COMPARATIVE KINEMATICS AND HYDRODYNAMICS OF ODONTOCETE CETACEANS: MORPHOLOGICAL AND ECOLOGICAL CORRELATES WITH SWIMMING PERFORMANCE

FRANK E. FISH*

Department of Biology, West Chester University, West Chester, PA 19383, USA
*e-mail: ffish@wcupa.edu

Summary

Propulsive morphology and swimming performance were compared for the odontocete cetaceans *Delphinapterus leucas*, *Orcinus orca*, *Pseudorca crassidens* and *Tursiops truncatus*. Morphological differences were apparent among the whales. The general body contour and low-aspect-ratio caudal flukes of *D. leucas* indicated that this species was a low-performance swimmer compared with the other species. Propulsive motions were video-taped as animals swam steadily in large pools. Video tapes were analyzed digitally using a computerized motion-analysis system. Animals swam at relative velocities ranging from 0.4 to 2.4 body lengths s^{-1}. The stroke amplitude of the flukes decreased linearly with velocity for *D. leucas*, but amplitude remained constant for the other species. Tail-beat frequencies were directly related to relative swimming velocity, whereas the pitch angle of the flukes was inversely related to relative swimming velocity. Unsteady lifting-wing theory was used with regression equations based on kinematics to calculate thrust power output, drag coefficients and propulsive efficiency. Compared with other species, *O. orca* generated the largest thrust power (36.3 kW) and had the lowest drag coefficient (0.0026), whereas *T. truncatus* displayed the largest mass-specific thrust power (23.7 W kg^{-1}) and *P. crassidens* had the highest efficiency (0.9). *D. leucas* did not swim as rapidly as the other species and had a comparatively higher minimum drag coefficient (0.01), lower mass-specific thrust power (5.2 W kg^{-1}) and lower maximum efficiency (0.84). Minimum drag coefficients were associated with high swimming speeds, and maximum efficiencies corresponded with velocities in the range of typical cruising speeds. The results indicate that the kinematics of the propulsive flukes and hydrodynamics are associated with the swimming behaviors and morphological designs exhibited by the whales in this study, although additional factors will influence morphology.

Key words: cetacean, whale, dolphin, swimming, hydrodynamics, power output, efficiency.

Introduction

Swimming by cetaceans is described as a highly derived locomotor behavior in which the caudal flukes act as a hydrofoil to generate thrust (Fish and Hui, 1991). The swimming motions incorporate dorsoventral bending of the posterior third of the body in conjunction with pitching of the flukes, which follow a sinusoidal pathway (Fish, 1993*b*; Curren *et al.* 1994). This locomotor pattern was categorized as carangiform with lunate-tail (thunniform) swimming (Lighthill, 1969, 1970; Fish *et al.* 1988) and is typical of some of the fastest marine vertebrates, including scombrid fishes, laminid sharks, pinnipeds and cetaceans (Lighthill, 1969).

Large morphological differences exist within the Cetacea that could affect swimming kinematics and dynamics and thus influence their behavioral ecology (Fish, 1993*a*; Curren *et al.* 1994). However, there is a paucity of reliable data on comparative swimming performance in cetaceans (for a review, see Fish and Hui, 1991). Most studies of cetacean swimming were confined to measurements of maximal swimming speeds (Lang and Daybell, 1963; Lang and Norris, 1966; Lang and Pryor, 1966; Lang, 1975; Lockyer and Morris, 1987). Recent studies of swimming kinematics have been limited to examination of a single species or low speeds (Kayan and Pyatetsky, 1977; Videler and Kamermans, 1985; Fish, 1993*b*; Curren *et al.* 1994). Thus, studies of dolphin swimming have not considered the full range of speeds or compared the swimming kinematics of different morphologically distinct species. As a result, an incomplete picture of dolphin swimming kinematics, energetics and hydrodynamics has emerged.

The purpose of the proposed study was to compare the swimming kinematics of various cetacean species displaying diverse morphologies. Swimming motions of beluga whale (*Delphinapterus leucas*), killer whale (*Orcinus orca*) and false

killer whale (*Pseudorca crassidens*) were compared with data from bottlenose dolphin (*Tursiops truncatus*) (Fish, 1993*b*). It was expected that cetaceans possessing morphological characters that reduce drag and enhance thrust production would demonstrate increased swimming performance (i.e. high speed, high efficiency) (Fish, 1993*a*). To test predictions of the association between morphological design and swimming performance, the kinematic data were used with a hydrodynamic model (Chopra and Kambe, 1977) to compute the thrust power, propulsive efficiency and drag over a wide range of swimming speeds.

Materials and methods

Experimental animals

The swimming motions of three species of trained odontocete whales were recorded at Sea World in Orlando, FL, USA, and San Antonio, TX, USA. The species included the false killer whale (*Pseudorca crassidens* Owen), beluga whale (*Delphinapterus leucas* Pallus) and killer whale (*Orcinus orca* Linnaeus). Experiments were performed in large elliptical pools with maximum lengths of 27.4–48.8 m. The curved portions of each pool were constructed of glass panels. A water depth of 1.4–2.1 m was visible through the panels. The depth of the pools was 7.3–11.0 m, and water temperatures were maintained at 20–22 °C for *D. leucas* and *P. crassidens*, and at 14 °C for *O. orca*.

Prior to each swimming bout, the animals were marked with zinc oxide reference points on the lateral aspects of the caudal peduncle. Marks were separated by a measured distance of 0.1–0.39 m and served as the scale for video analysis. Whales swam along the curved wall of the pool routinely or under the direction of human trainers. All whales were trained to swim near the water surface. The speed of the animals varied in response to cues from trainers.

Morphological measurements were obtained for each species (Table 1). Body length (*L*, m) is the linear distance from rostral tip to fluke notch, and fluke span (*S*, m) is the linear distance between fluke tips. Body mass (*M*, kg) was determined routinely by training the animals to lie on a force platform; these data were made available by Sea World. The surface area of the body (*S*$_a$, m^2) was estimated from scaled photographs of the appendages and the lateral body profile, assuming an axisymmetrical body and flat peduncle. The planar surface area of the flukes (*F*$_a$, m^2) and maximum body diameter (*D*, m) were measured from scaled photographs. Fineness ratio (*FR*) was calculated as *L/D*. The aspect ratio of the flukes (*AR*) was calculated as *S*^{2}/*F*$_a$, and the root fluke chord (*C*, m) was measured as the centerline distance from the leading to the trailing edge of the flukes. The sweepback was measured according to Magnuson (1970) as the angle between the perpendicular to *C* and a line extending from 25 %*C* to the fluke tip.

Film analysis

Animals were filmed with either ciné or video cameras.

Ciné films were taken at 64 frames s^{-1} using a Bolex H-16 ciné camera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9, focal length 16–100 mm) using 16 mm film (Kodak 4-X Reversal film 7277, ASA 400). Film records were analyzed by sequentially projecting individual frames of film with a stop-action projector (Lafayette Instrument Co., model 00100) onto a digitizer tablet (GTCO, Digi-Pad 21A71D4) interfaced to an IBM PC microcomputer. Video recordings of swimming whales were made using a Panasonic camcorder (DV-510) at 60 fields s^{-1}. Sequential body and fluke positions were digitized from individual frames of video tape with an AT-compatible computer, Panasonic AG-7300 video recorder, Sony PVM 1341 monitor and a video analysis system (Peak 2D, Version 4.2.4, Peak Performance Technologies, Inc.).

Kinematic data from film or video-tape records included mean swimming velocity (*U*, m s^{-1}), stroke cycle frequency (*f*, Hz) and amplitude of heave (*h*, m). Amplitude of heave is the maximum amplitude of the trailing edge of the flukes in the vertical plane (Yates, 1983). Pitch angle (*α*, rad) was measured as the angle between the tangent of the chordwise plane of the flukes (i.e. leading to trailing edge) and the axis of forward progression (Yates, 1983; Romanenko, 1995) and was estimated at midstroke (Curren *et al.* 1994).

To adjust for size differences between the whales, data were analyzed with respect to specific velocity (*U/L*) and Reynolds number (*Re*). Reynolds numbers are based on the whale's length (*L*, m) and swimming velocity (*U*) and the kinematic viscosity (*ν*) of sea water (1.044×10^{-6} m^2 s^{-1}) using the equation:

$$Re = LU/\nu. \tag{1}$$

Submersion depth (*H*) was measured from the surface to the centerline of the body.

Calculation of power output, efficiency and drag coefficient

A hydromechanical model of lunate-tail propulsion based on three-dimensional unsteady wing theory with continuous loading (planform B2: Chopra and Kambe, 1977; Yates, 1983) was used to calculate thrust power output (*P*$_T$), coefficient of drag (*C*$_D$) and Froude efficiency (*η*). Froude efficiency is defined as the mean rate of mechanical work derived from mean thrust divided by the mean rate of all work that the animal is performing while swimming (Chopra and Kambe, 1977). This model, which uses lifting surface theory, gives good accuracy for low-aspect-ratio (*AR*) (<6) conditions (Liu and Bose, 1993).

In the model, the relationship between reduced frequency (*σ*) and proportional feathering parameter (*θ*) determines the coefficient of thrust (*C*$_T$) and *η*. The reduced frequency is a measure of the unsteady effects of flow about the flukes, and is:

$$\sigma = \omega C/U, \tag{2}$$

where *ω* is the radian frequency, equal to 2π*f* (Yates, 1983). The feathering parameter, *θ*, is the ratio of the maximum *α* to

the maximum angle ($\omega h/U$) achieved by the trajectory of the pitching axis of the flukes (Yates, 1983) and is:

$$\theta = \alpha U/\omega h. \qquad (3)$$

The mean thrust power output (P_T) is given by:

$$P_T = 0.5\rho C_T U^3 F_a (h/C)^2, \qquad (4)$$

where ρ is the density of sea water. For a body moving at constant U, P_T is equal to the power output expended in overcoming drag, and the dimensionless drag coefficient (C_D) is calculated as:

$$C_D = P_T/0.5\rho S_a U^3. \qquad (6)$$

Because whales swimming near the water surface would have experienced increased drag due to wave formation, a drag coefficient corrected for submergence depth (C_{Dd}) was calculated (Hertel, 1966; Au and Weihs, 1980) as:

$$C_{Dd} = C_D/\gamma. \qquad (7)$$

The drag augmentation factor, γ, varies with relative submergence depth H/D, ranging from 1 to 5. A maximum value for γ occurs at $H/D=0.5$; minima occur at $-0.5>H>3$.

Results

Body and fluke design

Species varied in general appearance. *D. leucas* was elongate with relatively small paddle-like flippers, no dorsal fin and a skin with numerous folds. *O. orca* had a compact body with large rounded flippers and a moderately sweptback dorsal fin. *P. crassidens* was elongate with highly sweptback dorsal fin and flippers which tapered to a point at the tip. All three species had short rostra, whereas the rostrum of *T. truncatus* was long. *T. truncatus* had the general body form typical of the Delphinidae, which is long and stocky with a sweptback dorsal fin and medium-sized flippers that are rounded at the tips (Minasian *et al.* 1984).

Means and ranges of morphometric data are presented in Table 1. Means were computed either from values based on the number of individuals within a species or from values based on the total number of observations for all individuals within a species. The latter method calculated a weighted mean (Sokal and Rohlf, 1981) and was used to reflect the bias presented for the unequal number of sequences analyzed between individuals within a species. The weighted means were used in the calculation of least-squared regression equations for use in the model.

Body length among species varied 2.2-fold from 2.5 to 5.6 m, and body mass varied 12-fold from 192.8 to 2331.5 kg (Table 1). *O. orca* had the lowest mean *FR* of 4.81, followed in ascending order by *T. truncatus*, *D. leucas* and *P. crassidens*. The relatively long body and small maximum diameter of *P. crassidens* combined to produce a mean *FR* of 6.5. The estimated mean surface areas for *D. leucas*, *O. orca* and *P. crassidens* were 2.9, 15.7 and 13.5 % greater, respectively, than

Table 1. *Morphometrics of odontocetes tested*

Dimension	*Delphinapterus leucas*	*Orcinus orca*	*Pseudorca crassidens*	*Tursiops truncatus*
Number of individuals	3	6	5	5
Body mass (kg)	671.3 (664.2)	1601.7 (1645.4)	486.9 (535.8)	225.0 (214.9)
	589.7–725.7	841.9–2331.5	349.3–792.9	192.8–263.1
Body length (m)	3.64 (3.55)	4.74 (4.76)	3.75 (3.75)	2.61 (2.58)
	3.25–4.12	3.81–5.57	3.55–3.99	2.51–2.70
Maximum body diameter (m)	0.66 (0.66)	0.98 (0.99)	0.58 (0.60)	0.51 (0.51)
	0.62–0.70	0.80–1.15	0.53–0.69	0.48–0.58
Fineness ratio	5.53 (5.37)	4.81 (4.82)	6.50 (6.36)	5.15 (5.09)
	4.66–6.22	4.57–4.91	5.76–6.80	4.69–5.63
Surface area (m²)	5.85 (5.53)	11.98 (11.26)	5.12 (5.47)	2.70 (2.80)
	4.80–7.51	7.10–16.99	4.14–7.25	2.45–2.99
Fluke span (m)	0.85 (0.83)	1.19 (1.19)	0.82 (0.86)	0.66 (0.64)
	0.77–0.91	1.12–1.33	0.74–1.04	0.58–0.73
Planar fluke surface area (m²)	0.21 (0.20)	0.34 (0.32)	0.14 (0.15)	0.11 (0.10)
	0.17–0.24	0.28–0.53	0.11–0.20	0.09–0.12
Fluke chord (m)	0.32 (0.31)	0.40 (0.39)	0.26 (0.26)	0.22 (0.22)
	0.28–0.35	0.34–0.53	0.22–0.28	0.20–0.28
Fluke aspect ratio	3.43 (3.44)	4.38 (4.61)	4.83 (5.13)	4.06 (4.00)
	3.31–3.56	3.26–4.97	4.13–5.40	3.61–4.69
Sweepback (degrees)	28.91 (29.11)	20.74 (20.55)	29.81 (28.88)	30.95 (32.59)
	27.68–29.91	13.40–27.69	26.00–33.08	25.37–38.78

T. truncatus data are from Fish (1993*b*).

Values are means based on individuals, with the range given below. Values in parentheses are the weighted mean based on the total number of observations for all individuals within a species.

estimates of surface area based on the prediction equation of Fish (1993*b*).

P. crassidens had narrow flukes with a relatively long span, resulting in a high mean *AR* of 4.83. The one male *P. crassidens* examined had an *AR* of 5.40. The lowest mean *AR* (3.43) was found for *D. leucas*, which had relatively broad flukes with a relatively small span. Although of similar body length, the chords measured for all individuals of *D. leucas* were greater than those for *P. crassidens* (Table 1).

Sweepback of the flukes for *D. leucas*, *P. crassidens* and *T. truncatus* varied from 25.37 to 38.78 ° (Table 1), and mean values were not significantly different (*t*-test) between the three species. *O. orca* had significantly less sweepback than each of the other species (*P*<0.05; *t*-test).

Swimming speeds and kinematics

Ninety-six swimming sequences for *D. leucas*, *O. orca* and *P. crassidens* in which animals maintained continuous propulsive motions of the flukes were used for kinematic analysis.

The whales swam steadily parallel to and 2–3 m from the glass walls of the pools at depths of 0.3–2.5*D*. The time to swim a complete circuit of the pool was greater than 10 s. Velocities ranged from 1.54 to 7.91 m s^{-1} (*Re*=6.08×10^6 to 3.91×10^7). *D. leucas* was the slowest swimmer (*U*=1.54–3.83 m s^{-1}). *O. orca* had the highest swimming velocity (7.91 m s^{-1}), followed by *P. crassidens* (7.46 m s^{-1}) and *T. truncatus* (6.01 m s^{-1}). However, relative to body length,

P. crassidens (2.10 *L* s^{-1}) and *T. truncatus* (2.39 *L* s^{-1}; Fish, 1993*b*) exhibited faster speeds compared with *O. orca* and *D. leucas* at 1.53 and 1.08 *L* s^{-1}, respectively.

The frequency of the propulsive cycle (*f*) increased linearly with increasing *U*/*L* for all species (Fig. 1; Table 2). Analysis of covariance (Zar, 1984) showed that the slopes were not equal (*P*<0.001). Frequency increased with *U*/*L* fastest for *D. leucas* followed by *P. crassidens*, *T. truncatus* and *O. orca*, respectively.

Amplitude, *h*, was not significantly correlated with *U*/*L* for *O. orca*, *P. crassidens* and *T. truncatus* (Fig. 2; Table 2). Mean values of *h* were 0.49±0.06 m, 0.34±0.05 m and 0.26±0.05 m (means ± S.D.) for *O. orca*, *P. crassidens* and *T. truncatus*, respectively. *D. leucas* showed a significant negative relationship between *h* and *U*/*L* (Fig. 2; Table 2). The mean peak-to-peak amplitude (*A*=2*h*) as a percentage of body length was 20–21 % for *D. leucas*, *O. orca* and *T. truncatus*, but 18 % for *P. crassidens*.

The pitch angle (α) showed a significant linear decrease (*P*<0.01) with increasing *U*/*L* for all species examined (Fig. 3; Table 2). *D. leucas* showed the largest decrease in α with *U*/*L*, whereas *T. truncatus* had the shallowest slope.

Regression equations of the kinematic variables (Table 2) were used to compute reduced frequencies (σ) and feathering parameters (θ). Reduced frequency decreased curvilinearly with increasing swimming speed (Fig. 4A). Over the range of length-specific velocities tested, *P. crassidens* exhibited the lowest values of σ, whereas the largest decrease was computed
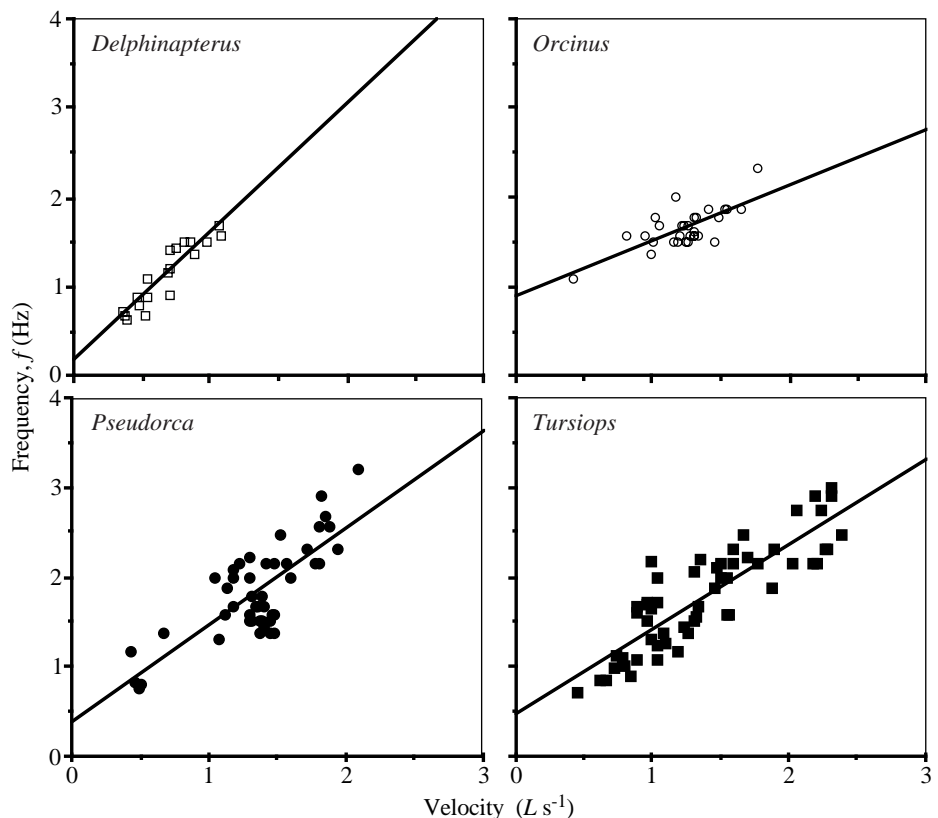

Fig. 1. Tail-beat frequency, *f* (Hz), as a function of length-specific swimming velocity, *U*/*L* (*L* s^{-1}), where *L* is body length and *U* is swimming velocity. Regression lines are plotted for all data sets in which the regression was statistically significant. Regression equations are provided in Table 2.
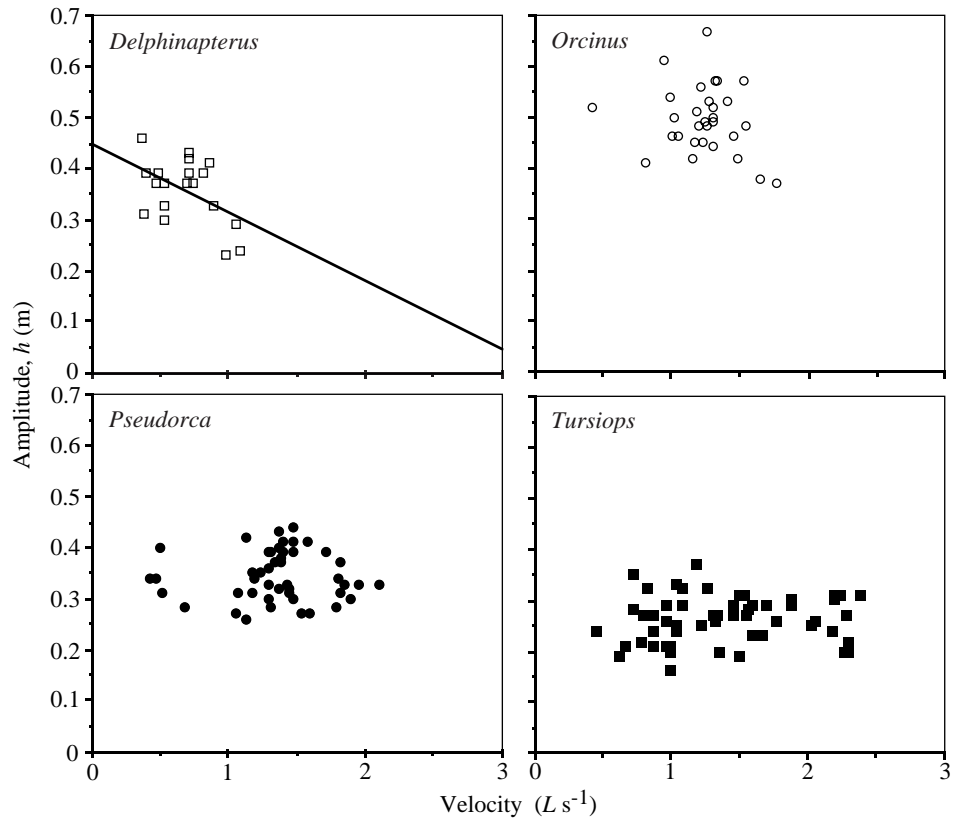
Fig. 2. Relationship between the amplitude of heave, h (m), and length-specific swimming velocity, U/L ($L\,\mathrm{s}^{-1}$), where L is body length and U is swimming velocity. The regression line is plotted for the data set in which the regression was statistically significant. Regression equations are provided in Table 2.

for *O. orca*. Values of σ for all species indicated that unsteady effects dominate the fluid forces associated with the oscillating propulsors (Yates, 1983; Daniel and Webb, 1987; Daniel *et al.* 1992). High values of σ were limited to low swimming speeds, which were rarely observed.

Values of θ increased with increasing swimming speed, reaching maxima between 0.7 and $1.4\,L\,\mathrm{s}^{-1}$ before decreasing (Fig. 4B). *P. crassidens* had the highest maximum θ of approximately 0.67, and *T. truncatus* had the lowest value measured of 0.37. At $\theta=0$, the motion of the flukes is pure heaving in which the angle of attack is zero; at $\theta=1$, the fluke is perfectly feathered and the fluke chord is tangential to the trajectory of the pitching axis (Lighthill, 1969; Yates, 1983).

Thrust power, drag coefficient and efficiency

The hydrodynamic model using unsteady lifting wing theory (Chopra and Kambe, 1977; Yates, 1983) related both C_T and η to σ for isopleths of θ. The calculated P_T from equation 4 showed a curvilinear increase with increasing U/L for all species (Fig. 5). P_T was found to be mass-dependent. *O. orca* had the highest P_T of 36.3 kW at $U=8\,\mathrm{m\,s}^{-1}$. This represented a mass-specific power output of $22.0\,\mathrm{W\,kg}^{-1}$. *P. crassidens* and *T. truncatus* had maximum mass-specific power outputs of 22.5 and $23.7\,\mathrm{W\,kg}^{-1}$, respectively. The computed value for *T. truncatus* was 22% lower than the maximum value ($30.5\,\mathrm{W\,kg}^{-1}$) at the same swimming speed previously reported by Fish (1993*b*). Although *D. leucas* had higher values of P_T compared with *P. crassidens* and *T. truncatus* over equivalent swimming speeds, higher maximum P_T values were reached

by the latter two species as they swam at higher speeds. Maximum P_T for *D. leucas* was 3.4 kW, with a mass-specific power output of $5.2\,\mathrm{W\,kg}^{-1}$.

Depth-corrected drag coefficients, C_{Dd}, plotted against Re are displayed in Fig. 6. C_{Dd} decreased with increasing Re for all species. The lowest minimum C_{Dd} of 0.0026 was found for *O. orca* at a Re of 3.65×10^7. The minimum values of C_{Dd} for *D. leucas*, *P. crassidens* and *T. truncatus* were 4.7, 1.6 and 2.9 times higher, respectively, than C_{Dd} for *O. orca*. Over a given range

Table 2. *Regression equations for kinematics*

Species	Regression equation	r^2
Delphinapterus leucas	$f=0.143+1.454U/L$	0.857***
$N=19$	$h=0.448-0.134U/L$	0.238*
	$\alpha=42.113-16.459U/L$	0.405**
Orcinus orca	$f=0.892+0.613U/L$	0.527***
$N=30$	$h=0.564-0.056U/L$	0.047
	$\alpha=43.373-11.448U/L$	0.332***
Pseudorca crassidens	$f=0.344+1.089U/L$	0.624***
$N=46$	$h=0.342+0.002U/L$	0
	$\alpha=38.654-6.917U/L$	0.430***
Tursiops truncatus	$f=0.463+0.945U/L$	0.738***
$N=56$	$h=0.254+0.007U/L$	0.006
	$\alpha=31.000-4.864\,U/L$	0.510***

f, frequency of the propulsive cycle; h, amplitude of heave; α, pitch angle; U, swimming speed; L, body length.
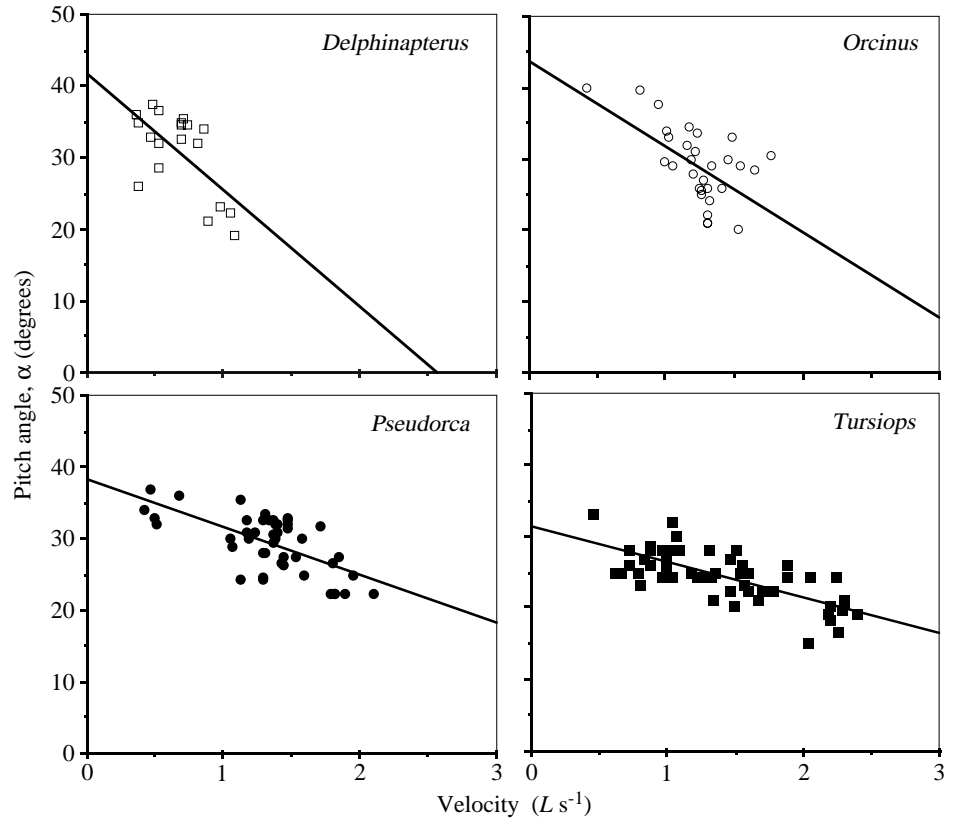***$P<0.001$; **$P<0.01$; *$P<0.05$.

Fig. 3. Relationship between the maximum angle of pitch, α (degrees), and length-specific swimming velocity, U/L ($L\,s^{-1}$), where L is body length and U is swimming velocity. Regression lines are plotted for all data sets in which the regression was statistically significant. Regression equations are provided in Table 2.

Table 3. *Expected and experimentally determined performance rankings of cetaceans based on morphology and kinematics*

Species	Factors affecting resistance	Expected drag ranking	Actual ranking based on minimum C_{Dd}	Factors affecting thrust production	Expected thrust ranking	Actual ranking based on maximum efficiency
Delphinapterus leucas	FR=5.5, bulbous head and loose skin increase parasite drag; paddle-like flippers increase induced drag	4	4	Fluke AR=3.4, giving lower lift production; moderate fluke sweep reduces lift	4	4
Orcinus orca	FR=4.8, lenticular head and tight skin reduce parasite drag; large paddle-like flippers increase induced drag	2	1	Fluke AR=4.4, giving intermediate lift production; low fluke sweep increasing lift production	2	2
Pseudorca crassidens	FR=6.5 increases parasite drag; lenticular head and tight skin reduce parasite drag; highly tapered flippers reduce induced drag	3	2	Fluke AR=4.8 increases lift production; moderate fluke sweep reduces lift	1	1
Tursiops truncatus	FR=5.2, lenticular head and tight skin reduce parasite drag; highly tapered flippers reduce induced drag	1	3	Fluke AR=4.1, giving intermediate lift production; moderate fluke sweep reduces lift	3	3

FR, fineness ratio; AR, aspect ratio; C_{Dd}, depth-corrected drag coefficient.

Expected and actual drag rankings are the comparative rankings, where 1 represents the lowest values of drag and 4 represents the highest values of drag.

Expected and actual thrust and efficiency rankings are the comparative rankings, where 1 represents the highest values of thrust or efficiency and 4 represents the lowest values.
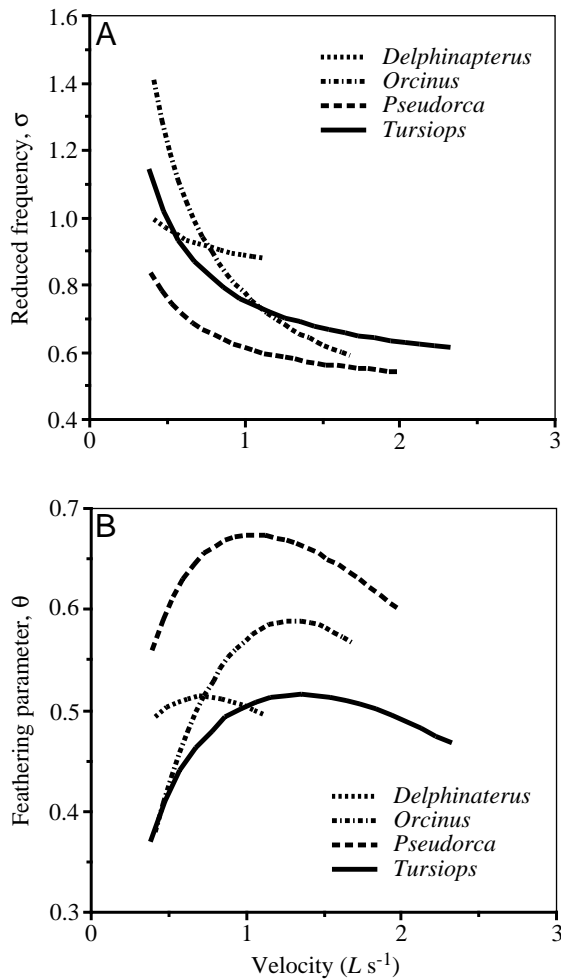
Fig. 4. Reduced frequency, σ (A), and feathering parameter, θ (B), plotted as a function of length-specific swimming velocity, *U/L* ($L\,s^{-1}$), where *L* is body length and *U* is swimming velocity. Data for calculation of σ and θ were obtained from the regression equations given in Table 2.

Fig. 5. Thrust power, P_T (W), as a function of length-specific swimming velocity, *U/L* ($L\,s^{-1}$), where *L* is body length and *U* is swimming velocity.

over the range of velocities obtained, such that the minimum η was within 1.5 % of the maximum η.

Discussion

Morphology and swimming speed

Morphology varied among the four odontocete species in relation to their kinematics and swimming performance (Table 3). However, expected rankings based on factors affecting resistance and thrust production only moderately reflected actual rankings based on minimum C_{Dd} and maximum efficiency. Whereas these factors accurately predicted that *D. leucas* would show the poorest performance, the low actual ranking of minimum C_{Dd} for *T. truncatus* was not predicted from the morphological characteristics affecting resistance. The differences between actual and predicted rankings indicate that additional factors may influence morphology. These factors would include differences due to phylogenetics, foraging behaviors (i.e. solitary hunter *versus*

of *Re*, *D. leucas* had the highest C_{Dd}. In the mid-range of *Re*, *O. orca* had a higher C_{Dd} than *P. crassidens* and *T. truncatus*.

Values of C_{Dd} for the cetaceans were 1.2–8.0 times higher than theoretical values for a flat plate of equivalent S_a and *Re* with turbulent boundary layer flow because of body shape (parasite drag), interference and induced drag from appendages, and oscillations of the flukes and body while swimming (Lighthill, 1971; Webb, 1975; Fish, 1993*b*; Romanenko, 1995). These results are in agreement with drag coefficients measured or calculated previously for dolphins (Webb, 1975; Fish and Hui, 1991).

Whales showed minimum values of propulsive efficiency, η, at swimming speeds less than $0.5\,L\,s^{-1}$ (Fig. 7). With increasing velocity, η increased rapidly to a maximum, at which it remained or eventually decreased. *P. crassidens* exhibited the highest η at 0.90, whereas maximum values of η for *O. orca*, *T. truncatus* and *D. leucas* were 0.88, 0.86 and 0.84, respectively. For *D. leucas*, η was relatively consistent
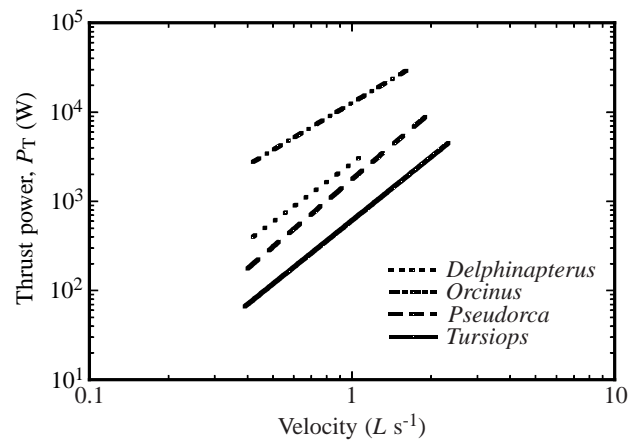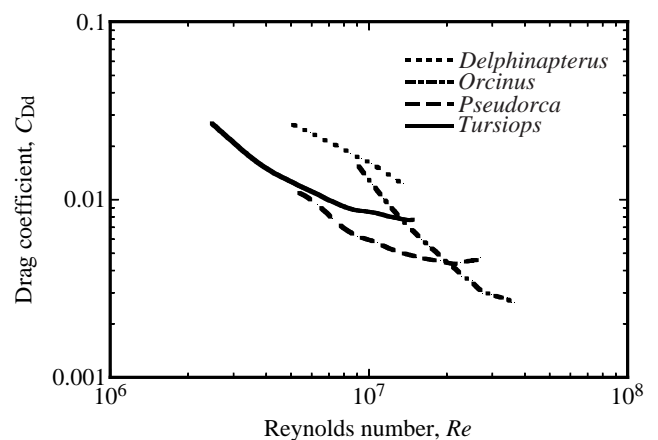

Fig. 6. Submergence-depth-corrected drag coefficient, C_{Dd}, as a function of Reynolds number, *Re*.
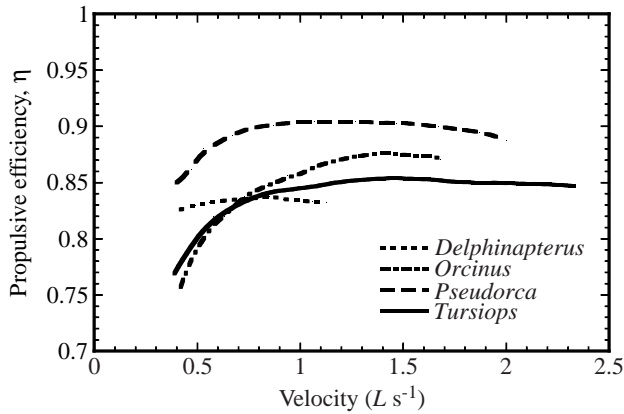
Fig. 7. Propulsive efficiency, η, as a function of length-specific swimming velocity, U/L ($L s^{-1}$), where L is body length and U is swimming velocity.

Fig. 8. Relationship between propulsive efficiency, η, and pitch angle, α (degrees). Vertical lines indicate the region from 20 to 30° in which efficiency is expected to be maximal according to Liu and Bose (1993).

use of coordinated hunts), prey size and abundance, social behavior, sexual dimorphism, habitat (i.e. pack ice, open ocean), maneuverability (Fish, 1996) and swimming speed.

The highest measured swimming speed with respect to body length decreased with increasing size. Despite the ability of *O. orca* and *P. crassidens* to swim $1 m s^{-1}$ faster than *T. truncatus*, the smaller dolphin was able to swim at higher length-specific speeds. In summarizing data from a variety of sources, Webb (1975) showed that there is a marked dependence of length-specific swimming speed on size for cetaceans. However, Bose *et al.* (1990) questioned the relationship between size and burst speed in cetaceans and asserted that the design of the flukes in conjunction with the morphology of the body were the major determinants of swimming performance.

Swimming speeds of *O. orca*, *P. crassidens* and *T. truncatus* in this study were within the range of speeds reported previously (Table 4) and generally lower than previously reported maxima. Shipboard observations of *O. orca* estimated that a single animal swam at 12.5–$15.4 m s^{-1}$ for 20 min (Johannessen and Harder, 1960), but this may include bow-riding. Bow-riding allows dolphins to swim at higher speeds with less effort than when swimming in undisturbed water (Fish and Hui, 1991; Williams *et al.* 1992). *O. orca*, however, does appear to swim rapidly when hunting slower-swimming *D. leucas* and large whales (Brodie, 1989; George and Suydam, 1998) as well as faster-swimming *Lagenorhynchus obscurus* (Constantine *et al.* 1998).

Swimming speed is related to duration (Lang and Norris, 1966). *T. truncatus* can swim at $3.08 m s^{-1}$ indefinitely, at $6.09 m s^{-1}$ for 50 s, at $7.01 m s^{-1}$ for 10 s and at $8.3 m s^{-1}$ for 7.5 s (Lang, 1975). The maximum speed of $6.0 m s^{-1}$ for a swimming bout longer than 10 s by *T. truncatus* in this study matches the speed measured by Lang and Norris (1966). However, speeds as high as $15 m s^{-1}$ were reported for burst swims by *T. truncatus* made from cliff-top observations (Lockyer and Morris, 1987).

Although smaller than *O. orca* but larger than *T. truncatus*, *D. leucas* displayed comparatively lower absolute and relative
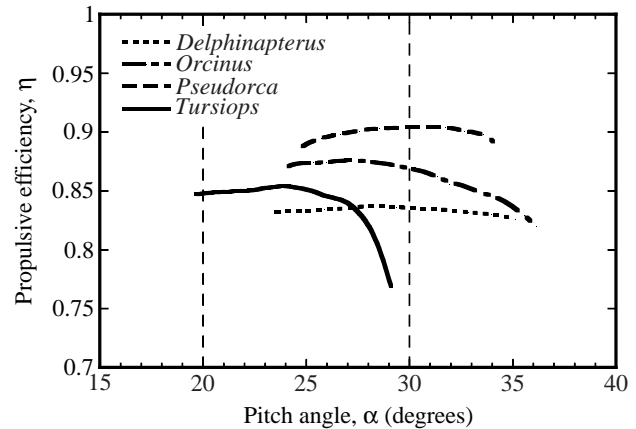
swimming velocities. *D. leucas* is not considered a fast swimmer (Brodie, 1989). Migrating *D. leucas* tracked using satellite-monitored radio transmitters swam at 0.6–$1.1 m s^{-1}$, with a fastest sustained swimming speed of $1.6 m s^{-1}$ (Martin *et al.* 1993). During dives to depths as great as 300 m, swimming speed increases for deeper dives with mean descent and ascent rates of less than $2 m s^{-1}$ and 2.2–$3 m s^{-1}$, respectively (Shaffer *et al.* 1997). Maximum burst speeds were estimated at 5.6–$6.1 m s^{-1}$ (Table 4). Indeed the low aspect ratio of the flukes, mobile neck, prominent creases and folds of fat and paddle-shaped flippers indicate a low-performance existence (Table 3; Brodie, 1989; Carwardine, 1995).

Its comparatively poor swimming performance may reflect phylogenetic differences, because *D. leucas* is a member of the family Monodontidae, whereas the other odontocetes studied are in the family Delphinidae. *D. leucas* is a shallow-water, coastal species which is associated with slow swimming. The other member of the Monodontidae is the narwhal *Monodon monoceros*, which is regarded as a very slow swimmer that seldom exceeds speeds of $1.7 m s^{-1}$ (Minasian *et al.* 1984). Members of the Delphinidae are generally pelagic, offshore species which are regarded as fast swimmers (Leatherwood and Reeves, 1983; Curren *et al.* 1994).

Kinematics

Swimming speed in cetaceans is controlled by modulation of a combination of f and α. The only exception was *D. leucas*, which adjusts h in addition to the other two kinematic parameters.

The positive linear relationship between f and U/L for cetaceans is similar to results found for fish and other marine mammals (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb *et al.* 1984; Feldkamp, 1987; Fish *et al.* 1988; Scharold *et al.* 1989). Data for *T. truncatus* corresponded with frequency values reported by Videler and Kamermans (1985).

The thunniform mode of swimming or carangiform with lunate tail uses propulsion derived from heaving and pitching motions of an oscillating hydrofoil with α varying throughout

the propulsive cycle (Lang and Daybell, 1963; Lighthill, 1969; Videler and Kamermans, 1985). Values of α of approximately 20–30° maximize efficiency (Liu and Bose, 1993) and were typical of the four cetaceans studied at swimming speeds between routine and maximum velocities (Fig. 8). Videler and Kamermans (1985) found a similar range of pitch angles for *T. truncatus*. Higher pitch angles for *Phocoena phocoena* (34°) and *Lagenorhynchus acutus* (33°) were reported by Curren *et al.* (1994), although these animals were swimming at relatively low speeds ($<1.6\,L\,s^{-1}$), where efficiency is low.

Peak-to-peak amplitude (*A*) remained a constant proportion of *L* (*A/L*=0.18–0.21) for three of the species examined. This was similar to previous results for *T. truncatus* with *A/L*=0.16–0.21 (Kayan and Pyatetsky, 1977; Fish, 1993*b*). *D. leucas* exhibited a decrease in *A/L* from 0.27 to 0.13 with increasing *U/L*. Despite the change in *A/L* for *D. leucas*, these values are typical for thunniform swimmers in which *A/L* is 0.16–0.34 (Fierstine and Walters, 1968; Fish *et al.* 1988; Dewar and Graham, 1994).

Thrust power

As expected, P_T of the four whales was mass-dependent, with the largest animal, *O. orca*, generating the greatest P_T. However, with the exception of *D. leucas*, the mass-specific power outputs for the whales were nearly equivalent at 22.0–$23.7\,W\,kg^{-1}$. These values are lower than the maximum total power output of $85.6\,W\,kg^{-1}$ reported for an accelerating *Stenella attenuata* by Lang and Pryor (1966). This high power output by a $52.7\,kg$ *S. attenuata* was attained at a maximum speed of $11.05\,m\,s^{-1}$ during a $1.5\,s$ acceleration. The data from *S. attenuata* imply that the species examined in the present study may not have reached their maximum power output. Power outputs lower than the maximum capability may explain the discrepancy between the maximum swimming speeds reported in the literature (Table 4) and the maximum speeds attained by the whales in this study.

Table 4. *Comparative swimming speeds, the speeds at which minimum drag and maximum efficiency occur*

| Species | Swimming speed (m s⁻¹) | | | |
	Cruising	Maximum	Minimum C_{Dd}[j]	Maximum efficiency[j]
Delphinapterus leucas	0.6–2.5[a,g,h]	5.6–6.1[a,g,h,i]	4.0	3.0
Orcinus orca	2.8–5.1[a,c,h]	12.5–15.4[b,h]	7.8	6.5
Pseudorca crassidens	3.1[c]	7.5[j]	6.0	3.8
Tursiops truncatus	1.1–5.6[d,e,f]	8–15[d,e,f]	5.8	3.8

C_{Dd}, depth-corrected drag coefficient.

[a]Tomilin (1957); [b]Johannessen and Harder (1960); [c]Norris and Prescott, (1961); [d]Lang and Norris (1966); [e]Wursig and Wursig (1979); [f]Lockyer and Morris (1987); [g]Brodie (1989); [h]Nowak (1991); [i]Martin *et al.* (1993); [j]this study.

Drag coefficient and efficiency

The differences in C_{Dd} are consistent with variations in morphology and kinematics affecting swimming performance (Table 3). *D. leucas*, with its high C_{Dd}, possesses a bulbous head which would increase the area of high pressure and therefore increase drag. In addition, the folds of fat along the lateral and ventral aspects of the body would act to increase drag (Aleyev, 1977). For the other species that possess a tighter skin and smoother body contour, C_{Dd} was lower at any specified *Re* (Fig. 6). At high *Re*, *O. orca* displayed the lowest C_{Dd}. This species has an *FR* closest to the optimum of 4.5 for minimum drag with maximum body volume (Webb, 1975). Despite the higher *FR* for *P. crassidens*, C_{Dd} was lower than for the other species at low and intermediate *Re*. *FR* for *P. crassidens* falls within the range of *FR* (3–7) in which drag increases by only approximately 10 % from the minimum value (Webb, 1975).

Minimum C_{Dd} for all species occurred at or close to the maximum speeds measured in the present study and above the normal cruising speeds (Table 4). Reduced drag at high *U* would facilitate burst swimming, particularly during foraging. The lower values of C_{Dd} for *O. orca*, *P. crassidens* and *T. truncatus* would aid these animals, which feed on large and rapidly swimming prey (Evans, 1987). A higher C_{Dd} can be tolerated by *D. leucas*, because this cetacean feeds on slower-moving prey, including crustaceans and annelids (Brodie, 1989).

Whereas the minimum drag characteristics of the body are associated with operation at high speeds, maximum efficiency of the propulsor occurs at lower speeds (Table 4). At the lowest speeds, η was reduced for all animals except *D. leucas*. *D. leucas* had a relatively stable efficiency over a more restricted range of low swimming speeds, which is in accordance with its limited swimming capabilities. At low speeds, *O. orca*, *P. crassidens* and *T. truncatus* had a reduced η but, after rapidly reaching a maximum, η remained relatively high and stable over a wide speed range. The speeds associated with maximum η for *D. leucas*, *P. crassidens* and *T. truncatus* approximated their cruising speeds. Although maximum η for *O. orca* occurred at $6.5\,m\,s^{-1}$, which was above the normal range of cruising speeds (Table 4), there was a reduction of less than 5 % in η from the maximum at a cruising speed of $3.5\,m\,s^{-1}$.

Maximum η at cruising speeds would be beneficial in reducing energy costs during transit between widely dispersed feeding sites or during migration. Cetaceans should swim at speeds that maintain the greatest efficiencies (Fish and Hui, 1991). The cost of transport is inversely related to efficiency and represents the energetic cost to move a unit mass a unit distance (Fish, 1992). The minimum cost of transport thereby defines the theoretical speed that provides the maximum distance traveled per unit power input (Williams *et al.* 1993). Williams *et al.* (1993) found that the minimum cost of transport of captive *T. truncatus* corresponded to swimming speeds measured from wild populations. Similarly, gray whales *Eschrichtius robustus* and minke whales *Balaenoptera acutorostrata* cruise at the speed of the lowest cost of transport (Sumich, 1983; Blix and Folkow, 1995).

Overall, the flukes of cetaceans provide a high η of 75–90 %,

which surpasses most manufactured propellers which have η as high as 70 % (Liu and Bose, 1993). Such values of η for the four cetaceans studied here are similar or slightly lower than values reported previously for cetaceans (Wu, 1971; Webb, 1975; Chopra and Kambe, 1977; Yates, 1983; Bose and Lien, 1989; Liu and Bose, 1993). Differences in efficiencies are explained by the use of models using alternative analyses (e.g. two-dimensional theory, unsteady quasi-vortex lattice method), indirect estimates of swimming kinematics and wing designs inconsistent with the morphology of the flukes (e.g. rectangular planform, high AR).

The magnitude of η is dependent on the design of the flukes, with AR being the most important morphological variable (Table 3; Bose and Lien, 1989). High AR and tapering of the flukes reduces drag while maximizing thrust (Webb, 1975; Daniel *et al.* 1992). With the largest AR, *P. crassidens* exhibited the highest maximum η of 0.9, and maximum η decreased with decreasing AR for each of the other species tested. Using the quasi-vortex-lattice method, Liu and Bose (1993) found the fin whale *Balaenoptera physalus*, with $AR=6.1$, to have a maximum propulsive efficiency of 0.96. However, they also found an equivalent efficiency of 0.96 for the white-sided dolphin *Lagenorhynchus acutus*, with $AR=2.7$, and an efficiency of 0.9 for *D. leucas*, with $AR=3.25$. Although this method gave higher values than reported in the present study, the differences between the three species were accounted for by the influence of sweep in the fluke design.

The combination of low sweep with high AR allows for high-efficiency rapid swimming, whereas high sweep may compensate for the reduced lift production of low-AR flukes (Azuma, 1983; Liu and Bose, 1993). A tapered wing with sweepback or a crescent design can achieve improved efficiency by reducing induced drag by 8.8 % compared with a wing with an elliptical planform (van Dam, 1987). Minimal induced drag occurs in swept wings with a triangular planform approximating the design of cetacean flukes (Chopra and Kambe, 1977; Fish, 1998). Highly swept back, low-AR wings produce maximum lift when operating at large angles of attack, when low-sweep, high-AR designs would fail (Hurt, 1965). This feature aids in the maintenance of high efficiency at slow sustained speeds (Magnuson, 1978), as observed for *D. leucas* (Fig. 7). Although increasing efficiency, the high sweep angle will reduce thrust. Maintenance of thrust would be facilitated by a higher AR as in *O. orca*, *P. crassidens*, and *T. truncatus*, which can swim at higher sustained speeds.

References

ALEYEV, Y. G. (1977). *Nekton*. The Hague: Junk.

AU, D. AND WEIHS, D. (1980). At high speeds dolphins save energy by leaping. *Nature* **284**, 548–550.

AZUMA, A. (1983). Biomechanical aspects of animal flying and swimming. In *Biomechanics VIII-A: International Series on Biomechanics*, vol. 4A (ed. H. Matsui and K. Kobayashi), pp. 35–53. Champaign, IL: Human Kinetics Publishers.

BAINBRIDGE, R. (1958). The speed of swimming fish as related to size and to frequency and amplitude of the tail beat. *J. exp. Biol.* **35**, 109–133.

BLIX, A. S. AND FOLKOW, L. P. (1995). Daily energy expenditure in free living minke whales. *Acta physiol. scand.* **153**, 61–66.

BOSE, N. AND LIEN, J. (1989). Propulsion of a fin whale (*Balaenoptera physalus*): why the fin whale is a fast swimmer. *Proc. R. Soc. Lond. B* **237**, 175–200.

BOSE, N., LIEN, J. AND AHIA, J. (1990). Measurements of the bodies and flukes of several cetacean species. *Proc. R. Soc. Lond. B* **242**, 163–173.

BRODIE, P. F. (1989). The white whale *Delphinapterus leucas* (Pallas, 1776). In *Handbook of Marine Mammals*, vol. 4 (ed. S. H. Ridgway and R. Harrison), pp. 119–144. London: Academic Press.

CARWARDINE, M. (1995). *Whales, Dolphins and Porpoises*. London: Dorling Kindersley.

CHOPRA, M. G. AND KAMBE, T. (1977). Hydrodynamics of lunate-tail swimming propulsion. Part 2. *J. Fluid Mech.* **79**, 49–69.

CONSTANTINE, R., VISSER, I., BUURMAN, D., BUURMAN, R. AND MCFADDEN, B. (1998). Killer whale (*Orcinus orca*) predation on dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *Mar. mammal. Sci.* **14**, 324–330.

CURREN, K. C., BOSE, N. AND LIEN, J. (1994). Swimming kinematics of a harbor porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*). *Mar. mammal. Sci.* **10**, 485–492.

DANIEL, T. L., JORDON, C. AND GRUNBAUM, D. (1992). Hydromechanics of swimming. In *Advances in Comparative and Environmental Physiology*, vol. 11 (ed. R. McN. Alexander), pp. 17–49. Berlin: Springer-Verlag.

DANIEL, T. L. AND WEBB, P. W. (1987). Physical determinants of locomotion. In *Comparative Physiology: Life in Water and on Land* (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 343–369. New York: Liviana Press.

DEWAR, H. AND GRAHAM, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. III. Kinematics. *J. exp. Biol.* **192**, 45–59.

EVANS, P. G. H. (1987). *The Natural History of Whales and Dolphins*. New York: Facts On File.

FELDKAMP, S. D. (1987). Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool., Lond.* **212**, 43–57.

FIERSTINE, H. L. AND WALTERS, V. (1968). Studies of locomotion and anatomy of scombrid fishes. *Mem. S. Calif. Acad. Sci.* **6**, 1–31.

FISH, F. E. (1992). Aquatic locomotion. In *Mammalian Energetics:*

Interdisciplinary Views of Metabolism and Reproduction (ed. T. E. Tomasi and T. H. Horton), pp. 34–63. Ithaca, NY: Cornell University Press.

FISH, F. E. (1993a). Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Aust. J. Zool.* **42**, 79–101.

FISH, F. E. (1993b). Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *J. exp. Biol.* **185**, 179–193.

FISH, F. E. (1996). Comparative turning performance of odontocete cetaceans. *Am. Zool.* **36**, 90A.

FISH, F. E. (1998). Biomechanical perspective on the origin of cetacean flukes. In *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea* (ed. J. G. M. Thewissen), pp. 303–324. New York: Plenum (in press).

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

FISH, F. E., INNES, S. AND RONALD, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. exp. Biol.* **137**, 157–173.

GEORGE, J. C. AND SUYDAM, R. (1998). Observations of killer whale (*Orcinus orca*) predation in Northeastern Chukchi and Western Beaufort Seas. *Mar. mammal. Sci.* **14**, 330–332.

HERTEL, H. (1966). *Structure, Form and Movement.* New York: Rheinhold.

HUNTER, J. R. AND ZWEIFEL, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus* and other fishes. *Fishery Bull. Fish. Wildl. Serv. U.S.* **69**, 253–266.

HURT, H. H., JR (1965). *Aerodynamics for Naval Aviators.* U.S. Navy, NAVWEPS 00-80T-80.

JOHANNESSEN, C. L. AND HARDER, J. A. (1960). Sustained swimming speeds of dolphins. *Science* **132**, 1550–1551.

KAYAN, V. P. AND PYATETSKY, V. YE. (1977). Kinematics of bottlenosed dolphin swimming as related to acceleration mode. *Bionika* **11**, 36–41.

LANG, T. G. (1975). Speed, power and drag measurements of dolphins and porpoises. In *Swimming and Flying in Nature* (ed. T. Y. Wu, C. J. Brokaw and C. Brennen), pp. 553–571. New York: Plenum Press.

LANG, T. G. AND DAYBELL, D. A. (1963). Porpoise performance tests in a seawater tank. *Nav. Ord. Test Sta. Tech. Rep.* **3063**, 1–50.

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

LANG, T. G. AND PRYOR, K. (1966). Hydrodynamic performance of porpoises (*Stenella attenuata*). *Science* **152**, 531–533.

LEATHERWOOD, S. AND REEVES, R. R. (1983). *The Sierra Club Handbook of Whales and Dolphins.* San Francisco: Sierra Club Books.

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

LIGHTHILL, M. J. (1970). Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid Mech.* **44**, 265–301.

LIGHTHILL, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. B* **179**, 125–138.

LIU, P. AND BOSE, N. (1993). Propulsive performance of three naturally occurring oscillating propeller planforms. *Ocean Eng.* **20**, 57–75.

LOCKYER, C. AND MORRIS, R. (1987). Observation on diving behaviour and swimming speeds in a wild juvenile *Tursiops truncatus. Aquat. mammal.* **13**, 31–35.

MAGNUSON, J. J. (1970). Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. *Copeia* **1970**, 56–85.

MAGNUSON, J. J. (1978). Locomotion by scombrid fishes: hydrodynamics, morphology and behaviour. *In Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 239–313. London: Academic Press.

MARTIN, A. R., SMITH, T. G. AND COX, O. P. (1993). Studying the behaviour and movements of high Arctic belugas with satellite telemetry. *Symp. zool. Soc. Lond.* **66**, 195–210.

MINASIAN, S. M., BALCOMB, K. C. AND FOSTER, L. (1984). *The World's Whales.* Washington, DC: Smithsonian Books.

NORRIS, K. S. AND PRESCOTT, J. H. (1961). Observations of Pacific cetaceans of California and Mexican waters. *Univ. Calif. Publ. Zool.* **63**, 291–402.

NOWAK, R. M. (1991). *Walker's Mammals of the World.* Baltimore: Johns Hopkins University Press.

ROMANENKO, E. V. (1995). Swimming of dolphins: experiments and modelling. In *Biological Fluid Dynamics* (ed. C. P. Ellington and T. J. Pedley), pp. 21–33. Cambridge: The Company of Biologists.

SCHAROLD, J., LAI, N. C., LOWELL, W. R. AND GRAHAM, J. B. (1989). Metabolic rate, heart rate and tailbeat frequency during sustained swimming in the leopard shark *Triakis semifasciata. Exp. Biol.* **48**, 223–230.

SHAFFER, S. A., COSTA, D. P., WILLIAMS, T. M. AND RIDGWAY, S. H. (1997). Diving and swimming performance of white whales, *Delphinapterus leucas*: an assessment of plasma lactate and blood gas levels and respiratory rates. *J. exp. Biol.* **200**, 3091–3099.

SOKAL, R. R. AND ROHLF, F. J. (1981). *Biometry.* New York: Freeman.

SUMICH, J. L. (1983). Swimming velocities, breathing patterns and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus. Can. J. Zool.* **61**, 647–652.

TOMILIN, A. G. (1957). *Mammals of the U.S.S.R. and Adjacent Countries*, vol. IX, *Cetacea.* Moskva: Izdatel'stvo Akademi Nauk SSSR.

VAN DAM, C. P. (1987). Efficiency characteristics of crescent-shaped wings and caudal fins. *Nature* **325**, 435–437.

VIDELER, J. AND KAMERMANS, P. (1985). Differences between upstroke and downstroke in swimming dolphins. *J. exp. Biol.* **119**, 265–274.

WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.

WEBB, P. W., KOSTECKI, P. T. AND STEVENS, E. D. (1984). The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. exp. Biol.* **109**, 77–95.

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., FRIEDL, W. A., HAUN, J. E. AND CHUN, N. K. (1993). Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). *Symp. zool. Soc. Lond.* **66**, 383–394.

WU, T. Y. T. (1971). Hydromechanics of swimming propulsion. Part 2. Some optimum shape problems. *J. Fluid Mech.* **46**, 521–544.

WURSIG, B. AND WURSIG, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bull. Fish Wildl. Serv. U.S.* **77**, 399–412.

YATES, G. T. (1983). Hydrodynamics of body and caudal fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 177–213. New York: Praeger.

ZAR, J. H. (1984). *Biostatistical Analysis.* Second edition. Englewood Cliffs, NJ: Prentice-Hall.