

RESEARCH ARTICLE

Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes

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ABSTRACT

Exponential increases in hydrodynamic drag and physical exertion occur when swimmers move quickly through water, and underlie the preference for relatively slow routine speeds by marine mammals regardless of body size. Because of this and the need to balance limited oxygen stores when submerged, flight (escape) responses may be especially challenging for this group. To examine this, we used open-flow respirometry to measure the energetic cost of producing a swimming stroke during different levels of exercise in bottlenose dolphins (*Tursiops truncatus*). These data were then used to model the energetic cost of high-speed escape responses by other odontocetes ranging in mass from 42 to 2738 kg. The total cost per stroke during routine swimming by dolphins, $3.31 \pm 0.20 \text{ J kg}^{-1} \text{ stroke}^{-1}$, was doubled during maximal aerobic performance. A comparative analysis of locomotor costs (LC; in $\text{J kg}^{-1} \text{ stroke}^{-1}$), representing the cost of moving the flukes, revealed that LC during routine swimming increased with body mass (M) for odontocetes according to $\text{LC} = 1.46 \pm 0.0005M$; a separate relationship described LC during high-speed stroking. Using these relationships, we found that continuous stroking coupled with reduced glide time in response to oceanic noise resulted in a 30.5% increase in metabolic rate in the beaked whale, a deep-diving odontocete considered especially sensitive to disturbance. By integrating energetics with swimming behavior and dive characteristics, this study demonstrates the physiological consequences of oceanic noise on diving mammals, and provides a powerful tool for predicting the biological significance of escape responses by cetaceans facing anthropogenic disturbances.

KEY WORDS: Beaked whale, Diving, Dolphin, Energetics, Oceanic noise, Swimming

INTRODUCTION

For a wide variety of highly active semi-aquatic and aquatic vertebrates, the comparative ease of swimming slowly contrasts with the marked metabolic and kinematic challenges of swimming fast. From athletic teleost fish (Lee et al., 2003; Clark and Seymour, 2006; Blank et al., 2007) to aquatic birds (Culik et al., 1994), small mammals (Williams, 1983; Fish and Baudinette, 1999) and large

marine mammals (Feldkamp, 1987; Williams et al., 1991, 1992; Kriete, 1995; Otani et al., 2001), the energetic cost of swimming increases exponentially when moving at progressively higher speeds. This effect is apparent to coaches and swimming athletes trying to simultaneously achieve peak endurance and speed in competition (Toussaint and Truijens, 2005), as well as to diving mammals that must balance speed and the duration of breath-hold with limited onboard oxygen stores needed to support metabolic processes during submergence (Kooyma, 1989).

The non-linear escalation in effort with locomotor speed for swimmers differs from that of runners, and has been attributed to the exponential rise in hydrodynamic drag that resists forward movement through water as speed increases (Fig. 1A). Indeed, for harbor seals (*Phoca vitulina*), in which hydrodynamic (Williams and Kooyma, 1985) and energetic and kinematic (Davis et al., 1985) parameters have been measured, we find that the non-linear relationship between oxygen consumption and swimming speed tracks that of body drag (Fig. 1). Because stroke frequency increases linearly with speed over the same range, there is a profound change in the energetic cost per stroke as the seals move faster (Fig. 1B,C). In view of this, it is not surprising that many species of marine mammal regardless of size routinely swim at comparatively slow preferred speeds (averaging $<1.5\text{--}2.5 \text{ m s}^{-1}$) that promote an economy of movement (Williams, 2009). Even the most active dolphins and largest whales (Goldbogen et al., 2006) tend to cruise within this range.

However, there are many occasions when high-speed swimming is demanded by free-ranging marine mammals. Locating and chasing prey (Williams et al., 2004; Guinet et al., 2007; Aguilar de Soto et al., 2008), as well as flight responses to avoid predators (Ford et al., 2005) or anthropogenic disturbance (DeRuiter et al., 2013; Goldbogen et al., 2013), can result in significant short- and long-term increases in swimming speed. In particular, many odontocete cetaceans will engage in short, extraordinary bouts of high-speed performance. For example, killer whales (*Orcinus orca*) can maintain speeds exceeding 3.7 m s^{-1} when chasing tuna (Guinet et al., 2007), and short-finned pilot whales (*Globicephala macrorhynchus*), named the ‘cheetahs of the deep sea’, can sprint up to 9.0 m s^{-1} while chasing deep-water prey (Aguilar de Soto et al., 2008).

Escape from aversive stimuli, most notably predators such as killer whales (Ford et al., 2005) and oceanic sound, can also instigate unusual swimming patterns and prolonged levels of increased physical exertion by cetaceans. High-speed swimming, elevated stroke frequencies and rapid ascent from depth are commonly reported for wild, tagged cetaceans following exposure to noise (Todd et al., 1996; DeRuiter et al., 2013), and have been suggested as causative factors for marine mammal strandings

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List of symbols and abbreviations

ACC	accelerometer
ECG	electrocardiogram
f_H	heart rate (beats min^{-1})
f_S	stroke frequency (strokes min^{-1})
D	dive duration (min)
MR	metabolic rate
LC	locomotor cost of stroking (without maintenance costs, $\text{J kg}^{-1} \text{stroke}^{-1}$)
$\text{LC}_{\text{aerobic max}}$	locomotor cost during maximum aerobic performance ($\text{J kg}^{-1} \text{stroke}^{-1}$)
$\text{LC}_{\text{preferred}}$	locomotor cost during routine swimming ($\text{J kg}^{-1} \text{stroke}^{-1}$)
$\text{O}_{2,\text{TOT recovery}}$	total O_2 consumed during a dive (measured during recovery, $\text{ml O}_2 \text{kg}^{-1}$)
S	number of strokes taken during a dive
T_{air}	air temperature
T_{water}	water temperature
\dot{V}_{O_2}	rate of O_2 consumption ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$)
$\dot{V}_{\text{O}_2,\text{dive}}$	rate of O_2 consumption during a dive ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$)
$\dot{V}_{\text{O}_2,\text{recovery}}$	rate of O_2 consumption during post-dive recovery ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$)

(Frantzis, 1998; Jepson et al., 2003). Less certain is how these responses translate into physiological costs to the escaping animal.

Although such changes in swimming performance from routine to elevated levels are theoretically associated with an increase in energetic costs (Fig. 1), they have rarely been measured or estimated in dolphins or whales. This is due in part to the difficulty of simultaneously measuring metabolic rate and behavior in free-ranging cetaceans. Indirect and comparative evidence (i.e. Ponganis et al., 1993; Williams et al., 1993; Crocker et al., 1997; Acevedo-Gutierrez et al., 2002) and theoretical models (Williams et al., 1996) have provided some insights. Regardless, the cost of a swimming stroke across the range of speeds for swimming and diving remains unknown for cetaceans. Furthermore, how these costs affect normal diving behavior or flight responses of whales and dolphins have not been determined.

To address this, we measured the energetic cost of producing a swimming stroke by exercising and diving bottlenose dolphins. Oxygen consumption and stroking kinematics of trained dolphins were measured simultaneously during static exercise while pushing on a load cell and during submerged swimming at 10 m depth. The inter-relationship between swimming performance and energetics for dolphins was determined and then used to model the cost of stroking during routine and aerobic flight speeds for larger and smaller odontocetes ranging in size from 42 to 2738 kg. These data were subsequently used to investigate the changes in the energetic cost of diving in a beaked whale exposed to anthropogenic sound, and thus provide a new metric for predicting the energetic cost of escape by wild cetaceans.

MATERIALS AND METHODS**Animals and experimental design**

Six adult, male bottlenose dolphins [*Tursiops truncatus* (Montagu 1821)] and one adult, female killer whale [*Orcinus orca* (Linnaeus 1758)] participated in these trials. The animals were housed in saltwater pools at Long Marine Laboratory (University of California, Santa Cruz) and collaborating aquariums that maintained water temperatures at 20.0–26.0°C (dolphins) and 12.6–13.7°C (killer whale) with depths ranging from 3 to 13 m depending on species. All cetaceans were fed multiple times daily on a mixed fish diet supplemented with vitamins, which included mackerel, herring, squid and capelin depending on the facility. The dolphins and the killer

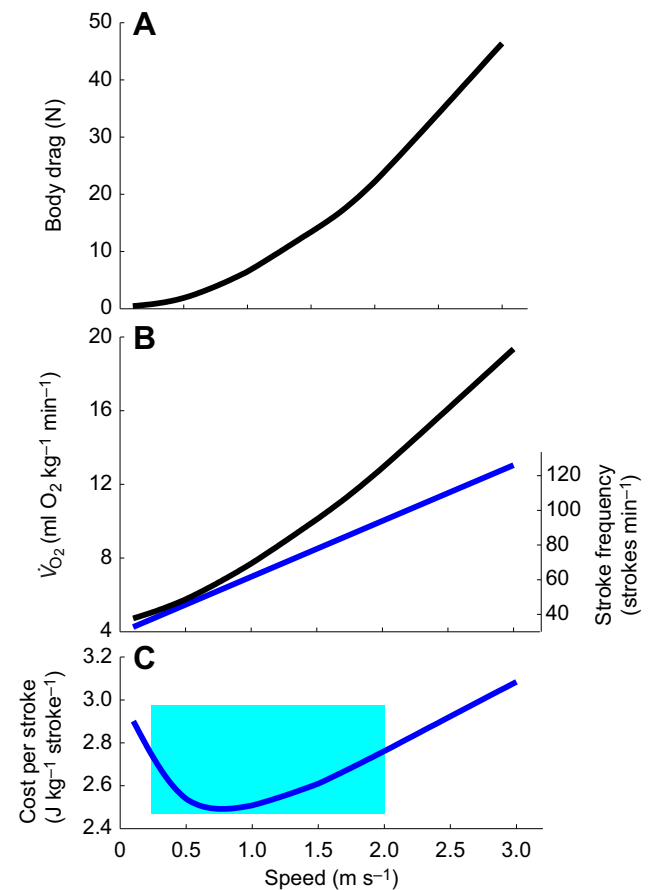


Fig. 1. The inter-relationship between energetics, biomechanics and hydrodynamics in a swimming marine mammal. (A) Hydrodynamic drag, (B) oxygen consumption and stroke frequency and (C) the energetic cost per stroke are shown in relation to speed for the harbor seal. All data were collected on a trained, adult seal swimming horizontally in a flume or an annular saltwater tank. Lines are the least squares regressions as described in Williams and Kooyman (1985) and Davis et al. (1985). Note the effect of the non-linear increase in oxygen consumption (black line in B) and the linear increase in stroke frequency (blue line in B) on stroking costs in C. The shaded blue box in C denotes the preferred swimming speeds of the seal.

whale were trained over at least 6 months using positive reinforcement and operant conditioning to voluntarily rest or exercise at various levels prior to data collection. All procedures were approved by the University of California Santa Cruz Institutional Animal Care and Use Committee and animal use committees of the collaborating institutions following National Institutes of Health guidelines. This study was conducted under Marine Mammal Permits through the US NOAA Fisheries Office of Protected Species.

The energetic costs associated with swimming and diving by bottlenose dolphins were determined by simultaneously measuring the rate of oxygen consumption (\dot{V}_{O_2}) and stroking mechanics (stroke frequency and amplitude, swimming gait) during static exercise and free diving. During static exercise, the time course and magnitude of force generation during swimming movements were determined for dolphins trained to voluntarily push against a load cell mounted on the side of a pool (Goforth, 1990; Williams et al., 1993) (Fig. 2A). These data were compared with data from performances of similarly sized dolphins freely swimming at 10 m depth in large saltwater pools while wearing a three-axis accelerometer recorder or electrocardiogram (ECG)–accelerometer (ACC) recorder (Williams et al., 2015a). Corresponding

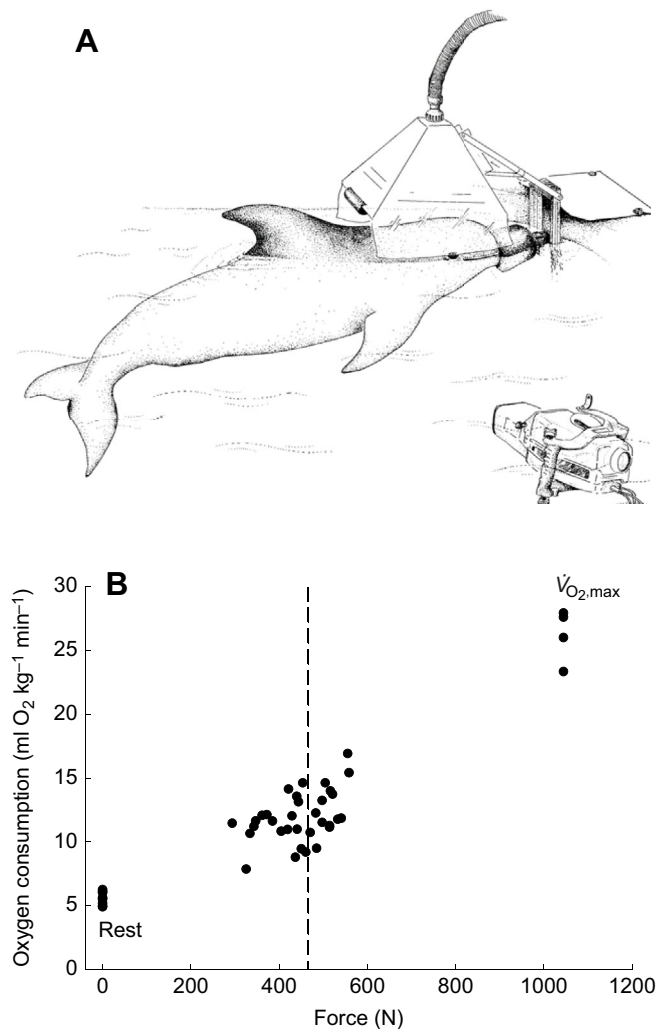


Fig. 2. Experimental setup and oxygen consumption of bottlenose dolphins voluntarily swimming against a load cell. (A) By positioning in front of the load cell, expired air of exercising dolphins was collected in a metabolic hood mounted overhead; stroking movements were monitored simultaneously with a submersible camera. (B) Oxygen consumption of resting, preferred exercise loads and maximum exercise by dolphins plotted in relation force produced by pushing against a load cell. Each point represents a separate trial ($n=46$ from rest to maximum). The dashed vertical line denotes the average force level selected by the dolphins for all trials.

measurements of \dot{V}_{O_2} were used to determine the energetic cost per stroke under each exercise condition and then compared to values calculated for larger and smaller odontocetes.

Energetic cost of force production in exercising dolphins

Two dolphins (average body mass during the study=182 kg) were trained over a 2-year period to use swimming movements to voluntarily push against a padded load cell (Transducer Techniques, HSW series, Temecula, CA, USA) (Fig. 2A) mounted at water level on the side of a pool. The animals were positioned by a trainer in a straight-line axis with the load cell, and remained submerged except for the top of the blowhole and dorsal fin. The dolphins selected the preferred load level during the first 5 s of each trial and maintained the same level of effort for 5–18 min. Signal output from the load cell was amplified and continuously recorded at 600 Hz on a computer (Peak Performance Technologies, Inc., Englewood, CO, USA). The output signals were also used to provide feedback about performance levels to the trainers

and the exercising dolphin through acoustic cues using a computer-controlled hydrophone (Goforth, 1990). Swimming movements (fluke mechanics, stroke frequency) of the dolphins on the load cell were recorded simultaneously with a digital camera (Panasonic CL350, Secaucus, NJ, USA) mounted in an underwater housing, and synchronized to the load cell output using a motion analysis system (Peak Performance Technologies). The entire system was calibrated using known weights and by comparing the timing of movements with a digital clock placed in the field of view. Oxygen consumption of the exercising dolphins (see below) was measured during 37 load cell trials using a metabolic hood placed on the water surface and open-flow respirometry following the procedures of Williams et al. (1993).

Energetic cost of diving and stroke production in swimming dolphins

Four adult, male bottlenose dolphins (mean body mass=229.3±7.5 kg) were studied under three experimental conditions: (1) voluntary rest on the water surface, (2) rest while submerged and (3) during voluntary submerged swimming and diving exercise. Resting measurements were taken while the dolphins floated dorsal side up next to a dock or as they stationed in front of a trainer at approximately 8 m depth and then returned to a metabolic hood on the water surface. During active diving tests, the dolphins descended to 10 m, performed a horizontal steady-state swim through submerged hoops positioned on the bottom of the pool, and then directly ascended to a metabolic hood on the water surface. Each experimental session began with a 1–5 min period of surface resting followed by diving and then a 10–15 min recovery period upon resurfacing. Individual dives were randomly divided into submerged resting or swimming trials ranging in duration from 1 to 6.5 min with the dolphins selecting preferred speeds for swimming.

In a subset of trials the dolphins were trained to wear a submersible three-axis accelerometer recorder (3×2.5×0.5 cm, Hobo Pendant G Waterproof Data Logger, Onset Computer Corporation, Bourne, MA, USA) attached to a neoprene and Velcro strap worn around the peduncle, or a custom-designed heart rate unit (16 cm long×3 cm diameter tube, ECG-ACC depth recorder; UUB/4-EIAP ECG/IBI/Acceleration/Pressure Recording System, UFI, Morro Bay, CA, USA) in a neoprene vest (Williams et al., 2015a). Signals from each transducer were recorded at 50–100 Hz. Two suction cup electrodes (5 cm diameter with a 2 cm diameter silver plate electrode) were used for ECG monitoring as described in Williams et al. (2015a). To avoid potential complications with additional drag owing to the vest, the low-profile peduncle accelerometer was used during trials when oxygen consumption was measured for assessment of stroking costs. The ECG-ACC with vest was used only during trials assessing heart rate responses in relation to stroking mechanics.

Oxygen consumption

Aerobic costs of swimming and diving were determined from the rate of oxygen consumption, as measured by open-flow respirometry following the protocols of Williams et al. (2004). Dolphins were trained over an 8-month period to rest quietly while breathing in a Plexiglas metabolic hood (35×50×75 cm) mounted next to a floating deck. On each experimental day, the dolphin voluntarily performed a dive in the morning following their normal overnight fast. This was followed by their typical morning feeding session. A second post-prandial dive was conducted in the afternoon with measurements scheduled to prevent identical tests on sequential days. Air temperature (T_{air}) was 24.0°C and water temperature (T_{water}) was 26.0°C during the trials.

Ambient air was drawn through the hood at 250–300 l min⁻¹ with a calibrated vacuum pump (Sable Systems International, Inc., Henderson, NV, USA). At these flow rates, the fractional concentration of oxygen in the hood remained above 0.2000 except for the initial seconds immediately following a dive. Samples of air from the exhaust port of the hood were dried (Drierite®) and scrubbed of carbon dioxide (Sodasorb®) before entering an oxygen analyzer (FMS, Sable Systems International, Inc.). The percentage of oxygen in the expired air was monitored continuously and recorded once per second with a personal computer using Sable Systems Expedata software. Oxygen consumption was then calculated using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77 based on other marine mammals on a mixed fish diet (Davis et al., 1985; Williams et al., 2004). All values were corrected to STPD, and the entire system was calibrated daily with dry ambient air (20.94% O₂) and every week with dry N₂ gas according to Fedak et al. (1981) and Davis et al. (1985).

For resting measurements, the lowest metabolic rate maintained for a minimum of 10 min was used as a baseline. Oxygen consumption during a dive was calculated from the difference between total recovery oxygen consumption and the resting rates in water following the procedures of Scholander (1940) and Williams et al. (2004). Baseline post-absorptive oxygen consumption rates were determined for each dolphin resting on the water surface and used to determine the duration of post-dive recovery. Following each voluntary dive, oxygen consumption was monitored continuously, and diving metabolism calculated from the recovery oxygen consumed in excess of resting rates for either post-absorptive or post-prandial dolphins as appropriate. In separate tests of similar dive duration, we measured post-dive blood lactate concentration (range=1.42–4.69 mmol l⁻¹) from blood vessels located on the ventral surface of the dolphin's fluke to ensure sub-maximal metabolic conditions. Previously, we reported that exercise performance in adult bottlenose dolphins declines when the concentration of lactate exceeds 11.2 mmol l⁻¹ (Williams et al., 1993).

Measurements of resting oxygen consumption were conducted similarly for an adult female killer whale (body mass=1837 kg) to provide a baseline for stroke cost calculations. A larger Plexiglas metabolic hood (40×145×170 cm) was constructed for the whale and mounted on the edge of a saltwater pool. Flow rate through the hood was 425–450 l min⁻¹, with $T_{\text{air}}=11.0\text{--}17.8^{\circ}\text{C}$ and $T_{\text{water}}=12.6\text{--}13.7^{\circ}\text{C}$ during the trials.

Analyses and statistics

Stroke costs in bottlenose dolphins

The energetic cost per stroke for diving bottlenose dolphins swimming at routine preferred speeds was determined for each animal by dividing the total post-dive oxygen consumed by the corresponding number of strokes taken during the dive (S) as recorded by the three-axis accelerometers (described in 'Energetic cost of diving and stroke production in swimming dolphins', above). These values were compared with average stroking costs computed from three test methods: (1) static exercise on the load cell in which the oxygen consumed during preferred loads was divided by mean stroke frequency, (2) the slope of the relationship between total post-dive oxygen consumed and the number of strokes taken during a dive (S) (Williams et al., 2004) and (3) a hydrodynamic analysis based on summing resting maintenance metabolism (present study) and thrust power (Fish, 1998) at the same preferred speed. Maximum aerobic stroke costs were calculated from Williams et al. (1992) for bottlenose dolphins trained to follow a boat at 3.0 m s⁻¹. Stroke frequency at this speed was

77 strokes min⁻¹ and metabolic rate was based on the heart rate– \dot{V}_{O_2} relationship reported in the same study.

Comparative stroking costs in odontocetes

The energetic cost per stroke was calculated for a variety of odontocetes with the goal of developing a predictive allometric regression for swimming cetaceans. In addition to stroking costs determined in the present study for bottlenose dolphins, we used published and new data for metabolic rates and kinematics of odontocetes ranging in mass from 42.5 kg harbor porpoises (*Phocoena phocoena*) to a 2738 kg female killer whale to determine stroking costs across species. Calculations for the smallest species, the harbor porpoise, were based on dividing the reported average oxygen consumption at preferred and maximum swimming speeds (10.7 and 36.0 ml O₂ kg⁻¹ min⁻¹, respectively, from Otani et al., 2001) by the speed-matched stroke frequencies (99 and 132 strokes min⁻¹, respectively; Curren, 1994). In the absence of $\dot{V}_{\text{O}_{2,\text{max}}}$ measurements, we assumed that the aerobic scope of harbor porpoises from minimum preferred swimming to maximum \dot{V}_{O_2} is similar to that measured for *Tursiops* (~4.5 times resting levels; see Fig. 2B and Williams et al., 1993).

Similar analyses were conducted for beluga whales and killer whales. Owing to the similarity in metabolic rates for surface resting and routine swimming speeds for cetaceans (Williams et al., 1992; Yazdi et al., 1999; Otani et al., 2001; Kriete, 1995), resting values were used as a proxy for metabolism at slow preferred swimming speeds for those cetaceans for which swimming metabolic values were unavailable. Metabolic rate estimated for 645 kg beluga whales swimming next to a boat (5.1 ml O₂ kg⁻¹ min⁻¹ at 1.6 m s⁻¹; Shaffer et al., 1997) was divided by the speed-matched stroke frequency for similarly sized belugas (45.9 strokes min⁻¹ from Fish, 1998). Maximum aerobic stroking cost was calculated from 4.5 times this minimum surface \dot{V}_{O_2} and a stroke frequency of 83 strokes min⁻¹ at 3.0 m s⁻¹ (from Fish, 1998), representing the fastest aerobic speed for freely swimming, open ocean belugas (Shaffer et al., 1997).

For killer whales, we used our measured metabolic rates for an 1837 kg adult female trained to rest on the water surface beneath a metabolic hood as described above. Mean surface resting metabolic rate was divided by an average stroke frequency for wild killer whales (25.8 strokes min⁻¹) swimming at a routine speed of 1.4 m s⁻¹ (Sato et al., 2007). Maximum aerobic stroking costs were based on 4.5 times resting rates, as described above for other odontocetes, divided by stroke frequency at 4.0 m s⁻¹ (66 strokes min⁻¹ from Rohr and Fish, 2004). Stroking costs were also determined for a larger 2738 kg female killer whale whose metabolic rates for resting and maximum swimming were determined from breath-by-breath oxygen consumption by Kriete (1995). These values for \dot{V}_{O_2} were divided by kinematic data from Rohr and Fish (2004) for preferred and maximum aerobic swimming.

In addition to these calculations for total metabolic cost per stroke, we determined the energy expended for locomotion alone, termed the locomotor cost (LC), by subtracting maintenance metabolic costs (based on Kleiber, 1975) from oxygen consumption for preferred and maximum aerobic performance. The resulting net metabolic cost was divided by stroke frequency as described above and in Williams et al. (2004). All values are reported in J kg⁻¹ stroke⁻¹ using a conversion factor of 20.1 J per ml O₂ for comparison with previous studies.

Oxygen stores of beaked whales

To determine the proportion of onboard oxygen stores used by a Cuvier's beaked whale (*Ziphius cavirostris* Cuvier 1823) exposed to

anthropogenic noise in our example of flight responses, we calculated the total body oxygen available in the lungs, blood and muscle of a 2500 kg whale. Currently, this class of deep-diving odontocete is considered unique in terms of the comparatively high levels of muscle myoglobin in the skeletal muscle as well as the high proportion of body mass composed of muscle (Velten et al., 2013). To account for this, we assumed that skeletal muscle mass of the Cuvier's beaked whale was proportionately the same as reported for other deep-diving beaked whales (48% of body mass) and that myoglobin content was 73.4 g Mb kg⁻¹ muscle (Velten et al., 2013). Multiplying by the oxygen carrying capacity of mammalian myoglobin (1.34 ml O₂ g⁻¹ Mb) results in 118 liters of O₂ available in the beaked whale's skeletal muscles. This muscle oxygen store is only a portion of the total body oxygen store of the odontocete, which ranges from 30% of the total store (Noren and Williams, 2000) to 54% (Velten et al., 2013); we used a mean value of 40% as the conservative estimate for this study, with a resulting total body oxygen store of 295 liters of O₂ for a 2500 kg Cuvier's beaked whale.

Statistics

Least-squares methods (SYSTAT, 2005) were used to examine the relationships between oxygen consumption rates during recovery and during diving with stroke frequency, heart rate, number of strokes taken during a dive and dive duration. Because of the non-linear effect of body drag on metabolic rate in swimming mammals (Fig. 1), we used an iterative analysis to compare linear and non-linear models for evaluating the correlation between oxygen consumption rates and both heart rate and stroke frequency; in each case, the best-fit regressions are reported. Allometric regressions for locomotor costs in relation to body mass were determined for preferred and maximum aerobic performance levels using linear models only. All mean values are reported as means±1 s.e.m. unless noted. Statistical data are tabulated in the text (Table 1), with electronic versions available upon request from the senior author through the UCSC Mammal Physiology Project database.

RESULTS

Energetic cost of force production in exercising dolphins

Results from the static exercise tests on the load cell demonstrated that oxygen consumption increases with force production by fluke

movements of dolphins (Fig. 2B). The preferred level of peak force generated by bottlenose dolphins on the load cell ranged from 294 to 559 N (Fig. 2B), with a mean voluntary selected force of 465±5 N ($n=119$ trials). Stroke frequency during the preferred loads was 53.0±0.6 strokes min⁻¹. Corresponding oxygen consumption ranged from 7.84 to 16.90 ml O₂ kg⁻¹ min⁻¹ (mean=11.56±0.39 ml O₂ kg⁻¹ min⁻¹ for 37 trials). This level of oxygen consumption was 2.1 times resting values and only 39.2% of the maximum oxygen consumption measured for dolphins pushing on a load cell (Fig. 2B) (Williams et al., 1993).

Energetic cost of recovery, diving, and stroke production in swimming dolphins

The post-dive recovery period of the bottlenose dolphins was characterized by tachycardia and a consistent elevated \dot{V}_{O_2} compared with surface resting levels ($\dot{V}_{O_2,rest}=6.35\pm 0.17$ ml O₂ kg⁻¹ min⁻¹, $n=4$ dolphins). As reported previously, the heart rate of the diving dolphins declined from approximately 130 beats min⁻¹ pre-dive to 30–60 beats min⁻¹ depending on the level of exercise upon submergence (Williams et al., 2015a); it then ranged from 80 to 132 beats min⁻¹ during recovery (Fig. 3). Variability in heart rate during the post-dive phase corresponded to the breathing patterns of the dolphins, with the highest heart rates associated with the exhalation–inspiration transition. The animals recovered to resting physiological levels within 5–10 min of surfacing after a dive, and showed a relatively narrow range of values for the rate of oxygen consumption ($\dot{V}_{O_2,recovery}=11–18$ ml O₂ kg⁻¹ min⁻¹) during the post-dive recovery period. There was a modest increase in $\dot{V}_{O_2,recovery}$ with duration of the dive as described by:

$$\dot{V}_{O_2,recovery} = 11.70 + 0.74D, \quad (1)$$

where $\dot{V}_{O_2,recovery}$ is in ml O₂ kg⁻¹ min⁻¹ and D is dive duration (min) ($n=22$, $r^2=0.15$, $P=0.07$; Fig. 3 inset).

To determine the relationship between the rate of oxygen consumption during the dive ($\dot{V}_{O_2,dive}$) and heart rate (f_H), we first calculated heart rate from measured stroke frequencies (f_S) using the relationship $f_H=2.46+0.99f_S$ ($n=88$, $r^2=0.72$), reported previously for these dolphins (Davis and Williams, 2012). These values were then related to the stroke-matched rate of oxygen consumption

Table 1. Energetic cost of diving by a wild Cuvier's beaked whale exposed to experimental mid-frequency sonar

	Depth (m)	Duration (min)	Dive cost (J kg ⁻¹)	Dive cost (liters O ₂)	Dive MR (ml O ₂ kg ⁻¹ min ⁻¹)	Maintenance cost (%)	Preferred stroking cost (%)	Max. aerobic stroking cost (%)
Pre forage	1734	66	4315	537	3.25	43.4	26.8	29.8
Pre 1	437	31	2109	262	3.38	41.8	29.6	28.5
Pre 2	364	32	1570	195	2.44	57.8	35.4	6.9
Pre 3	348	25	1726	215	3.43	41.1	18.5	40.4
Pre 4	311	25	1589	198	3.16	44.6	25.1	30.3
Mean	365	28.3	1749	218	3.10	46.3	27.2	26.5
s.e.m.	26.4	1.9	125	15.5	0.23	3.9	3.6	7.0
During	1125	69	4547	566	3.28	43.0	26.0	31.1
Post 1	245	17	1588	197	4.65	30.3	10.7	58.9
Post 2	273	13	1367	170	5.23	27.0	7.9	65.1
Post 3	444	26	2273	283	4.41	31.9	16.7	51.4
Mean	320	18.7	1742	216	4.76	29.7	11.8	58.5
s.e.m.	62.2	3.8	272	33.7	0.24	1.4	2.6	4.0

Sequential dives include a deep foraging dive followed by four pre-exposure dives (Pre 1–4), a deep dive interrupted by sonar (During), and lastly three dives immediately after sonar exposure (Post 1–3). Except for the pre-foraging dive, time–depth profiles are provided in Fig. 7B. Data include the depth and duration of the dive, the energetic cost of the dive from Eqn 8, the oxygen store expended (liters O₂), metabolic rate (MR) during the dive, and the percentage of the dive cost used to support maintenance functions (Maintenance), preferred stroking periods and aerobic maximum stroking periods. Means±1 s.e.m. are shown for each dive grouping and category where appropriate.

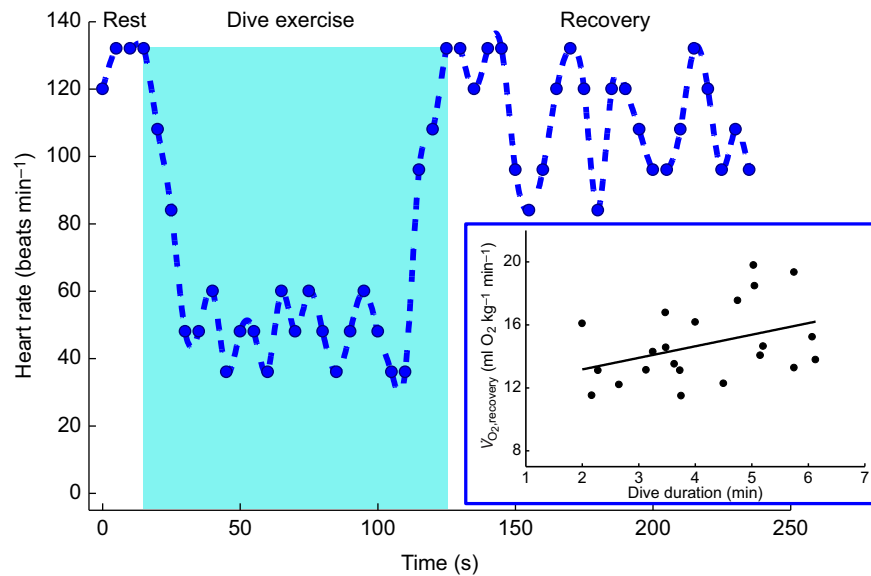


Fig. 3. Cardiac and metabolic recovery from diving in bottlenose dolphins. Representative sequential changes in heart rate in relation to time diving are presented for an adult dolphin. Pre-dive rest on the water surface, voluntary diving exercise (blue background) and post-dive recovery periods are shown. Each point represents the instantaneous heart rate recorded over a 5 s period, with trend lines shown between sequential points. The inset illustrates the rate of oxygen consumption recorded during the recovery period in relation to the duration of the dive. Each point in the inset denotes a single dive, with data for four dolphins combined; the line is the least squares regression as described by Eqn 1.

during the dive ($\dot{V}_{O_2, \text{dive}}$; ml O₂ kg⁻¹ min⁻¹). As predicted, $\dot{V}_{O_2, \text{dive}}$ increased non-linearly with both heart rate (f_H ; beats min⁻¹) and stroke frequency (f_S ; strokes min⁻¹) (Fig. 4), suggesting an underlying hydrodynamic effect on energetics as in Fig. 1. The best fit regressions ($n=20$, $r^2=0.51$, $P=0.0026$; and $n=20$, $r^2=0.51$, $P=0.0026$, respectively) were:

$$\dot{V}_{O_2, \text{dive}} = 9.98 - 0.34f_H + 0.006f_H^2 \quad (2)$$

and

$$\dot{V}_{O_2, \text{dive}} = 9.19 - 0.30f_S + 0.006f_S^2. \quad (3)$$

In contrast, the total recovery oxygen consumed ($O_{2, \text{TOTrecovery}}$; ml O₂ kg⁻¹), an indicator of oxygen store depletion during the dive, increased linearly with dive duration and the number of strokes taken on a dive (Fig. 5). The relationship between $O_{2, \text{TOTrecovery}}$ and dive duration was highly variable ($n=21$, $r^2=0.38$, $P=0.0031$), where:

$$O_{2, \text{TOTrecovery}} = 8.95 + 4.98D. \quad (4)$$

This variability was explained in part by differences in swimming effort by the dolphins as reflected in the relationship between total O₂ recovery and the number of strokes taken during a dive (S) ($n=20$, $r^2=0.66$, $P<0.0001$):

$$O_{2, \text{TOTrecovery}} = 5.77 + 0.14S. \quad (5)$$

Following the procedures of Williams et al. (2004), the slope of this relationship provides a value of 2.81 J kg⁻¹ stroke⁻¹ for the mass-specific energy expended per stroke by the dolphins swimming submerged at routine preferred speeds.

Energetic cost per stroke in bottlenose dolphins

The total cost per stroke for individual bottlenose dolphins in this study was also determined by dividing the oxygen consumed during recovery by S . The results ranged from 2.32 ± 0.13 to 3.89 ± 0.37 J kg⁻¹ stroke⁻¹ among the four dolphins (Fig. 6; $n=3$ for each animal). The mean value for all four animals was 3.31 ± 0.20 J kg⁻¹ stroke⁻¹ ($n=12$). This value is comparable to 3.14 J kg⁻¹ stroke⁻¹ reported for freely swimming dolphins

following a boat at a cruising speed of 2.0 m s⁻¹ (Williams et al., 1992), and 3.20 J kg⁻¹ stroke⁻¹ calculated from a hydrodynamic model in which we summed the calculated thrust power of dolphins

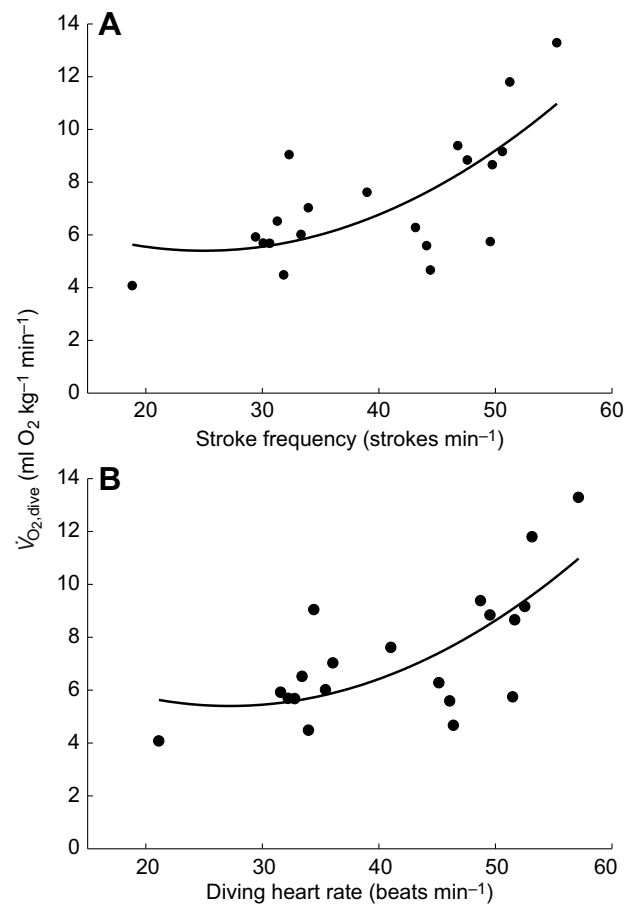


Fig. 4. Metabolic responses of voluntary diving bottlenose dolphins. The rate of oxygen consumption during a dive is plotted in relation to two metrics of performance, stroke frequency (A) and heart rate (B), for four dolphins combined. Each point denotes the average value for a single dive by an individual animal. Solid lines are the least squares non-linear regressions as described by Eqns 2 and 3.

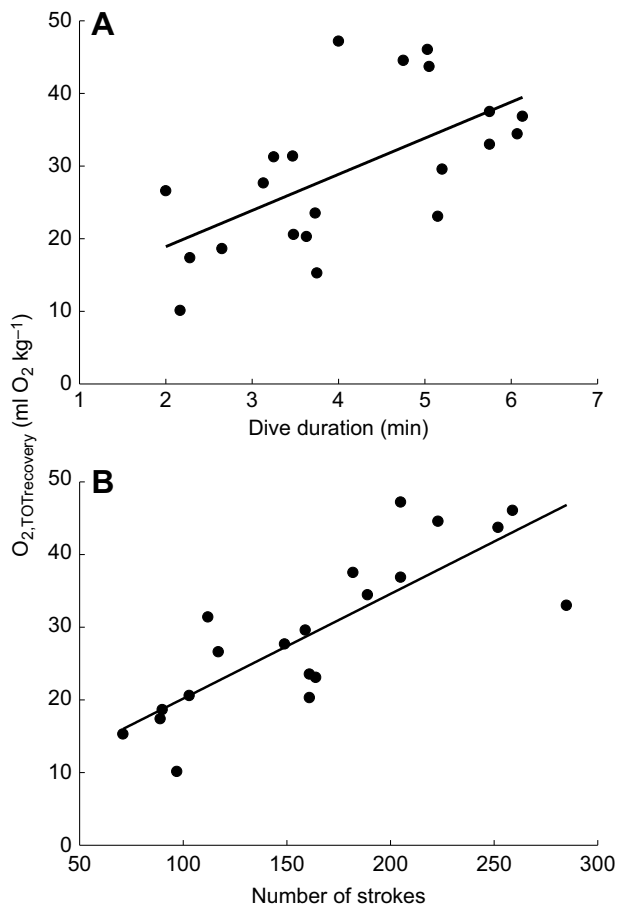


Fig. 5. The energetic cost of diving in bottlenose dolphins. Total recovery oxygen consumed in relation to dive duration (A) and number of strokes taken during a dive (B) by bottlenose dolphins is shown. Because baseline oxygen consumption during recovery is removed, the data represent the total oxygen demanded during the dive only. Each point denotes the value for a single dive by an individual animal with data for four dolphins combined. Solid lines are the least squares linear regressions as described by Eqns 4 and 5.

(Fish, 1998) and resting metabolism measured in the present study. The maximum aerobic stroking cost was $6.41 \text{ J kg}^{-1} \text{ stroke}^{-1}$ as calculated from stroke frequency and oxygen consumption rates reported for dolphins freely swimming next to a boat (Fig. 6) (Williams et al., 1992).

Resting metabolic rate of a female killer whale

Mean surface resting metabolic rate of the 1837 kg female killer whale was $4.34 \pm 0.14 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ ($n=4$ trials). This value was 2.7 times the predicted value based on Kleiber (1975), and follows trends for smaller odontocetes and other marine mammals (Williams et al., 2001; McNab, 2008). This differs from the results of Worthy et al. (2014), who reported no difference between predicted values and measured basal metabolic rate for a 5318 kg male killer whale.

Calculated stroking costs for other odontocetes

The calculated energetic cost per stroke for harbor porpoises based on the average oxygen consumption at preferred and maximum swimming speeds (Otani et al., 2001) and speed-matched stroke frequencies (Curren, 1994) was $2.20 \text{ J kg}^{-1} \text{ stroke}^{-1}$ during preferred swimming and $5.48 \text{ J kg}^{-1} \text{ stroke}^{-1}$ during maximum aerobic performance (Fig. 6). In comparison, the stroking costs for

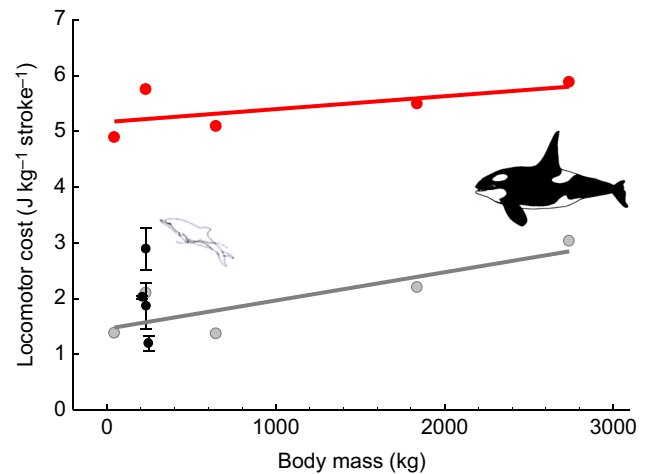


Fig. 6. Locomotor cost per stroke in relation to body mass for odontocetes. Measured values for bottlenose dolphins (black symbols for individual dolphins with the mean denoted by the grey symbol) are compared with calculated values for other odontocetes. Data for preferred swimming (grey symbols and line) are compared with values determined for maximum aerobic performance (red symbols and line). The solid lines are the least squares linear regressions as described by Eqns 6 and 7. Data points denote values for 42 kg harbor porpoises, 229 kg bottlenose dolphins, 645 kg beluga whales, and 1837 and 2738 kg female killer whales as described in the Results.

645 kg beluga whales ranged from $2.23 \text{ J kg}^{-1} \text{ stroke}^{-1}$ at preferred speeds to $5.57 \text{ J kg}^{-1} \text{ stroke}^{-1}$ for maximum aerobic performance during open-ocean swimming. Stroking costs were highest for the largest odontocete in this study, the killer whale. Stroking cost during preferred swimming for an 1837 kg adult female killer whale was $3.38 \text{ J kg}^{-1} \text{ stroke}^{-1}$, based on our measured metabolic rate presented above; maximum aerobic stroking cost was $5.95 \text{ J kg}^{-1} \text{ stroke}^{-1}$ for this animal (Fig. 6). To provide a comparison with wild killer whales, we also calculated stroking costs for a similarly sized, free-ranging subadult male killer whale instrumented with a customized suction-cup tag with onboard accelerometry (Cade et al., 2016) in northern Norway. Routine stroke frequency measured for this animal was $34.8 \text{ strokes min}^{-1}$, with an average speed of $<1.5 \text{ m s}^{-1}$ and a sustained maximum speed of $3.5\text{--}4.0 \text{ m s}^{-1}$ (D. E. Cade, Stanford University, personal communication). Using our metabolic data and these kinematic values, we found that the resulting stroking costs of this wild animal were within 26% of the values calculated for the adult female here. Lastly, stroking costs for a larger 2738 kg female killer whale, based on breath-by-breath oxygen consumption (Kriete, 1995) and kinematic values from Rohr and Fish (2004), were $4.11 \text{ J kg}^{-1} \text{ stroke}^{-1}$ during preferred swimming and $6.30 \text{ J kg}^{-1} \text{ stroke}^{-1}$ during maximum aerobic swimming performance (Fig. 6).

DISCUSSION

The cost of high level performance during swimming and diving

For obvious logistical reasons, direct measurements of the rate of oxygen consumption (\dot{V}_{O_2}) of diving marine mammals are limited primarily to non-cetacean species including pinnipeds (Kooyman et al., 1980; Castellini et al., 1992; Ponganis et al., 1993; Williams et al., 2004; Fahlman et al., 2008) and sea otters (*Enhydra lutris*; Yeates et al., 2007). For dolphins and whales, the \dot{V}_{O_2} for surfacing in shallow pools has been directly measured for harbor porpoises (Worthy et al., 1987; Otani et al., 2001) and bottlenose dolphins

(Yazdi et al., 1999). Both species demonstrated an economy of movement at preferred swimming speeds. Indeed, there is often little change in \dot{V}_{O_2} between rest and routine swimming speeds that is likely facilitated by the exceptional body streamlining of these cetaceans (Fish, 1998).

In the present study, we examined the combined effect of swimming and diving to 10 m on the \dot{V}_{O_2} of bottlenose dolphins. As reported for the surface-swimming porpoises and dolphins, \dot{V}_{O_2} changed little from resting to swimming at low stroke frequencies (<35 strokes min^{-1} ; Fig. 4A). Conversely, as would be predicted from hydrodynamic theory (Fig. 1), there was a marked increase in \dot{V}_{O_2} for higher level performances and stroke frequencies by the dolphins (Fig. 4) that ultimately affected the total amount of oxygen utilized during a dive (Fig. 5).

In view of this, it is not surprising that fast-swimming cetaceans often display a suite of behavioral strategies for minimizing body drag and mitigating the associated metabolic costs when swimming near the water surface and submerged. During high-speed surface swimming, dolphins will leap clear of the water (Au and Weihs, 1980) and wave-ride (Williams et al., 1992) to avoid the work of continuous stroking to move quickly. Similarly, passive gliding owing to changes in buoyancy with depth enables many species of marine mammals (Williams et al., 2000) including dolphins (Skrovan et al., 1999) to conserve limited on-board oxygen reserves while submerged. An important component of these strategies, particularly when submerged, is a change in swimming gait. Thus, high-speed swimming dolphins (Skrovan et al., 1999), as well as deep divers including Weddell seals (*Leptonychotes weddellii*; Williams et al., 2015a,b) and beaked whales (Martin López et al., 2015), switch between gliding, continuous stroking and burst-and-glide gaits throughout a dive.

In the present study, we found that such gait changes modify the energetic cost of stroking and of a dive. For the odontocetes examined here, the energetic cost per stroke was not constant as typically reported for stepping costs in terrestrial mammals (Taylor et al., 1982). Rather, it changes with stroke frequency, speed and body mass as expected from theoretical models for swimmers (Fig. 1C). This is evident by examining the locomotor cost of stroking (LC), which separates the energy expended for maintenance functions from the energetics of moving the flukes (Fig. 6). At slower preferred speeds when cruising, LC of odontocete cetaceans increases with body mass (M) from harbor porpoises to killer whales. Values ranged from 1.38 to 3.03 $\text{J kg}^{-1} \text{stroke}^{-1}$, respectively, as described by:

$$\text{LC}_{\text{preferred}} = 1.46 + 0.0005M, \quad (6)$$

where LC is in $\text{J kg}^{-1} \text{stroke}^{-1}$ and M is in kg ($n=5$ across 4 species, $r^2=0.72$, $P=0.069$). As cetaceans change to nearly constant stroke frequencies at higher performance levels, the relative energetic cost increases and the locomotor cost per stroke is described by a second allometric regression ($n=5$ across 4 species, $r^2=0.40$, $P=0.254$):

$$\text{LC}_{\text{aerobic,max}} = 5.17 + 0.0002M. \quad (7)$$

Clearly, not all strokes are equal in terms of energy expended for cetaceans, and are influenced by the swimming gait used by the animal.

A case study: the energetics of flight responses in the beaked whale

Because of the different locomotor costs for preferred and maximum aerobic swimming (Fig. 6) and the exponential

increase in energetic cost for high level performance by dolphins (Fig. 4), it is likely that the cost of flight by odontocetes is more complicated than simply counting the number of swimming strokes taken during a dive. Rather, the stroking gait of the animal must be considered. By predicting locomotor costs for different levels of swimming, Eqns 6 and 7 provide a means of assessing energetic costs that may be incurred as free-ranging cetaceans alter gaits during flight responses.

As a test, we examined how the energetic cost of a dive changes prior to and after exposure to anthropogenic noise in the Cuvier's beaked whale (*Ziphius cavirostris*), a deep-diving odontocete considered especially sensitive to environmental perturbation (Tyack et al., 2011; Pirota et al., 2012). Using accelerometer–depth data from DeRuiter et al. (2013), we calculated the locomotor costs for stroking by a 2500 kg beaked whale from Eqns 6 and 7 presented here. The resulting locomotor costs at preferred swimming gaits ($2.71 \text{ J kg}^{-1} \text{stroke}^{-1}$ for stroke frequencies <14 strokes min^{-1}) and at maximum aerobic performance during constant stroking ($5.67 \text{ J kg}^{-1} \text{stroke}^{-1}$ when stroke frequency ≥ 16 strokes min^{-1}) were then used to calculate the total energetic cost of a dive (C_{dive}) from:

$$C_{\text{dive}} = 20.1(9.98M^{-0.25})D + 2.71S_{\text{preferred}} + 5.67S_{\text{max}}, \quad (8)$$

based on Williams et al. (2004). Here, the diving cost in J kg^{-1} is separated into maintenance costs using mass-specific basal metabolic rate as a minimum level during diving (Hurley and Costa, 2001) multiplied by the duration of the dive (D , min), and stroking costs calculated from locomotor cost and S , the number of strokes taken during routine ($S_{\text{preferred}}$) and maximum aerobic (S_{max}) swimming gaits (see Williams et al., 2004 for details). Using the conversion factor of 20.1 J per ml of O_2 consumed, we then converted the resulting values into oxygen stores utilized during each dive.

Calculations included the energetic costs for dives matched for depth and duration occurring before and after experimental exposure to mid-frequency sonar (Table 1, Fig. 7) (DeRuiter et al., 2013). As reported previously, the beaked whale showed a shift in swimming gait from primarily burst and glide to nearly constant stroking following exposure to noise (Fig. 7A). For two matched dives to approximately 440 m, the most obvious behavioral effect was an 18.3% decrease in dive time and an increase in the range and mean stroke frequency (pre-exposure 437 m dive= 7.2 ± 1.6 strokes min^{-1} during an 11 min descent and 13.6 ± 0.8 strokes min^{-1} during a 19 min ascent; post-exposure 444 m dive= 10.2 ± 1.0 strokes min^{-1} during a 9 min descent and 16.9 ± 0.9 strokes min^{-1} during a 15 min ascent). Importantly, the whale spent over 4 min gliding on descent during the pre-exposure dive, and did not use this energy-saving gait during post-exposure diving.

These changes resulted in a concomitant increase in energetic costs (Table 1, Fig. 7C). Using Eqn 8 and the total number of strokes taken for each gait, a dive to 437 m before noise exposure required 2019 J kg^{-1} (262 liters O_2) to complete, while a 444 m dive after exposure demanded 2273 J kg^{-1} (283 liters O_2). Calculated metabolic rate during the post-exposure dive was 30.5% higher than before exposure. Furthermore, for all post-exposure dives examined there was a marked shift in the proportion of the dive cost used to support maintenance or stroking demands. Regardless of depth, dives occurring before or partially during noise exposure were supported by metabolic rates averaging $3.16 \pm 0.15 \text{ ml } O_2 \text{ kg}^{-1} \text{min}^{-1}$ ($n=6$ dives) that were partitioned as 45% for maintenance costs with the remainder divided nearly equally into preferred and maximum aerobic stroking costs for most dives (Table 1). For post-exposure dives, metabolic rate increased to

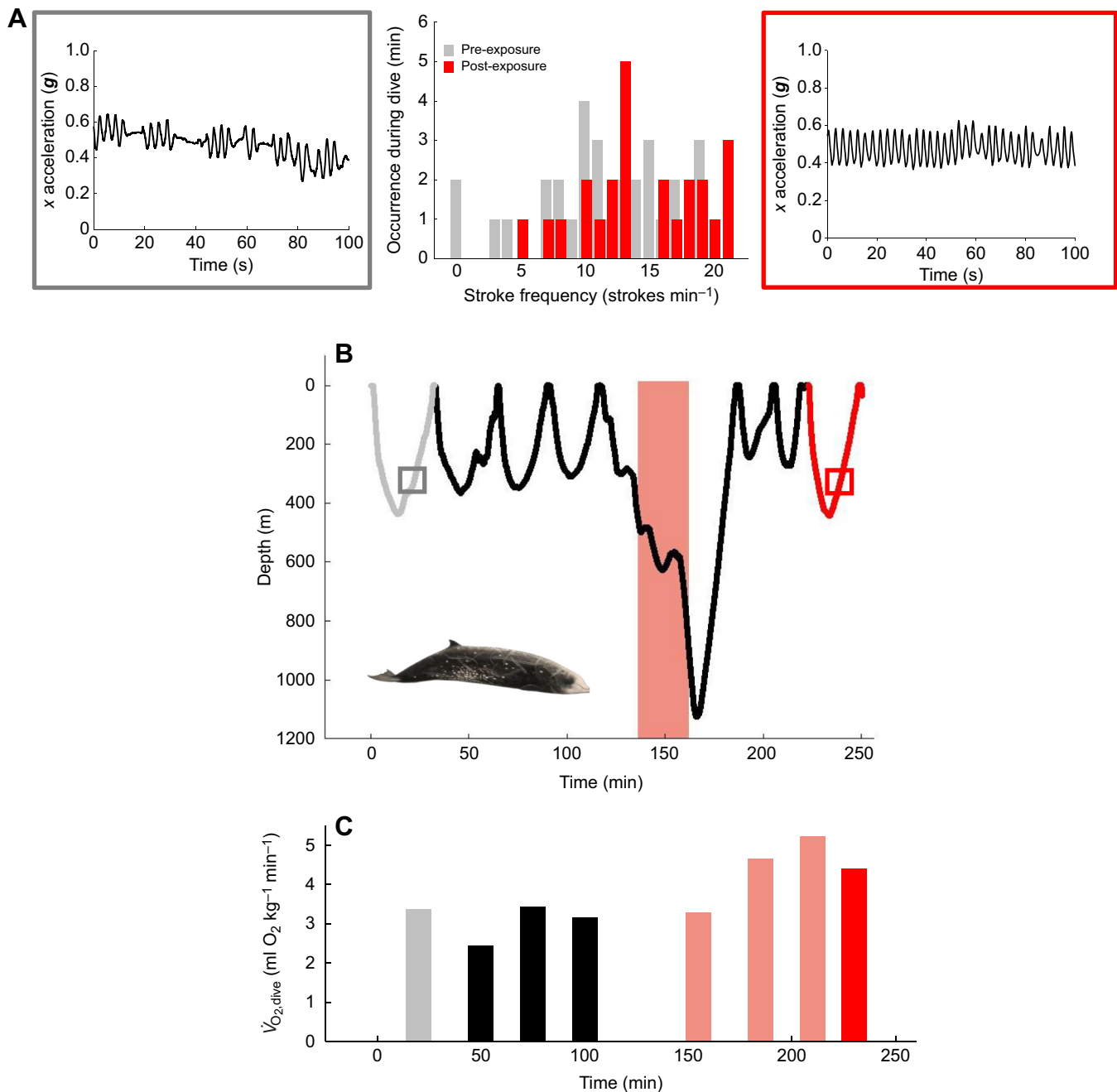


Fig. 7. Integrative effects of unanticipated noise on a deep-diving odontocete cetacean. Kinematic (A), behavioral (B) and energetic (C) responses to anthropogenic noise by a diving Cuvier's beaked whale are shown. (B) The 4-h sequential dive pattern of an adult beaked whale before, during and after exposure to mid-frequency sonar is shown. The timing of sonar exposure is denoted by the pink background. Matched dives to approximately 440 m are drawn in grey (pre-exposure) and red (post-exposure) (data from DeRuiter et al., 2013). Small boxes on the ascent portion of two matched dives in B correspond to the colored boxes in A showing the prevalent stroking gait pattern from the accelerometer during each period. The middle graph in A illustrates the shift in the range of stroke frequencies for these two matched pre- (grey) and post-exposure (red) dives. Here, the height of the bars corresponds to the occurrence of each level of stroke frequency (calculated per minute) during the entire dive. In C, the calculated rate of oxygen consumption in relation to sequential dive time as shown in B is compared for pre-exposure dives (grey and black bars), and dives taking place during and immediately after exposure (pink bars) and nearly 2 h post-exposure (red bar). (Whale illustration redrawn from P. Folkens.) Detailed data for the dives are presented in Table 1.

4.76 ± 0.24 ml O₂ kg⁻¹ min⁻¹ ($n=3$ dives), with maintenance and preferred stroking costs dropping to 29.7% and 11.8% of the diving cost, respectively, and maximum stroking costs increasing to 58.5%. This shift in energetic partitioning was apparent even 1.7 h following exposure to a single sonar event.

By comparing the sequence of dives before, during and after experimental sonar exposure (Fig. 7B, Table 1), we found that the

beaked whale tended to defend its theoretical dive limit, and hence remain aerobic, even during the post-exposure escape period. This was accomplished by reducing the depth and duration of post-exposure dives while increasing the use of energetically costly high-speed stroking. In this way, the proportion of the oxygen store expended remained below the total calculated store of 295 liters O₂ that would lead to prolonged anaerobiosis and lactate accumulation.

However, exceptionally long, deep dives (exceeding 1 h and 1000 m in depth), as occurred during pre-exposure foraging or during sonar exposure, exceeded these stores (Table 1), suggesting the involvement of anaerobic metabolism and possibly a reduction in maintenance metabolism through changes in non-essential organ function (Davis et al., 1983). Interestingly, a common strategy for reducing energetic costs during these extreme dives was prolonged (>9 min) gliding during descent, which demonstrates the crucial role of this gait in such deep-diving species.

Admittedly, this is just one example for one species of diving odontocete. However, it illustrates the power of integrating energetics with swimming behavior and dive characteristics to assess the impact of anthropogenic disturbance on a wild cetacean. It is likely that different species of cetaceans, including mystecete whales and highly active, coastal or deep diving marine mammals with different oxygen stores (Noren and Williams, 2000) and oxygen carrying globins (Williams et al., 2008), will have unique behavioral responses to disturbance. However, by using the integrated energetics approach described here, the physiological consequences and biological significance of these responses can be predicted.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.M.W.; Methodology: all authors; Investigation: all authors; Writing - original draft preparation: T.M.W.; Writing - review and editing: T.M.W., T.K., B.R., J.J., M.A.S.; Funding acquisition: T.M.W.; Resources: T.M.W., K.O., M.A.S.; Supervision: T.M.W., T.K., K.O., M.A.S.

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