THE PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*): HEART RATE, METABOLIC RATE AND PLASMA LACTATE CONCENTRATION DURING EXERCISE

TERRIE M. WILLIAMS, W. A. FRIEDL and J. E. HAUN

*NOSC Hawaii Laboratory, PO Box 997, Code 511, Kailua, HI 96734, USA*

Summary

Despite speculation about the swimming efficiency of cetaceans, few studies have investigated the exercise physiology of these mammals. In view of this, we examined the physiological responses and locomotor energetics of two exercising adult *Tursiops truncatus*. Oxygen consumption, heart rate, respiratory rate and post-exercise blood lactate concentration were determined for animals either pushing against a load cell or swimming next to a boat. Many of the energetic and cardiorespiratory responses of exercising dolphins were similar to those of terrestrial mammals. Average heart rate, respiratory rate and oxygen consumption for dolphins pushing against a load cell increased linearly with exercise levels up to 58kg for a female dolphin and 85kg for a male. Oxygen consumption did not increase with higher loads. Maximum rate of oxygen consumption ($\dot{V}_{O_2max}$) ranged from 19.8 to 29.4 ml O_2 kg^{-1} min^{-1}, which was 7–11 times the calculated standard metabolic rate ($\dot{V}_{O_2std}$) of the dolphins. Blood lactate concentration increased with exercise loads that exceeded $\dot{V}_{O_2max}$. The maximum lactate concentration was 101.4 mg dl^{-1} (11.3 mmol l^{-1}) for the male, and 120.6 mg dl^{-1} (13.6 mmol l^{-1}) for the female. When swimming at 2.1 m s^{-1}, heart rate, respiratory rate and post-exercise blood lactate concentration of the dolphins were not significantly different from values at rest. The cost of transport at this speed was 1.29±0.05 J kg^{-1} min^{-1}. The energetic profile of the exercising bottlenose dolphin resembles that of a relatively sedentary mammal if the exercise variables defined for terrestrial mammals are used. However, the energetic cost of swimming for this cetacean is low in comparison to that of other aquatic and semi-aquatic mammals.

Introduction

A hydrodynamic body shape and high-speed locomotion have led to the perception that dolphins are unusually efficient and powerful swimmers (Fish and Hui, 1991). The streamlined characteristics of the dolphin's body have been studied experimentally (Lang, 1974; Purves *et al.* 1975) and described theoretically (Lighthill, 1969; Nachtigall, 1981). The fusiform body shape of these marine mammals is considered to be 'ideal' for drag reduction during high-speed swimming (Hertel, 1966). Several morphological
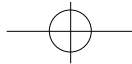
features for reducing drag have been proposed for cetaceans. These include cutaneous ridges (Shoemaker and Ridgway, 1991), speed-induced skin folds (Essapian, 1955) and subdermal mechanical properties of the skin (Kramer, 1960; Haun *et al.* 1984). Each of these features may influence the transition between laminar and turbulent flow across the boundary layer surrounding the dolphin's body. This, in turn, will influence the energetic cost of swimming.

Low body drag enables swimmers to achieve and maintain high swimming speeds. Anecdotal accounts have reported remarkably high swimming speeds for dolphins in the wild, but provide little information about the duration of effort. Furthermore, it is difficult to assign average or preferred swimming speeds to wild dolphins, because of (1) differences in the performance levels of individual species, (2) the inability of observers to discriminate between burst and sustained swimming effort, (3) difficulties in monitoring swimming speed from a moving boat, and (4) assisted propulsion during wave-riding. Many factors appear to influence the routine swimming speeds of bottlenose dolphins (*Tursiops truncatus*). Lang (1974) and Lockyer and Morris (1987) found that speed depended on the duration of effort. Sustained (lasting more than 5min) swimming speed ranged from 2.8 to $5.6\,\mathrm{m\,s^{-1}}$ for an immature male bottlenose dolphin in the coastal waters of Wales (Lockyer and Morris, 1987). A lower range of speeds ($1.4–4.8\,\mathrm{m\,s^{-1}}$) was reported for the same species off the coast of Argentina and was correlated with water depth (Würsig and Würsig, 1979). The mean sustained speed of this group, $1.7\,\mathrm{m\,s^{-1}}$, was similar to the relatively slow speeds ($<1.5\,\mathrm{m\,s^{-1}}$) measured for dolphins in Florida (Shane, 1990). In comparison, a similarly sized bottlenose dolphin trained to follow a boat was able to maintain a speed of $3.1\,\mathrm{m\,s^{-1}}$ for extended periods (Lang and Norris, 1966).

To evaluate the energetics of swimming in dolphins and the ability of these animals to attain high swimming speeds, we need to understand the exercise physiology of cetaceans. Unfortunately, little is known about the physiological responses of active cetaceans. Neither the physiological limits of dolphins exercising under controlled conditions nor the energetic demands of swimming have been defined. Only metabolic (Worthy *et al.* 1987) and cardiovascular (Elsner *et al.* 1966) responses of cetaceans swimming in small pens or pools have been measured. Although physiological changes associated with diving (Ridgway *et al.* 1969; Ridgway and Howard, 1979) and the skeletal muscle characteristics of the dolphin (Goforth, 1986) have been investigated, these studies provide little information about the metabolism of swimming in dolphins.

We determined the physiological limits of swimming in bottlenose dolphins by measuring aerobic costs and the onset of lactate accumulation during exercise. Heart rate, respiratory rate, metabolic rate and blood lactate concentration were assessed for animals pushing against a load cell and swimming next to a boat. The results of this study show that the energetic profile of the bottlenose dolphin resembles that of a relatively sedentary terrestrial mammal. Swimming at routine speeds is energetically economical for bottlenose dolphins. Minimum transport costs for the dolphin are lower than values for other aquatic and semi-aquatic mammals.
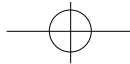
Materials and methods

Animals

Two adult Atlantic bottlenose dolphins (*Tursiops truncatus* Montagu) were used in both static exercise and open-water swimming tests. The animals (one male, one female each weighing 145kg) were housed in open-water floating pens (7 m×7m×3 m deep) in a salt-water bay, and were fed 2–3 times daily on mackerel, herring and smelt, supplemented with vitamins. Average water temperature in the pens during the experimental period was 24.6±1.20˚C (s.d.).

Experimental design

The dolphins were studied under three experimental conditions: (1) resting in water, (2) static exercise against a load cell and (3) swimming in open water. Resting measurements were made as the animals floated quietly under a metabolic hood while stationed in front of the load cell. The animals were trained for the exercise tests over a 2 year period using standard operant conditioning techniques. Physical condition of the animals was maintained by exercise on the load cell or in open water at least 4 days per week.

Each session on the load cell consisted of a 2min rest period, followed by 5–7min of steady-state exercise at a constant load and a 3min recovery period. The recovery period was omitted if blood samples were collected for post-exercise lactate analyses. Heart rate, respiratory rate and metabolic rate were measured simultaneously throughout the session. The dolphins performed three to four exercise sessions per day with a 30–40min rest period between each session. Target levels on the load cell ranged from 22 to 182kg and were randomly varied.

Open-water swimming sessions began with a 5min pre-exercise rest period and a 5–6min warm-up swim (approx. 0.5km at $2.1\,\mathrm{m\,s^{-1}}$) to the experimental site. This was followed by 10–25min of swimming at a constant speed. Swimming speeds during the experimental sessions ranged from 2.1 to $3.8\,\mathrm{m\,s^{-1}}$. Most sessions covered approximately 1–2 nautical miles (1.8–3.7km) in a straight line. Heart rate and respiratory rate of the dolphin were monitored continuously during the sessions. Blood samples were taken immediately after each experimental swimming period. The dolphins were used in two swimming sessions per day with a 20–40min rest period between each session.

Static exercise

Training techniques and equipment for static exercise by bottlenose dolphins have been described in detail by Goforth (1990). Each dolphin was trained to push its rostrum against a padded load cell (Lebow, model 3169-110, force transducer) mounted at water level in a floating net pen. Threshold force levels and tail-beat frequency were predetermined by the investigator for each experimental session. The dolphins were required to maintain the predetermined level of effort for a minimum of 5min. Tail-beat frequency and the force produced with each tail beat were measured by transmitting signals from the force transducer to a differential amplifier (Princeton Applied Research) and a personal computer (Compaq). The computer compared these signals with the
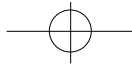
predetermined criteria for performance. Feedback on performance was provided to the trainer and the exercising dolphin through acoustic cues using a computer-controlled hydrophone. Thus, the system simultaneously analysed and stored data from the load cell while providing behavioural feedback on the animal's performance.

To ensure that the total force produced by each tail beat was measured, the trainer aligned the long axis of the dolphin's body with the maximum force vector of the load cell. While pushing on the load cell, the body and tail of the dolphin remained submerged; the top of the head and blowhole remained above the surface, permitting unrestricted breathing. Mean maximum force of all tail beats was calculated from the data following each exercise session. The load cell was calibrated daily using lead weights.

Although the dorsal-to-ventral flexion of the dolphin's tail simulated the movements of swimming, we do not consider this representative of free swimming behaviour (Goforth, 1990). Instead, the load cell was used to assess the physiological limits of the exercising dolphin during controlled, graded work.

Open-water swimming

The dolphins were trained to match their swimming speed with that of a motorboat (Boston Whaler, model 21 foot). Position of the animals relative to the boat was determined by a trainer and maintained by a series of acoustic signals presented through a submerged hydrophone. Individual dolphins were positioned 3–10m abeam of the boat outside of the wake zone. When submerged, the swimming dolphin remained approximately 1m (>2.5 body diameters) below the surface of the water. At this depth, the augmentation in drag from surface wave interference is considered to be negligible (Hertel, 1966).
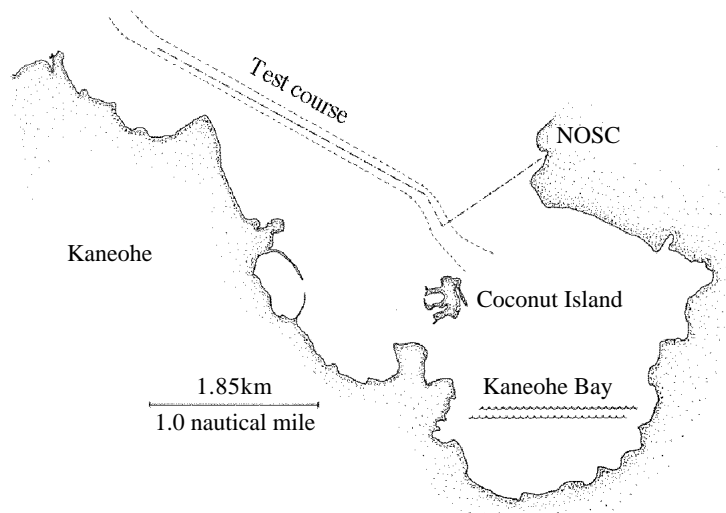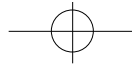

Fig. 1. Test course for open-water swimming experiments with bottlenose dolphins. The path of the test boat is shown between the dashed lines. A warm-up swim was conducted between NOSC facilities and the ship channel (dotted and dashed line). This was followed by an experimental swimming session along the ship channel.

The open-water experiments were conducted in a 14m deep ship channel in Kaneohe Bay, Oahu, Hawaii (Fig. 1). Water currents in this area are generally less than $0.3 \, \text{m s}^{-1}$ and were insignificant during the tests. In a previous study, Lang and Norris (1966) reported that water currents in Kaneohe Bay had little effect on the swimming speed of dolphins during their tests of cetacean performance. The speed of the boat was monitored with a speed log recorder that was calibrated before and after the experiments by timed trials over a measured course in Kaneohe Bay.

Heart rate

Electrocardiograph (ECG) signals were recorded continuously during rest, static exercise and swimming. We used two cross-thorax surface electrodes placed on the sternum between the pectoral fins and on the mid-lateral axillary area. Each electrode consisted of a 3.0cm diameter copper plate mounted in an 8.5cm suction cup. Insulated wires from the electrodes were braided and trailed to the side of the resting or exercising animal. Signals from the electrodes were amplified and recorded at $2.5 \, \text{cm s}^{-1}$ with a Birtcher heart rate monitor (model 365).

During swimming, a nylon harness was used to keep the suction cup electrodes in position. Care was taken to design a streamlined, low-profile (<5% of the frontal area of the dolphin) harness for minimum drag augmentation (Culik and Wilson, 1991). Respiratory rates and blood lactate concentrations for dolphins swimming with and without the harness at speeds lower than $2.9 \, \text{m s}^{-1}$ were not significantly different (at $P < 0.05$). As a result, we assumed that there was little additional energetic cost associated with the harness at these relatively low speeds. The effect of the harness undoubtedly increases with speed, but was not assessed in this study.

Respiratory rate

The duration of breath-holds and the respiratory rate of the dolphins were recorded by observers with stopwatches and with an event marker on the electrocardiograph (ECG)

Fig. 2. Representative electrocardiographic traces for an adult bottlenose dolphin during swimming at two different speeds. *B* denotes the point at which the animals surfaced to breathe, and corresponds to a shift in the ECG baseline. The dolphins remained submerged for the remainder of the period. Note the increase in the *r*-to-*r* interval as bradycardia developed during prolonged submergence at $2.0 \, \text{m s}^{-1}$. This was not observed at the higher swimming speed.
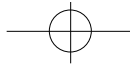
trace. Mean respiratory rate was determined for 1min periods at 5min intervals during the tests. In addition, respiratory movements were superimposed on the ECG trace (Fig. 2). Respiratory rate was determined from these traces by counting the number of respiratory deflections over 5min intervals.
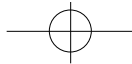
Blood lactate

Samples for lactate analyses were taken from blood vessels located on the ventral surface of the dolphin's fluke. Collection was facilitated by training the animals to present their flukes voluntarily for sampling. After exercise or swimming, the animals immediately swam to the side of the pen or boat for fluke presentation to the trainer. Using this technique, we obtained the samples within 2–4min after completion of exercise. Serial blood samples taken on four occasions showed that peak lactate concentrations were obtained during this period. Chilled samples (10–12ml in SST vacutainers; Becton Dickinson) were centrifuged (approx. $1000\,g$ for 10min) and the plasma was analysed for total lactate concentration (YSI Industrial Analyzer, model 27). The analyzer was calibrated daily with lactate standards ranging from 0 to $133.6\,\mathrm{mgdl}^{-1}$ (0–$15.0\,\mathrm{mmoll}^{-1}$).

Metabolic rate

Each dolphin was fasted overnight before experimental sessions. During the sessions the animals were rewarded with small pieces of fish. Preliminary results show that the peak in the heat increment of feeding for dolphins is longer than 3h and is less than 30% of resting metabolic rate (D. P. Costa, personal communication). In view of this, the short duration of the experimental period and the small size of the fish rewards, the effects of digestion on exercise metabolism are considered insignificant in this study.

The rate of oxygen consumption ($\dot{V}_{O_2}$) was determined for quiescent dolphins stationed on the water surface in front of the load cell and for active animals pushing against the load cell. We used an open-flow respirometry system in which breathing was restricted to an acrylic metabolic hood (57cm $\times$ 57cm base $\times$ 57cm slant height) placed on the water (Fedak et al. 1981). Air was drawn into the hood by a vacuum pump. Flow rate was monitored with a pitot tube (Dwyer flow sensor, DS-100) attached to a needle gauge and was maintained at approximately $100\,\mathrm{lmin}^{-1}$. At this flow rate, the content of oxygen in the dome remained above 20%. Samples of the exhaust air from the hood were dried (Drierite) and scrubbed of carbon dioxide (Sodasorb) before entering an oxygen analyzer (Ametek S3-A). The percentage of oxygen in the sample line was monitored continuously during the experiments and recorded with a computer (Franklin Ace, 1200). The output from the oxygen analyzer was monitored every 2s and averaged each minute. These values were converted to $\dot{V}_{O_2}$ using the equations from Fedak et al. (1981). All values are corrected to STPD.

The entire system was calibrated daily with dry, ambient air (20.94% O_2) and nitrogen gas (100% N_2). The theoretical fraction of O_2 leaving the dome was calculated (Davis et al. 1985; Fedak et al. 1981) and compared with measured values from the oxygen analyzer. The flow of calibration gases into the dome was controlled by an electronic flowmeter (Omega, model FMA-772v) that was accurate to within 1% of flow. The

flowmeter was calibrated before and after the experiments using nitrogen gas and a calibrated rotameter (Cole-Palmer Instruments).

Data analyses

Data for heart rate, blood lactate concentration and oxygen consumption are presented as mean ± 1 s.D. Differences between means were tested by paired *t*-tests according to Zar (1974). Linear and non-linear relationships were calculated by least-squares procedures, with plateau regions defined by the intersection of the regressions.

Heart rate was calculated by dividing the total number of ECG waveforms or fractions thereof by the test interval according to Chabot *et al.* (1989). To distinguish between periods of respiratory tachycardia at the surface and bradycardia while submerged, heart rates were calculated for two discrete intervals; (1) 5–7s immediately following inspiration, and (2) the remainder of the period between breaths (Fig. 2). Average heart rate was also determined for 1min periods. Calculations were made at 2min intervals for static exercise tests and at 5min intervals for open-water tests.

Results

Static exercise

The changes in metabolic rate of dolphins pushing against a load cell were similar in pattern to those of other exercising mammals. Oxygen consumption increased linearly with exercise loads up to 58kg for the female dolphin and 85kg for the male (Fig. 3). Least-squares regressions for these relationships are: $\dot{V}_{O_2}=6.99+0.19$load ($N=20$, $r=0.99$) for the female and $\dot{V}_{O_2}=7.37+0.26$load ($N=16$, $r=0.99$) for the male, where $\dot{V}_{O_2}$ is in mlO_2kg^{-1}min^{-1} and load is in kg.

Further increases in load did not result in a concomitant rise in oxygen consumption. The plateau region, representing the maximum oxygen consumption ($\dot{V}_{O_2max}$), was different for the two dolphins. Mean $\dot{V}_{O_2max}$ was 19.79 ± 1.35mlO_2kg^{-1}min^{-1} ($N=11$) for the female and 29.41 ± 2.09mlO_2kg^{-1}min^{-1} ($N=14$) for the male. The highest work loads achieved were 105kg and 192kg for the female and male dolphin, respectively.

Plasma lactate levels for the male dolphin averaged 25.8 ± 0.9mgdl^{-1} (2.9 ± 0.1mmol l^{-1}; $N=4$) at rest and with loads up to 82kg (Fig. 3). The mean blood lactate concentration for the female dolphin was 19.0 ± 3.1mgdl^{-1} (2.1 ± 0.3mmol l^{-1}; $N=3$) for loads less than 44kg. Above these loads, post-exercise blood lactate concentration showed a positive relationship with load. The relationships were described by the equations: lactate concentration=0.91load-22.6 ($N=6$; $r=0.99$) for the female dolphin and lactate concentration=0.63load-18.3 ($N=8$; $r=0.96$) for the male dolphin, where lactate concentration is in mgdl^{-1} and load is in kg.

Lactate level appeared to be an important factor in determining maximum exercise performance by the dolphins. When plasma lactate concentrations exceeded 100mgdl^{-1} (11.2mmol l^{-1}), the duration of effort declined. At the highest work load, 202kg, the male dolphin maintained exercise for only 4min and had a post-exercise blood lactate concentration of 101.4mgdl^{-1} (11.3mmol l^{-1}). The highest load for the female was
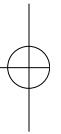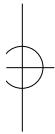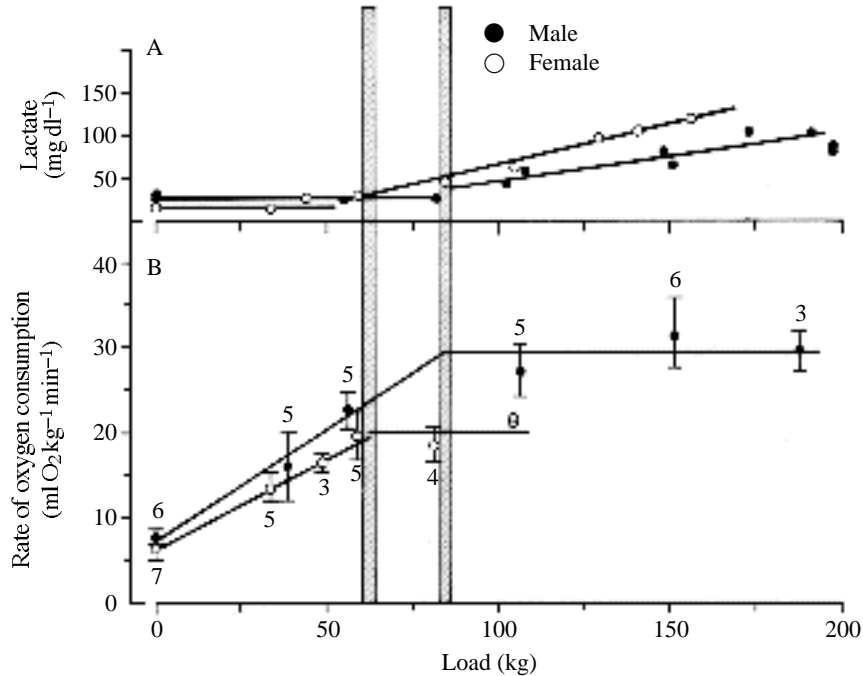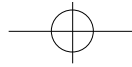
Fig. 3. Post-exercise blood lactate concentration (A) and rate of oxygen consumption (B) in relation to load for dolphins pushing against a load cell. Values for a male (●) and female (○) dolphin are shown. Solid lines are the least-squares linear regressions through the data points. In B, points and vertical lines represent the mean ± 1 S.D. Numbers denote the number of experimental sessions. In A, each point represents a single experimental session on the load cell. Vertical bars show the point of intersection for linear and plateau regions for each dolphin.

157kg, which resulted in a post-exercise lactate concentration of 120.6mgdl^{-1} (1.3mmol l^{-1}).

As found for blood lactate concentration, changes in respiratory rate correlated with the linear and plateau regions of $\dot{V}_{O_2}$ (Fig. 4). These changes were more apparent for the female dolphin. The respiratory rate of this animal increased from 5.9breathsmin^{-1} at rest to 12.5breathsmin^{-1} during exercise at a 47kg load. Respiratory rate did not change with further increases in load and averaged 12.1±2.0breathsmin^{-1} (N=24) over the range of 47–162kg on the load cell. The male dolphin showed only a 60% increase in respiratory rate between rest and exercise at 190kg. Mean respiratory rate over the plateau region was 5.9±0.7breathsmin^{-1} (N=17) for this animal.

Heart rate was indistinguishable for the two dolphins so the data were combined. The average heart rate of dolphins pushing against the load cell increased linearly with load up to 129kg (Fig. 4). The relationship for both animals was: heart rate=78.1+0.44load (N=94; r=0.98), where heart rate is in beatsmin^{-1} and load is in kg. Heart rate was 139.4±4.1beatsmin^{-1} (N=12) for loads over 129kg. Post-inspiratory tachycardia and breath-hold bradycardia were evident at low work loads (0–58kg). At these loads, heart
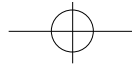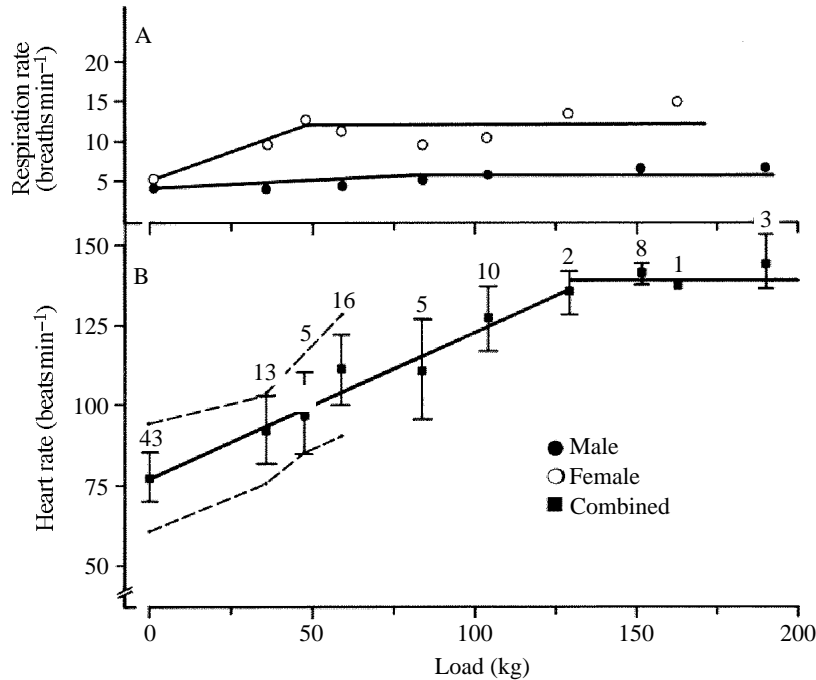
Fig. 4. Respiration rate (A) and heart rate (B) in relation to exercise load for dolphins pushing against a load cell. B shows mean ± 1 S.D. for average heart rate for both dolphins. Numbers represent the number of experimental sessions. Dashed lines are the corresponding levels of bradycardia and tachycardia at the lower work loads. Points representing mean respiration rate are shown in A. *N* for each of the points corresponds to the numbers in B. Solid lines are the least-squares linear relationships.

rates during the 5–7s following inspiration were 16% greater than average; heart rates during periods of bradycardia were 18% lower than the average rates. Neither tachycardia nor bradycardia was apparent at higher work loads.

Open-water swimming

Heart rate, respiration rate and post-exercise blood lactate concentration of swimming dolphins showed similar patterns as swimming speed changed (Fig. 5). We found no significant change (*P*<0.05) in these three variables between rest and swimming at 2.1 ms^{-1}. All three variables increased as swimming speed approached 2.9 ms^{-1}. At this speed, respiration rate was 66% faster, blood lactate concentration was 27% higher and average heart rate was 61% faster than the values at rest. The increases were statistically significant (*P*<0.05) for lactate concentration and heart rate.

The heart rate of swimming dolphins was biphasic and oscillated between periods of tachycardia and bradycardia (Figs 2, 5). At rest and at slow swimming speeds (<2.5 ms^{-1}) tachycardia occurred for 5–7s after inspiration. Bradycardia persisted during the remainder of the submerged period. Unlike seals (Hill *et al.* 1987; Williams *et al.* 1991), the dolphins did not show a pre-inspiratory increase in heart rate. The
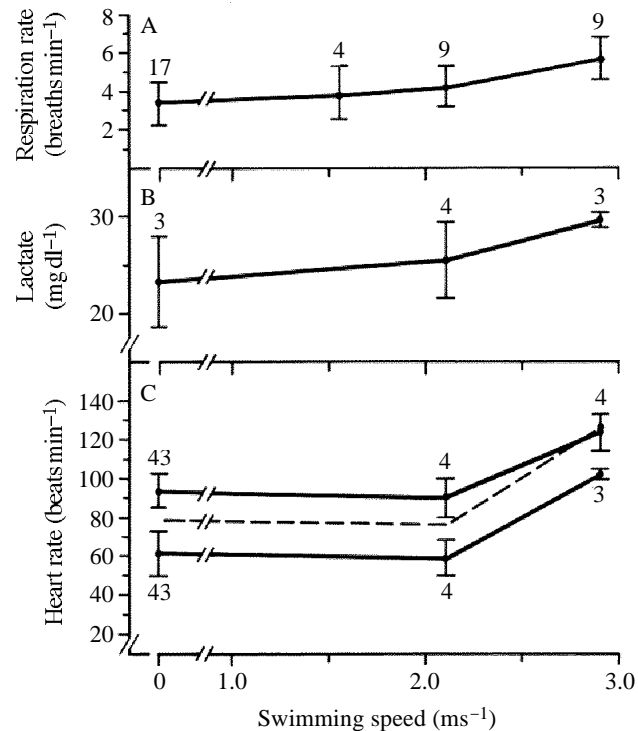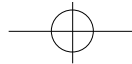
Fig. 5. Respiration rate (A), blood lactate concentration (B) and heart rate (C) in relation to swimming speed for bottlenose dolphins trained to follow a moving boat. Data for the male and female dolphin are combined. Values are presented for animals resting in water and swimming freely. Points and vertical lines are the mean ± 1 S.D. Numbers represent the number of experimental sessions. The two solid lines for heart rate represent values for surface tachycardia (top line) and submerged bradycardia (bottom line) at each speed. The dashed line denotes the average heart rate. Note that the period of bradycardia was reduced or absent at the highest swimming speed. Therefore, the average heart rate approximated the value for surface tachycardia.

biphasic heart rate pattern was most pronounced at rest and at slow swimming speeds. As swimming speed approached $3.0 \, \mathrm{ms^{-1}}$, the period of bradycardia was shortened or eliminated and heart rate remained elevated. Consequently, the average heart rate of dolphins swimming at $2.9 \, \mathrm{ms^{-1}}$ approximated the post-inspiratory tachycardia.

Discussion

Physiological limits of exercise performance in dolphins

The limit of oxygen consumption ($\dot{V}_{O_2 \mathrm{max}}$) of exercising terrestrial mammals is indicated by a plateau in $\dot{V}_{O_2}$ that does not change with increased exercise intensity. Under these conditions, the energetic demands of exercise are supplemented by anaerobic glycolysis, which is often manifested as an increase in blood lactate level (Margaria, 1976; Seeherman *et al.* 1981). Based on this definition, the dolphins in this study reached
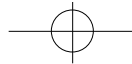
$\dot{V}_{O_2max}$ while pushing against the load cell (Fig. 3). Maximum values for oxygen consumption were $19.79 \pm 1.35\,\text{ml}\,O_2\,\text{kg}^{-1}\,\text{min}^{-1}$ for the female dolphin and $29.41 \pm 2.09\,\text{ml}\,O_2\,\text{kg}^{-1}\,\text{min}^{-1}$ for the male. These levels were 30–40% lower than
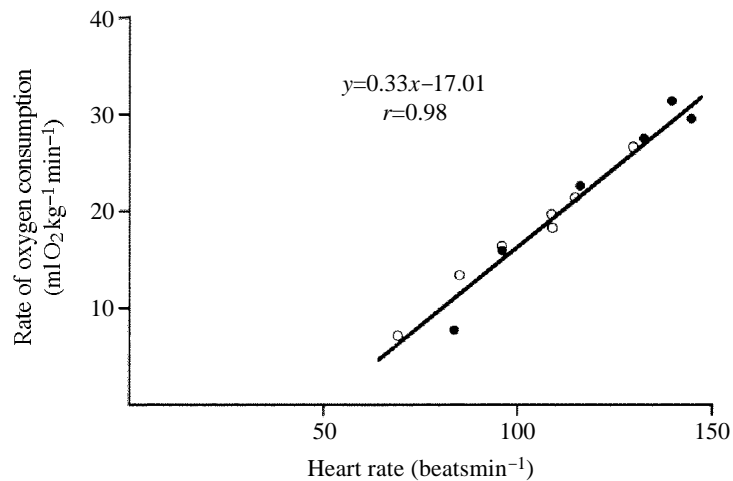

Fig. 6. Oxygen consumption in relation to average heart rate for an adult male (●) and female (○) dolphin pushing against a load cell. Each point represents the mean value from data in Figs 3 and 4. Values from 106 experimental sessions are represented in these means. The solid line is the least-squares linear regression through the data points.
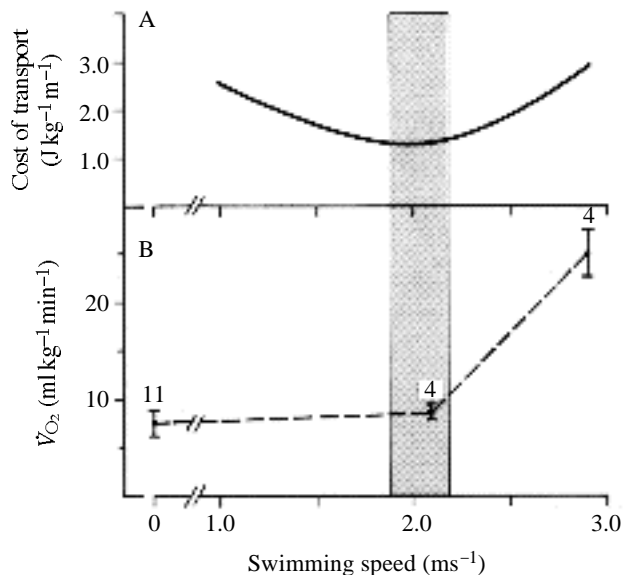

Fig. 7. Cost of transport (A) and oxygen consumption (B) in relation to speed for the swimming bottlenose dolphin. Values were calculated from the relationship presented in Fig. 6 and average heart rates measured during swimming (see text). The shaded area denotes the routine cruising speeds of coastal dolphins (Würsig and Würsig, 1979). Numbers in B represent the number of experimental sessions and values are mean ± S.D.
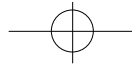
predicted values for the maximum oxygen consumption of running mammals (Taylor *et al.* 1980; Lindstedt *et al.* 1991).

A comparatively low $\dot{V}_{O_2max}$ for swimmers is not unusual. Depending on the type and degree of athletic training, the $\dot{V}_{O_2max}$ of swimming humans is 11% (McArdle *et al.* 1971) to 19% (Åstrand and Saltin, 1961) lower than that measured during running. Likewise, the $\dot{V}_{O_2max}$ of swimming mink is 3–14% lower than for the same animals running on a treadmill (Williams, 1983). Respiratory constraints and utilization of a smaller skeletal muscle mass during swimming are possible causes for the low $\dot{V}_{O_2max}$ of terrestrial and semi-aquatic mammals. It is unlikely that these are the only factors contributing to the low $\dot{V}_{O_2max}$ of dolphins, mammals that are adapted primarily for aquatic activity.

Terrestrial mammals also show considerably higher dynamic metabolic scopes ($\dot{V}_{O_2max}/\dot{V}_{O_2std}$, where $\dot{V}_{O_2std}$ is the standard rate of oxygen consumption from Kleiber, 1975) than observed for the dolphins. Athletic species such as dogs and ponies have dynamic scopes approaching 30, but the value is approximately 12 for sedentary species (goats, calves) (Taylor *et al.* 1987). In comparison, the maximum oxygen consumption of dolphins was only 3–4 times greater than the values for the animals resting in water.

The difference in dynamic metabolic scope between dolphins and terrestrial mammals may be due to the relatively low $\dot{V}_{O_2max}$ of swimmers or an elevated resting metabolic rate. $\dot{V}_{O_2}$ measured for quiescent dolphins stationed on the water surface in front of the load cell at a water temperature of 24.6˚C was $7.39\pm0.91\,ml\,O_2\,kg^{-1}\,min^{-1}$, a value that is 2.5 times the standard rate of oxygen consumption predicted from body mass (Kleiber, 1975). Such high 'resting' rates may be attributed in part to a pre-exercise anticipatory rise in $\dot{V}_{O_2}$ (Taylor *et al.* 1987).

Metabolic adaptations for the aquatic environment may also contribute to the high resting metabolic rate and, hence, low dynamic scope of marine mammals (Scholander, 1940; Kanwisher and Ridgway, 1983), although this has recently been questioned (Lavigne *et al.* 1986; Innes and Lavigne, 1991; Kasting, 1991). Irving (1969) speculated that the high resting metabolic rate of whales could only provide a three- to fourfold increase in metabolic rate during exercise. We have found that the minimum metabolic rate for post-absorptive dolphins resting in a metabolic chamber at a water temperature of 26.0˚C is $4.63\pm0.21\,ml\,kg^{-1}\,min^{-1}$ (N=6) (T. M. Williams, W. A. Friedl, J. E. Haun and S. Shippee, in preparation). This rate is 37% lower than that measured under the pre-exercise condition, but is 1.6 times the predicted standard metabolic rate.

If we use the predicted standard metabolic rate for mammals in our calculations, the resulting dynamic metabolic scope for dolphins pushing against the load cell ranges from 7 to 11. These levels are typical of relatively sedentary terrestrial species as described by Taylor *et al.* (1987).

To cope with a limited dynamic metabolic scope, marine mammals may preferentially rely on anaerobic metabolism during high work loads (Fig. 3; Elsner, 1986). In this respect, exercising dolphins and seals are similar to running lions (Chassin *et al.* 1976). These three species are capable of doubling exercise intensity while at $\dot{V}_{O_2max}$ (Seeherman *et al.* 1981; Elsner, 1986; present study). In contrast, human athletes (Åstrand and Rodahl, 1977) and smaller terrestrial mammals (Seeherman *et al.* 1981) fatigue quickly once $\dot{V}_{O_2max}$ has been reached.
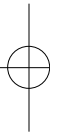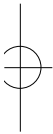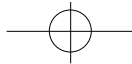
Despite a reliance on anaerobic processes, post-exercise lactate concentrations are not exceptionally high for exercising dolphins. Maximum lactate levels were 100–120mgdl^{-1} (11.2–13.5mmol1^{-1}) for dolphins pushing against a load cell (Fig. 3; Goforth, 1986). These levels are similar to those of human swimmers (Goodman *et al.* 1985) and cyclers (Knuttgen and Saltin, 1972), but are only 32–56% of values reported for a variety of terrestrial species run to exhaustion on a treadmill (Seeherman *et al.* 1981). The difference in peak lactate concentration between marine and terrestrial mammals may be related to (1) the relative muscle mass involved in the exercise, (2) enhanced buffering capacity and possibly lactate turnover in marine mammals (Castellini and Somero, 1981), or (3) the presence of large oxygen reserves in the lungs, blood or muscle. Oxygen reserves reportedly provide a short-term solution to inadequate oxygen delivery in diving marine mammals. Because such reserves are repaid during recovery, their contribution would have been overlooked in our study. The role of these reserves during steady-state swimming by dolphins awaits further investigation.

The energetics of swimming in cetaceans

Logistics prevented us from directly measuring the oxygen consumption of swimming dolphins at sea. An indirect measure is provided by using average heart rate to predict the metabolic rate of the animals. As observed for swimming seals and sea lions (Fedak *et al.* 1988; Williams *et al.* 1991), metabolic rate correlates with heart rate during static exercise by dolphins (Fig. 6). We can use this relationship to calculate metabolic rate from heart rates measured during free swimming. The results of these calculations are presented in Fig. 7. Like other swimmers (Williams, 1983; Davis *et al.* 1985; Williams *et al.* 1991), dolphins show a non-linear increase in oxygen consumption with swimming speed. The trend parallels the curvilinear increase in respiration rate, heart rate and lactate concentration with swimming speed (Fig. 5).

Transport costs for swimming dolphins, determined from metabolic rate divided by speed, showed a U-shaped curve with speed (Fig. 7A). The trough of this curve, representing the minimum cost of transport, was 1.29±0.05 J kg^{-1} min^{-1}, which is lower than values reported for a variety of aquatic and semi-aquatic mammals (Fish, 1982; Williams, 1989; Williams *et al.* 1992). The minimum cost of transport occurred at 2.1 m s^{-1}, approximating the mean cruising speed of coastal dolphins (Würsig and Würsig, 1979; Shane, 1990). At this speed, oxygen consumption, respiration rate and post-exercise lactate concentration of the dolphin vary little from resting levels.

Results from static exercise trials (Goforth, 1986; present study) and speed trials (Lang and Norris, 1966) indicate that bottlenose dolphins are capable of sustaining much higher work loads and energetic costs than those incurred during routine swimming. Wild bottlenose dolphins will maintain speeds that are 1.5–2.0 times cruising levels, but appear to limit this effort to short bouts (Würsig and Würsig, 1979; Lockyer and Morris, 1987). Often these animals use behavioural strategies, including positioning in currents (Shane *et al.* 1986) and wave-riding (Williams *et al.* 1992), to reduce the energetic cost of free swimming, especially at high speeds.

In summary, the energetic profile for the bottlenose dolphin is one of a comparatively sedentary mammal if exercise variables defined for terrestrial mammals are used. The
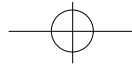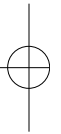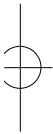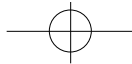
dolphins' behaviour, dynamic metabolic scope and level of maximal oxygen consumption fall short of those reported for elite terrestrial athletes such as horses and dogs (Taylor *et al.* 1987). It is possible that these definitions are not appropriate for the exercising marine mammal. The swimming dolphin may rely on metabolic pathways or oxygen reserves that were not identified by conventional methods of evaluation. Alternatively, physiological specialization may not be necessary in the bottlenose dolphin, whose body streamlining and behavioural strategies effectively reduce the cost of movement through water.

References

ÅSTRAND, P. O. AND RODAHL, K.(1977). *Textbook of WorkPhysiology*. 681pp. New York: McGraw-Hill Book Co.

ÅSTRAND, P. O. AND SALTIN, B.(1961). Maximal oxygen uptake and heart rate in various types of muscle activity. *J. appl. Physiol.* **16**, 977–981.

CASTELLINI, M. A. AND SOMERO, G. N. (1981). Buffering capacity of vertebrate muscle: Correlations with potentials for anaerobic function. *J. comp. Physiol.* **143**, 191–198.

CHABOT, D., BAYER, M. AND DE ROOS, A. (1989). The analysis of heart rate data: the effect of using interbeat intervals vs instantaneous heart rates. Proceedings from the Eighth Biennial Conference on the Biology of Marine Mammals. p. 11.

CHASSIN, P. S., TAYLOR, C. R., HEGLUND, N. C. AND SEEHERMAN, H. J. (1976). Locomotion in lions: Energetic cost and maximum aerobic capacity. *Physiol. Zool.* **49**, 1–10.

CULIK, B. AND WILSON, R. P. (1991). Swimming energetics and performance of instrumented Adélie penguins (*Pygoscelisadeliae*). *J. exp. Biol.* **158**, 355–368.

DAVIS, R. W., WILLIAMS, T. M. AND KOOYMAN, G. L. (1985). Swimming metabolism of yearling and adult harbor seals, *Phocavitulina*. *Physiol. Zool.* **58**, 590–596.

ELSNER, R.(1986). Limits to exercise performance: Some ideas from comparative studies. *Acta physiol. scand* **128** (Suppl. 556), 45–51.

ELSNER, R., KENNEY, D. W. AND BURGESS, K.(1966). Diving bradycardia in the trained dolphin. *Nature* **212**, 407–408.

ESSAPIAN, F. S.(1955). Speed-induced skin folds in bottle-nosed porpoise, *Tursiopstruncatus*. *Breviora, Mus. comp. Zool.* **43**, 1–4.

FEDAK, M. A., PULLEN, M. R. AND KANWISHER, J. (1988). Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. *Can. J. Zool.* **66**, 53–60.

FEDAK, M. A., ROME, L. AND SEEHERMAN, H. J. (1981). One-step-N_2 dilution technique for calibrating open-circuit O_2 measuring systems. *J. appl. Physiol.* **51**, 772–776.

FISH, F. E. (1982). Aerobic energetics of surface swimming in the muskrat (*Ondatra zibethicus*). *J. exp. Biol.* **110**, 183−201.

FISH, F. E. AND HUI, C. A.(1991). Dolphin swimming – A review. *Mammal Rev.* **21**, 181–195.

GOFORTH, H. W., JR (1986). Glycogenolytic responses and force production characteristic of a bottlenose dolphin (*Tursiops truncatus*), while exercising against a force transducer. PhD thesis, University of California, Los Angeles. 137pp.

GOFORTH, H. W., JR (1990). Ergometry (exercise testing) of the bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood and R. R. Reeves), pp. 559–574. San Diego: Academic Press, Inc.

GOODMAN, C., ROGERS, G. G., VERMAAK, H. AND GOODMAN, M. R.(1985). Biochemical responses after swimming 100m and 800m. *Europ. J. appl. Physiol.* **54**, 436–441.

HAUN, J. E., HENDRICKS, E. W., BORKAT, F. R., KATAOKA, R. W., CARDER, D. A., DOOLEY, C. A. AND LINDER, E. (1984). *Dolphin Hydrodynamics: FY83 and FY84 Report.* Technical Report 998. 165pp. San Diego: Naval Oceans System Center.

HERTEL, H.(1966). *Structure, Form, Movement.* New York: Reinhold Publishing Corporation. 251pp.

HILL, R. D., SCHNEIDER, R. C., LIGGINS, G. C., SCHUETTE, A. H., ELLIOTT, R. L., GUPPY, M., HOCHACHKA, P. W., QVIST, J., FALKE, K. J. AND ZAPOL, W. M. (1987). Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol.* **22**, R344–R351.

INNES, S. AND LAVIGNE, D. M. (1991). Do cetaceans really have elevated metabolic rates? *Physiol. Zool.* **64**, 1130–1134.

IRVING, L.(1969). Temperature regulation in marine mammals. In *The Biology of Marine Mammals* (ed. H. T. Andersen), pp. 147–174. New York: Academic Press.

KANWISHER, J. W. AND RIDGWAY, S. H. (1983). The physiological ecology of whales and porpoises. *Scient. Am.* **248**, 110–120.

KASTING, N. (1991). Reply to technical comment, Do cetaceans really have elevated metabolic rates? *Physiol. Zool.* **64**, 1135–1136.

KLEIBER, M. (1975). *The Fire of Life.* 453pp. Huntington, NY: R. E. Krieger Publ. Co.

KNUTTGEN, H. G. AND SALTIN, B.(1972). Muscle metabolites and oxygen uptake in short-term maximal exercise in man. *J. appl. Physiol.* **32**, 690–694.

KRAMER, M. O. (1960). Boundary layer stabilization by distributed damping. *J. Am. Soc. Naval Engrs* **72**, 25–33.

LANG, T. G. (1974). Speed, power and drag measurements of dolphins and porpoises. In *Swimming and Flying in Nature*, vol. 2 (ed. T. Y. Wu, C. J. Brokaw and C. Brennen), pp. 553–572. New York: Plenum Press.

LANG, T. G. AND NORRIS, K. S. (1966). Swimming speed of a Pacific bottlenose dolphin. *Science* **151**, 588–590.

LAVIGNE, D. M., INNES, S., WORTHY, G. A. J., KOVACS, K. M., SCHMITZ, O. J. AND HICKIE, J. P. (1986). Metabolic rates of seals and whales. *Can. J. Zool.* **64**, 279–284.

LIGHTHILL, M. J. (1969). Hydromechanics of aquatic animal propulsion. *A. Rev. Fluid Mech.* **1**, 413–446.

LINDSTEDT, S. L., HOKANSON, J. F., WELL, D. J., SWAIN, S. D., HOPPELER, H. AND NAVARRO, V. (1991). Running energetics in the pronghorn antelope. *Nature* **353**, 748–750.

LOCKYER, C. AND MORRIS, R. (1987). Observations on diving behavior and swimming speeds in a wild juvenile *Tursiops truncatus*. *Aquatic Mammals* **13**, 31–35.

MARGARIA, R. (1976). *Biomechanics and Energetics of Muscular Exercise*. 146pp. Oxford: Clarendon Press.

MCARDLE, W. D., GLASER, R. M. AND MAGEL, J. R. (1971). Metabolic and cardiorespiratory response during free swimming and treadmill walking. *J. appl. Physiol.* **30**, 733–738.

NACHTIGALL, W. (1981). Hydromechanics and biology. *Biophys. Struct. Mech.* **8**, 1–22.

PURVES, P. E., DUDOK VAN HEEL, W. H. AND JONK, A.(1975). Locomotion in dolphins. I. Hydrodynamic experiments on a model of the bottlenose dolphin, *Tursiops truncatus* (Mont.). *Aquatic Mammals* **3**, 5–31.

RIDGWAY, S. H. AND HOWARD, R. (1979). Dolphin lung collapse and intramuscular circulation during free diving: Evidence from nitrogen washout. *Science* **206**, 1182–1183.

RIDGWAY, S. H., SCRONCE, B. L. AND KANWISHER, J. (1969). Respiration and deep diving in the bottlenose porpoise. *Science* **166**, 1651–1654.

SCHOLANDER, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**, 1–131.

SEEHERMAN, H. J., TAYLOR, C. R., MALOIY, G. M. O. AND ARMSTRONG, R. B. (1981). Design of the mammalian respiratory system II. Measuring maximum aerobic capacity. *Respir. Physiol.* **44**, 11–23.

SHANE, S. H. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In *The*
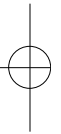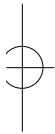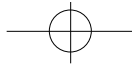
Bottlenose Dolphin (ed. S. Leatherwood and R. R. Reeves), pp. 245–265. New York, London: Academic Press.

SHANE, S. H., WELLS, R. S. AND WÜRSIG, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Mar. Mammal Sci.* **2**, 34–63.

SHOEMAKER, P. A. AND RIDGWAY, S. H. (1991). Cutaneous ridges in odontocetes. *Mar. Mammal Sci.* **7**, 66–74.

TAYLOR, C. R., KARAS, R. H., WEIBEL, E. R. AND HOPPELER, H. (1987). Adaptive variation in the mammalian respiratory system in relation to energetic demand. II. Reaching the limits to oxygen flow. *Respir. Physiol.* **69**, 7–26.

TAYLOR, C. R., MALOIY, G. M. O., WEIBEL, E. R., LANGMAN, V. A., KAMAU, J. M. Z., SEEHERMAN, M. J. AND HEGLUND, N. C. (1980). Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir. Physiol.* **44**, 25–37.

WILLIAMS, T. M. (1983). Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. exp. Biol.* **103**, 155–168.

WILLIAMS, T. M. (1989). Swimming by sea otters: Adaptations for low energetic cost locomotion. *J. comp. Physiol.* A **164**, 815–824.

WILLIAMS, T. M., FRIEDL, W. A., FONG, M. L., YAMADA, R. M., SEDIVY, P. AND HAUN, J. E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821–823.

WILLIAMS, T. M., KOOYMAN, G. L. AND CROLL, D. A. (1991). The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. comp. Physiol.* B **160**, 637–644.

WORTHY, G. A. J., INNES, S., BRAUNE, B. M. AND STEWART, R. E. A. (1987). Rapid acclimation of cetaceans to an open-system respirometer. In *Marine Mammal Energetics* (ed. A. C. Huntly, D. P. Costa, G. A. J. Worthy and M. A. Castellini), pp. 115–126. Society for Marine Mammalogy Special Publication no. 1. Allen Press: Lawrence, KS.

WÜRSIG, B. AND WÜRSIG, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the south Atlantic. *Fish. Bull.* **77**, 399–412.

ZAR, J. H.(1974). *Biostatistical Analysis.* 620pp. Englewood Cliffs, New Jersey: Prentice Hall, Inc.