADL, lactate production may exceed its turnover rate; hence, its conversion back to glucose or oxidation as a substrate could remain incomplete at the start of a subsequent dive. If no further lactate is metabolized during a subsequent dive, then residual lactate will carry over into the next surface interval. Continuing in this manner, lactate concentrations are likely to increase exponentially over a series of dives with a high DT/PDSI ratio. Eventually, the diver fatigues and must spend time at the surface in order to increase its oxygen intake to metabolize the lactate load.

The observed curvilinear relationship between swimming speed and dive depth (Fig. 2) is perhaps quite important in understanding the whales' diving behavior. On dives shallower than 30 m, water clarity permitted observation of the whales' swimming behavior from the surface. In most cases, the whales appeared to glide slowly down to the platform with little stroking effort. Conversely, the whales vigorously stroked out of view on deeper dives. Overall, the fastest descent rate was just above 3 m s^{-1}, which was very similar to that previously observed by Ridgway *et al.* (1984), but most dives to 100 m or deeper averaged 1.2–2.2 m s^{-1}. The observation that slower swimming speeds were used during descent suggests that the whales are conserving oxygen at the beginning of the dive. This is also inferred from the markedly faster ascent rates which the whales used when returning to the surface (Fig. 2B). If 2.4–3.0 m s^{-1} (mean ascent rates, Table 2) were the minimum COT speed, one would expect the whales to use these speeds routinely while diving to maximize bottom time. In fact, descent and ascent rates of 1.6–1.8 m s^{-1} are more commonly used by Arctic white whales (Martin *et al.* 1993).

In comparing the mean dive durations and the descent rates for all dives, it would appear that the whales chose to swim at speeds of 2 m s^{-1} or less to prolong the ADL. There were dives, however, that apparently challenged the ADL as the whales' blood lactate levels were 2–3 times the resting values in many of the diving sessions (Fig. 3). These increased blood lactate concentrations may result from individual dives exceeding the aerobic dive limit and/or to the short surface intervals, which could have precluded complete reoxygenation and incomplete metabolism of lactate between sequential dives. The voluntary breath-hold experiments also reconfirm the observation of Scholander *et al.* (1942) that lactate is sequestered during a dive and then released into the general circulation after breathing has resumed.

Post-dive hyperglycemia was observed during recovery on some dives; however, responses varied between sessions. Therefore, some cycling between lactate and glucose probably occurred during diving. Hyperglycemia has been observed in

the post-dive recovery of other species (Davis, 1983; Kooyman *et al.* 1980; Robin *et al.* 1981). In contrast, a different response was observed during recovery from exercise. The whales exhibited either a decreasing or a stable plasma glucose concentration, which is more similar to responses measured during post-exercise recovery in humans and dogs (MacRae *et al.* 1995; Issekutz *et al.* 1976).

Swimming performance and the effects of hydrodynamics on respiratory patterns

The results of this study suggest that white whales, in comparison with other dolphins and porpoises (Ridgway and Johnston, 1966; Williams *et al.* 1992, 1993*a*), are not well adapted for sustained high-speed travel at the water's surface. In the present study, we obtained mean travel speeds more than double those commonly used by Arctic white whales ($2–4\,km\,h^{-1}$ or $0.6–1.1\,m\,s^{-1}$; Martin *et al.* 1993) and observed a two- to threefold increase in lactate concentration ($0.7\,mmol\,l^{-1}$ at rest and $2.3\,mmol\,l^{-1}$ post-exercise) as well as a substantial effect on respiratory rate (Fig. 6). Animals can minimize locomotor costs by swimming at a depth (greater than 3 body diameters) that avoids the creation of a surface wave (Hertel, 1966). If the whales reduced the number of excursions to the surface to avoid surface waves when swimming speeds are high, breathing rate would subsequently decline during a period when muscular demand is greatest, thus creating an aerobic deficit. As a result, the whales would have to compensate by utilizing anaerobic glycolysis to facilitate muscle metabolism, which would produce a lactate burden and, further, cause fatigue.

Increasing locomotor effort generally elicits a concomitant increase in the breathing rate of exercising mammals (Taylor *et al.* 1987). Terrestrial animals show unique coupling between respiratory patterns and locomotor movements (Baudinette, 1991; Carrier, 1987). Marine mammals face a different set of challenges because they live in a fluid medium that influences both the timing of breathing and locomotor movements. Coupling between locomotor strokes and breathing was not observed in exercising whales, as they swam 1–2 m (i.e. 2–3 body diameters; Table 1) below the surface. As locomotor speed increased, the whales remained submerged longer, causing a decrease in respiratory rate (Fig. 6). Consequently, the respiratory patterns of these mammals appear to be linked to surface/submergence patterns rather than to locomotor movements *per se*.

In summary, serial diving in marine mammals is likely to involve strategies that maximize underwater time by minimizing the number of dives that exceed the ADL. This strategy requires optimizing speed without increasing oxygen consumption. White whales achieve this by swimming at speeds of $2\,m\,s^{-1}$ or less when diving and by utilizing slower speeds or swimming well below the surface when transiting between locations.

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