DESIGNS FOR SWIMMING: MORPHOMETRICS AND SWIMMING DYNAMICS OF SEVERAL CETACEAN SPECIES

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Designs for Swimming: Morphometrics and Swimming Dynamics of Several Cetacean Species.

by

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Abstract

Swimming is the only mode of locomotion available to whales and dolphins. Although all cetaceans live in an aquatic environment, large differences exist between the behavioural ecologies of different species; corresponding variation in morphology and in dynamical swimming characteristics is expected between species.

Morphological variation was examined within a sample (n=35) of harbour porpoise (*Phocoena phocoena*) to determine the values of several geometric parameters (including body volume, body surface area, volumetric coefficient, fineness ratio, fluke surface area, fluke aspect ratio and fluke sweep angle) for mature animals. Harbour porpoise showed significant variation in several non-dimensional parameters with age, suggesting that other cetacean species may display similar variation. In general, juvenile harbour porpoise displayed lower fineness ratios and lower fluke aspect ratios than adult harbour porpoise: these results imply a lower propulsive efficiency for juvenile porpoise.

The morphologies of sexually mature harbour porpoise were statistically compared with a sample (n=3) of Atlantic white-sided dolphins (*Lagenorhynchus acutus*). Harbour porpoise were found to have significantly lower fineness ratios than Atlantic white-sided dolphins, indicating a fatter body and a higher drag coefficient. Harbour porpoise also displayed higher fluke aspect ratios. This suggests that the flukes of the harbour porpoise may have a higher propulsive efficiency than those of Atlantic white-sided dolphins, although the white-sided dolphins' high fluke sweep angles may compensate for their lower aspect ratio.

The morphologies of harbour porpoise and Atlantic white-sided dolphins were qualitatively compared with several other cetacean species. The largest between-species differences were observed for volumetric coefficient, fluke aspect ratio and the ratio of body surface area : fluke area. These morphological differences may reflect differences in relative swimming performance.

Dynamical swimming parameters, including swimming speed, fluke oscillation frequency, and stride length, were measured from videotape for a harbour porpoise, an Atlantic white-sided dolphin and two long-finned pilot whales (*Globicephala melas*). Limited data on heave amplitude and maximum pitch angle of the flukes were also measured for the harbour porpoise and the white-sided dolphin. The results were compared with data from fish and cetacean swimming studies. The observed animals displayed a linear relationship between swimming speed and fluke oscillation frequency. Stride lengths were found to remain constant within species, and to vary significantly between species.

The upstroke and downstroke of the flukes were found to be equally long for all speeds measured.

Finally, a statistical method to test the hypothesis of wave energy absorption by whales was developed, and the method was applied to the track of a long-finned pilot whale when corresponding wave conditions were known. The whale was not found to increase its swimming speed or to adjust its heading with respect to wave direction in response to favourable wave conditions. Possible reasons for these results are reviewed.

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This thesis is dedicated to my family, who have always supported me without reservation even when it appeared that I'd lost my mind (*Carpe Diem!*) - to Meredith Curren, who never ceases to delight me; to Janet Stitt, who listens; and to Thomas Curren, who makes me laugh.

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A	body section with maximum area
C_p	prismatic coefficient
C_v	volumetric coefficient
f	frequency
g_{max}	maximum girth of body
h	heave amplitude of flukes
l	length
L	body length
Re	Reynolds number
s	half span of flukes
s	stride length
S	fluke planform area
v	velocity
V	body volume
θ	pitch angle of flukes
λ	sweep angle of flukes
μ	mean
ν	kinematic viscosity of water
σ	standard deviation
ξ	wave frequency
$S(\xi)$	wave spectral density

1. Introduction

1.1. Why study cetacean swimming?

Swimming is the only mode of locomotion available to whales and dolphins. Natural selection is expected to have acted upon cetaceans so as to optimize their swimming performance in accordance with ecological, genetic and physical constraints (Krebs and Davies, 1981). As a result, these animals are important models for understanding adaptations to an aquatic lifestyle (Fish and Hui, 1991). All cetaceans display the thunniform mode of swimming; that is, they are swimmers characterized by a streamlined body shape, warm muscle, and thrust produced exclusively by undulatory propulsive motions that are confined to a high aspect ratio caudal fin mounted on a slender peduncle (Blake, 1983; Webb and de Buffrénil, 1990). Since thrust may be produced almost continuously by fins that act as hydrofoils, and drag is minimized by the rigid, streamlined body, thunniform swimmers are regarded as representing the ideal design for sustained high-speed performance (Webb and de Buffrénil, 1990). The study of the swimming characteristics of cetaceans improves understanding of their locomotion, behavioural ecology and energetics. Information provided by these studies may also be applied to the design of oscillating propellers and drag reduction techniques (Bose, Lien and Ahia, 1990; Bushnell and Moore, 1991).

1.2. Locomotor forces

All cetaceans live within an aquatic environment, and are therefore subjected to its physical constraints. The forces associated with submerged cetacean swimming may be broken down into four components: friction drag, pressure drag, lift and acceleration reaction (Webb and de Buffrénil, 1990).

Friction drag is a result of the viscosity of the fluid the animal is moving through, and is due to the shear stresses within the fluid near a moving surface. Pressure drag, which is also viscous in origin, is the result of dynamic pressure differences upstream and downstream from the animal; this component of drag is dependent upon the form of the body, and may be reduced by streamlining. Lift arises from pressure differences on either side of the body and the hydrofoil. Acceleration reaction may be equated to an added mass of water that is moved by an accelerating body (Newman, 1977; Vogel, 1981; Webb and de Buffrénil, 1990).

The Reynolds number (Re), a dimensionless number defined in equation (1), evaluates the relative importance of inertial and viscous forces:

[1]

$$Re=\frac{v*l}{\nu},$$

where l is a characteristic length, usually total length; v is velocity; and ν is the kinematic viscosity of water (Newman, 1977). In general, viscous shear forces dominate at low Reynolds numbers, while inertial forces become increasingly important at high Reynolds numbers (Newman, 1977). Cetaceans swimming at even moderate speeds are subject to high values of this ratio of the order 10^6 - 10^8. At moderate and high Reynolds numbers, the magnitude of the pressure drag is much greater than friction drag for unstreamlined bodies. However, streamlining can reduce the pressure drag on a moving body to a few percent of its unstreamlined counterpart (Vogel, 1981). Longitudinal acceleration reaction forces are relatively small for large thunniform swimmers, while the lift forces of the flukes are very important for propulsion (Webb and de Buffrénil, 1990). Thus, cetacean adaptations to an aquatic environment are likely to be found in the morphology of the body, and in the shape and dynamics of the flukes.

1.3. Review of cetacean swimming

A brief review of previous work on cetacean swimming is given here. Detailed reviews of the literature directly relevant to the work in this thesis are presented at the beginning of each chapter.

Early interest in cetacean swimming was stimulated by a problem known as Gray's paradox (Gray, 1936). It was hypothesized that a swimming dolphin must either maintain a laminar flow of water over its body to reduce drag, or that its muscles must generate energy at a rate at least seven times greater than other mammalian muscle, to attain maximum reported speeds. Further studies indicated that the paradox existed only for cetaceans less than five metres in length (Gawn, 1948; Kermack, 1949; Parry, 1949). Many solutions were proposed to the problem, including a lower resistance for an actively swimming dolphin than a towed model (Gray, 1936, 1948; Parry, 1949; Purves, 1963), the compliant skin theory to reduce drag (Kramer, 1960), dermal ridges to alter the flow of water over the body (e.g. Purves, 1963; Shoemaker and Ridgway, 1991), and porpoising behaviour at high swimming speeds (Au and Weihs, 1980; Blake, 1983; Hester, Hunter and Whitney, 1963). All but the latter of these theories have been refuted (e.g. Fish and Hui, 1991; Hui, 1987; Lang and Pryor, 1966; Vogel, 1981). Gray's paradox appears to be due to inaccurately reported swimming speeds (Fish and Hui, 1991; Lang and Norris, 1966), assisted locomotion in the wakes of ships (Fejer and Backus, 1960; Lang, 1966; Williams *et al.*, 1992), and incomplete data on the duration of swimming effort (Fish and Hui, 1991; Johännessen and Harder, 1960; Lang and Pryor, 1966).

Few accurately measured swimming speeds exist for most cetacean species. Table 1 lists the available swimming speeds and duration of swimming effort for several species of whales and dolphins.

The dynamics of cetacean swimming have not been extensively examined. Theoretical models of propulsion have been developed for a range of dynamical parameters (e.g. Bose and Lien, 1989; Liu and Bose, 1992); however, only a few studies of dolphins are available which measure the parameters modelled (Fish, 1991; Lang and Daybell, 1963; Parry, 1949; Videler and Kamermans, 1985).

Dolphins and porpoises are well known for their habit of riding the bow and stern wakes of moving vessels, on wind and surf waves, and even in the wakes of larger cetaceans (Caldwell and Fields, 1959; Fejer and Backus, 1960; Norris and Prescott, 1961; Williams *et al.*, 1992). Several models have been proposed to explain the mechanics of wave riding (Fejer and Backus, 1960; Hayes, 1953; Norris and Prescott, 1961; Scholander, 1959), while physiological response measurements indicate that the energetic demands of wave-riding are significantly less than those of swimming at similar speeds (Williams *et al.*, 1992).

Table 1a. Swimming speeds and durations for several cetacean species.

Species	Speed (m/s)	Performance	Source
Stenella microps	7.1	burst	Hester, Hunter & Whitney, 1963
Stenella attenuata, Stenella longirostris	4.3	16 min.	Au & Perryman, 1982
S. attenuata	4.2	49 min.	Au & Perryman, 1982
S. attenuata	6.4 11.05	burst burst	Lang & Pryor, 1966
S. attenuata	1.8	sustained	Perrin, Evans & Holts, 1979
Stenella coeruleoalba	2.9	86 min.	Au & Perryman, 1982
"Dolphins" (species unknown)	8.8 7.3 8.5	8 min. 20 min. 25 min.	Johannessen & Harder, 1960
Lagenorhynchus obliquidens	7.76	burst	Lang & Daybell, 1963
L. obliquidens	4.9	prolonged	Pike, 1960
Tursiops gilli	8.3 7.01 6.09 3.08	7.5 s 10 s 50 s sustained	Lang & Norris, 1966
Tursiops truncatus	1.6	sustained	Hui, 1987
Delphinus bairdi	2.4	prolonged	Norris & Prescott, 1961

Table 1b. Swimming speeds and durations for several cetacean species.

Species	Speed (m/s)	Performance	Source
Orcinus orca	10.1	20 min.	Johannessen & Harder, 1960
O. orca	2	30 min.	Norris & Prescott, 1961
Pseudorca crassidens	2.9	not burst	Norris & Prescott, 1961
Globicephala scammoni	9.8	15 s	Norris & Prescott, 1961
Eschrichtius glaucus	4.2	1 hour	Norris & Prescott, 1961
E. glaucus	2.0	sustained	Sumich, 1983
Balaenoptera physalus	2.1	sustained	Watkins *et al.*, 1984
Balaenoptera musculus	10 7.1	10 min. 2 hours	Gawn, 1948

Large whales may have another method of assisted locomotion. It has been shown theoretically that the flukes of large cetaceans are capable of absorbing energy from ocean waves (Bose and Lien, 1990). Theoretical calculations demonstrated that energetic savings of up to 33% for a fin whale (*Balaenoptera physalus*) were possible in a fully developed seaway corresponding to a wind speed of 20 knots. Thus, energy absorbed from ocean waves may be significant for large cetacean species, and may be an important part of the energy budget of migrating whales.

1.4. Behavioural ecologies of cetaceans

Although all cetaceans live in an aquatic environment, tremendous differences exist between the behavioural ecologies of different species. Body size ranges from 1.5 metres for the harbour porpoise (*Phocoena phocoena*) to 30 metres for the blue whale (*Balaenoptera musculus*) (Katona, Rough & Richardson, 1983). Small dolphins are noted for their agility and maneuverability, while many species of large baleen whales make extensive annual migrations. For example, humpback whales (*Megaptera novaeangeliae*) in the northern Atlantic ocean travel as much as 6,000 km annually (Martin *et al.*, 1984), while gray whale (*Eschrichtius robustus*) migrations are the most extensive of any mammal, and may span 50° of latitude and cover 15,000 - 20,000 km

(Sumich, 1983). Baleen whales graze on plankton and shoaling fish, while toothed whales feed upon quick-moving prey such as fish or squid (Evans, 1987).

In light of these ecological and behavioural differences, corresponding variation may be found in the swimming characteristics between species. This variation may be manifested as behavioural, morphological, physiological and/or dynamical swimming differences.

1.5. Purpose of the study

The purpose of this thesis was to examine morphological and dynamical swimming differences within and between several species of cetaceans, and to test the hypothesis that swimming whales absorb energy from ocean waves.

Morphological variation was examined within a large sample (n=35) of harbour porpoise in an effort to determine the values of several geometric parameters for mature animals, and to look for trends in these parameters with age (Chapter 2). The morphologies of the harbour porpoise were also compared to those of a small sample of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) and several other cetaceans, and the differences found correlated with the behavioural ecologies of the species.

Dynamical swimming parameters were measured from a videotape of a harbour porpoise, an Atlantic white-sided dolphin and two long-finned pilot whales (*Globicephala melas*) swimming in captivity (Chapter 3). Measurements were possible at several different swimming speeds. The results were compared with similar data available from other fish and cetacean swimming studies.

A statistical method to test the hypothesis of wave energy absorption by whales was developed, and the method applied to the track of a tagged long-finned pilot whale when corresponding wave conditions were known (Chapter 4). Possible reasons for the negative results were reviewed.

2. Morphometrics

2.1. Introduction to cetacean morphometrics

In cetacean swimming, propulsive thrust is produced by movements of the flukes, while drag is largely the result of viscous shear stresses exerted by the water on the body surface (Wu, 1977). Differences in the morphologies of the body and flukes within and between species of cetaceans may significantly affect propulsive thrust and drag. However, limited geometrical data on the body and flukes of cetaceans has been reported. Quantitative morphological measurements also form valuable input data to theoretical models of cetacean swimming (e.g. Bose and Lien, 1989; Bose and Lien, 1990; Liu and Bose, 1992).

Body length, mass, body surface area, position of maximum body thickness and fineness ratio (see Section 2.2.3.) of a sample of harbour porpoise were examined by Yasui (1981). The average fineness ratio was 4.9 (σ=0.72), and the average position of maximum thickness was 0.423 (σ=0.015) of the body length from the beak. No trends with age were examined. The position of maximum body thickness for dolphins in general has been reported as in a range from 0.34 - 0.45 of body length from the anterior tip of the beak, and the fineness ratio as 3.85 - 5.55 (Hertel, 1966; Fish and Hui, 1991).

Bose *et al.* (1990) presented detailed morphometric data for ten animals representing nine species of cetaceans: harbour porpoise; Atlantic white-sided dolphin; white-beaked dolphin (*Lagenorhynchus albirostris*); common dolphin (*Delphinus delphis*); beluga whale (*Delphinapterus leucas*); Sowerby's beaked whale (*Mesoploden bidens*); minke whale (*Balaenoptera acutostrata*); fin whale; and sperm whale (*Physeter macrocephalus*). Values of body volume, mass, wetted-surface area, prismatic and volumetric coefficients, fineness ratio, fluke area, fluke aspect ratio and fluke sweep angles were estimated from the measurements taken. It was suggested that a species exhibiting a low volumetric coefficient, low ratio of (fluke area)$^{1/2}$: (volume)$^{1/3}$, high fluke aspect ratio, low ratio of fluke area : wetted-surface area, and a high fineness ratio is likely to be capable of high maximum speeds compared with other similarly sized species in similar conditions.

The purpose of this study was fourfold: (i) to present morphometric data for additional species of cetaceans; (ii) to examine within-species variation in several morphological parameters, including gender and age differences; (iii) to compare quantitatively the within- and between-species variation in parameters in cases where the number of specimens is sufficient for statistical evaluation; and, (iv) to compare the geometry of harbour porpoise, a relatively slow-swimming inshore species (Read and Gaskin, 1985) and Atlantic white-sided dolphins, a more pelagic species (Evans, 1987), to that of other cetaceans.

2.2. Materials and methods

2.2.1. Specimens

Body and fin morphometrics are presented for 42 animals representing six species. These include: humpback whale (one specimen); Sowerby's beaked whale (one specimen); harbour porpoise (33 specimens); Atlantic white-sided dolphin (3 specimens); beluga whale (one specimen) and long-finned pilot whale (three specimens).

The specimens were obtained from several sources. Dead harbour porpoise became available through the Harbour Porpoise Bycatch Survey run co-operatively by the Whale Research Group at the Memorial University of Newfoundland and the Department of Fisheries and Oceans. Measurements were taken from two live long-finned pilot whales temporarily held in captivity at the New England Aquarium in Boston, Massachusetts. Other dead cetaceans were collected opportunistically through an entrapment and stranding network run by the Whale Research Group, Memorial University of Newfoundland.

2.2.2. Measurements

Measurements were taken either in a laboratory or *in situ* if the size of the animal prohibited moving it. Recorded measurements included body girth measurements and fluke-planform offsets (Tables A1-A2).

Body length was measured as a straight line from the anterior tip of the skull to the fluke notch for all specimens except the humpback whale. Measurement of body length for the humpback whale was made over the belly of the animal. Body girths were recorded at equally spaced stations along the length of the animals (Figure 1). A linear interpolation between adjacent values was recorded in instances where a girth measurement was not possible. Full girth values for the humpback whale were obtained from half-girth measurements. Fluke planform offsets were measured at 23 stations across the fluke span (Figure 2) (Bose *et al.*, 1990). Masses were recorded for the harbour porpoise by using a spring balance.

2.2.3. Derived parameters

Several parameters were derived from the measurements taken; these included: body volume; estimated mass; wetted-surface area; fluke planform area; fluke planform sweep angle; fluke aspect ratio; prismatic coefficient; volumetric coefficient; fineness ratio; and position of maximum girth.

Figure 1

Example of the measurement of body girths at equally spaced stations along the body length of a cetacean (adapted from a sketch by Dawn Nelson). Lines marked with an asterisk represent stations where girth measurements are not possible; in these cases, linear interpolations between adjacent values are recorded.

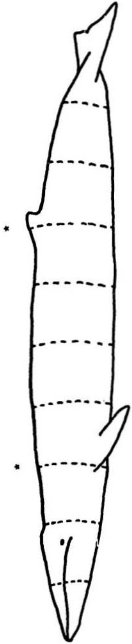
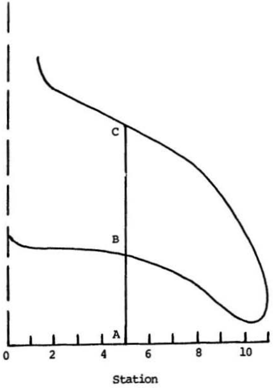


Figure 2

Measurement of fluke planform offsets of a cetacean (adapted from Figure 3, Bose *et al.* (1990)). Line AB represents the trailing edge offset at station 5, and line BC represents the chord length (see Table A2).


C
B
A
0
2
4
6
8
10
Station

1. Body volume was obtained from girth measurements. The girth measurements were used to obtain an estimate of the cross-sectional area of the body, assuming circular sections, at each station along the body length. These sectional areas were then integrated over the length of the body by using Simpson's rules (e.g. Rawson and Tupper, 1983). However, cetacean cross-sections at the ends of the body are not circular; thus, the assumption of circular sections gives a maximum estimate of body volume. Bose and Lien (1989) showed that the calculated body volume of a fin whale using elliptical sections at the ends of the body was about 2.5% less than the volume derived using circular sections. Cetacean body volume values reported here were reduced by this amount in an attempt to account for the elliptical shape at the ends of the body (Bose *et al.*, 1990).

2. By assuming that the bodies were close to neutrally buoyant, estimated mass was found by multiplying the body volume by the density of salt water; this was taken as 1025 kg/m^3 (Bose *et al.*, 1990).

3. Wetted-surface area of the body was obtained by integrating the whole girth measurements over the length of the body (Bose *et al.*, 1990). This value is used in the estimation of the friction drag of rigid bodies (e.g. Blake, 1983).

4. Fluke planform area was found by integrating the fluke planform chord lengths over the span from station 2 outwards (see Figure 2) (Bose *et al.*, 1990). This parameter is used in the calculation of the lift of an oscillating hydrofoil (e.g. Blake, 1983).

5. Sweep of the fluke planform (λ) (Figure 3) was defined as:

[2]
$$\lambda = \arctan \frac{(0.75c_3 + t_3) - (0.75c_{10} + t_{10})}{7h},$$

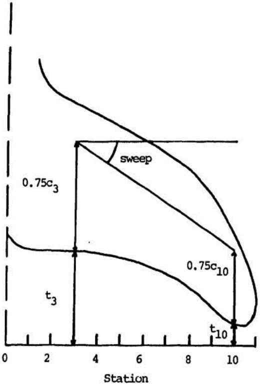
where c_3 and c_{10} are the fluke chord lengths at fluke stations 3 and 10; t_3 and t_{10} are the distances from the fluke's trailing edge to a datum line at the same stations; and h is the spacing between fluke stations (see Figure 3) (Bose *et al.*, 1990). Theoretical studies indicate that the efficiency of an oscillating hydrofoil is related to its sweep (Karpouzian, Spedding and Cheng, 1990; van Dam, 1987).

6. Fluke aspect ratio was defined as:

[3]
$$aspect\ ratio = \frac{4s^2}{S},$$

Figure 3

Fluke planform showing measurement of sweep angle of the flukes of a cetacean (adapted from Figure 3, Bose *et al.* (1990)).


sweep
0.75c3
0.75c10
t3
t10
0
2
4
6
8
10
Station

where s is the half span measured from fluke station 2 to station 11, and S is the planform area of both sides of the planform from station 2 outwards (see Figure 2) (Vogel, 1981; Bose *et al.*, 1990). The area of the fluke directly behind the peduncle was not included in the calculation of aspect ratio; since the fluke in this area has no leading edge and chord lengths are not clearly defined, this region is better thought of as part of the body rather than the hydrofoil (Bose *et al.*, 1990). Hydrodynamically, a high fluke aspect ratio means a high propulsive efficiency (van Dam, 1987).

7. Prismatic coefficient (C_p), a measure of fineness in the ends of the body, was defined as

[4] $$C_P = \frac{V}{LA},$$

where V is the body volume, L is the body length and A is the area of the section with maximum area (Bose *et al.*, 1990).

8. A volumetric coefficient (C_v) was found from:

[5] $$C_V = \frac{V}{(0.1L)^3}.$$

Volumetric coefficient is a measure of the stockiness or "fatness" of the body (Bose *et al.*, 1990).

9. The fineness ratio was found from:

[6]

$$\mathit{fineness\ ratio} = \frac{L(\pi)}{g_{\max}},$$

where g_{max} is the maximum girth of the animal. This ratio is used in the estimation of the drag of rigid bodies (*e.g.* Blake, 1983).

10. The position of maximum body girth was recorded as a fraction of body length from the anterior tip of the skull. For small cetaceans, the position of maximum girth can influence the percentage of the body surface area that will experience laminar flow; it is therefore a factor in determining the drag of the animal (Blake, 1983).

Values of derived parameters for all specimens are shown in Table 2.

Table 2a. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise F900871	Harbour Porpoise F900872	Harbour Porpoise M910710
Body length (m)	1.49	0.96	1.37
Volume (m^3)	0.048	0.015	0.046
Mass (kg)	48	14	45
Estimated mass (kg)	49	16	47
Surface area (m^2)	0.86	0.39	0.81
Fluke area (m^2)	0.0256	0.0114	0.0220
Fluke aspect ratio	2.85	2.43	3.85
Sweep angle (°)	37.5	41.8	29.4
C_v	14.7	18.4	18.1
C_p	0.47	0.51	0.51
Fineness ratio	5.03	4.71	4.71
Position of maximum girth (/body length)	0.4	0.42	0.44

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2b. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise F910711	Harbour Porpoise M910712	Harbour Porpoise M910740
Body length (m)	0.92	1.43	1.06
Volume (m^3)	0.019	0.058	0.028
Mass (kg)	19.5	55	27
Estimated mass (kg)	20.5	59.5	29
Surface area (m^2)	0.43	0.94	0.54
Fluke area (m^2)	0.0173	0.0209	0.0135
Fluke aspect ratio	2.27	3.45	3.21
Sweep angle (°)	46.2	34.6	37.2
C_v	24.4	19.8	23.5
C_p	0.49	0.51	0.49
Fineness ratio	3.99	4.52	4.04
Position of maximum girth (/body length)	0.43	0.42	0.38

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2c. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise M910741	Harbour Porpoise F910742	Harbour Porpoise F910743
Body length (m)	1.37	1.31	1.54
Volume (m^3)	0.042	0.037	0.050
Mass (kg)	39	36	50
Estimated mass (kg)	43	38	51
Surface area (m^2)	0.77	0.69	0.88
Fluke area (m^2)	0.0193	0.0192	0.0214
Fluke aspect ratio	3.36	2.57	3.19
Sweep angle (°)	34.2	41.9	35.7
C_v	16.3	16.6	13.8
C_p	0.52	0.50	0.52
Fineness ratio	5.00	4.85	5.42
Position of maximum girth (/body length)	0.36	0.38	0.33

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2d. <u>Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).</u>

Parameter	Identification number		
	Harbour Porpoise M910744	Harbour Porpoise M910745	Harbour Porpoise F910746
Body length (m)	1.42	1.24	1.61
Volume (m^3)	0.056	0.032	0.069
Mass (kg)	58	32	71
Estimated mass (kg)	57	33	71
Surface area (m^2)	0.92	0.64	1.09
Fluke area (m^2)	0.0248	0.0181	0.0323
Fluke aspect ratio	3.60	2.95	3.22
Sweep angle (°)	32.7	40.5	31.4
C_v	19.6	17.0	16.7
C_p	0.53	0.50	0.48
Fineness ratio	4.62	4.82	4.76
Position of maximum girth (/body length)	0.42	0.32	0.37

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number.

Table 2e. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise F910747	Harbour Porpoise F910748	Harbour Porpoise M910755
Body length (m)	1.23	1.36	1.47
Volume (m^3)	0.034	0.035	0.051
Mass (kg)	31	36	48
Estimated mass (kg)	35	36	52
Surface area (m^2)	0.64	0.67	0.88
Fluke area (m^2)	0.0176	0.0176	0.0226
Fluke aspect ratio	2.53	3.00	3.14
Sweep angle (°)	44.4	40.0	35.5
C_v	18.5	14.1	16.1
C_p	0.47	0.44	0.53
Fineness ratio	4.47	4.95	5.07
Position of maximum girth (/body length)	0.41	0.37	0.34

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2f. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise F910757	Harbour Porpoise M910758	Harbour Porpoise M910759
Body length (m)	1.15	1.42	1.33
Volume (m^3)	0.029	0.045	0.039
Mass (kg)	25	45	38
Estimated mass (kg)	30	46	40
Surface area (m^2)	0.59	0.80	0.74
Fluke area (m^2)	0.0159	0.0205	0.0197
Fluke aspect ratio	2.65	3.42	3.48
Sweep angle (°)	42.4	28.8	28.8
C_v	19.3	15.9	16.6
C_p	0.48	0.50	0.50
Fineness ratio	4.41	4.99	4.89
Position of maximum girth (/body length)	0.39	0.42	0.38

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2g. <u>Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).</u>

Parameter	Identification number		
	Harbour Porpoise F910760	Harbour Porpoise M910761	Harbour Porpoise M910762
Body length (m)	1.56	1.44	1.50
Volume (m^3)	0.059	0.049	0.058
Mass (kg)	57	52	54
Estimated mass (kg)	60.5	50	59.5
Surface area (m^2)	0.98	0.81	0.97
Fluke area (m^2)	0.0245	0.0270	0.0242
Fluke aspect ratio	3.40	3.57	3.65
Sweep angle (°)	35.6	35.1	30.5
C_v	15.5	16.4	17.4
C_p	0.49	0.46	0.52
Fineness ratio	4.98	4.71	4.87
Position of maximum girth (/body length)	0.38	0.35	0.40

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number.

Table 2h. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise M910763	Harbour Porpoise M910764	Harbour Porpoise F910765
Body length (m)	1.16	1.37	1.29
Volume (m^3)	0.030	0.042	0.032
Mass (kg)	26	41	29
Estimated mass (kg)	31	43	33
Surface area (m^2)	0.59	0.80	0.74
Fluke area (m^2)	0.0177	0.0232	0.0183
Fluke aspect ratio	2.68	3.49	3.06
Sweep angle (°)	39.8	35.9	39.2
C_v	19.5	16.5	15.1
C_p	0.50	0.48	0.50
Fineness ratio	4.48	4.79	5.08
Position of maximum girth (/body length)	0.35	0.40	0.31

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2i. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise M910766	Harbour Porpoise F910768	Harbour Porpoise M910820
Body length (m)	1.20	1.15	0.91
Volume (m^3)	0.026	0.030	0.016
Mass (kg)	28	27	14
Estimated mass (kg)	27	31	16
Surface area (m^2)	0.55	0.60	0.38
Fluke area (m^2)	0.0189	0.0141	0.0149
Fluke aspect ratio	2.47	2.99	2.33
Sweep angle (°)	44.8	40.1	43.2
C_v	15.0	19.7	21.6
C_P	0.44	0.49	0.54
Fineness ratio	4.77	4.43	4.44
Position of maximum girth (/body length)	0.33	0.35	0.33

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2j. Summary of geometric parameters for harbour porpoise, (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise F910734	Harbour Porpoise M910735	Harbour Porpoise F910736
Body length (m)	1.25	1.34	1.25
Volume (m^3)	N/A	N/A	N/A
Mass (kg)	29	35	30
Estimated mass (kg)	N/A	N/A	N/A
Surface area (m^2)	N/A	N/A	N/A
Fluke area (m^2)	0.0242	0.0210	0.0193
Fluke aspect ratio	2.70	3.08	2.97
Sweep angle (°)	38.7	37.8	38.9
C_v	N/A	N/A	N/A
C_p	N/A	N/A	N/A
Fineness ratio	N/A	N/A	N/A
Position of maximum girth (/body length)	N/A	N/A	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2k. Summary of geometric parameters for harbour porpoise. (*Phocoena phocoena*).

Parameter	Identification number		
	Harbour Porpoise M910737	Harbour Porpoise M910738	Harbour Porpoise M910739
Body length (m)	1.38	1.34	1.39
Volume (m^3)	N/A	N/A	N/A
Mass (kg)	41	36.5	47.5
Estimated mass (kg)	N/A	N/A	N/A
Surface area (m^2)	N/A	N/A	N/A
Fluke area (m^2)	0.0244	0.0216	0.0207
Fluke aspect ratio	3.17	3.31	3.60
Sweep angle (°)	37.3	34.3	29.8
C_v	N/A	N/A	N/A
C_p	N/A	N/A	N/A
Fineness ratio	N/A	N/A	N/A
Position of maximum girth (/body length)	N/A	N/A	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 21. Summary of geometric parameters for Atlantic white-sided dolphin, (*Lagenorhynchus acutus*).

Parameter	Identification number		
	White-sided Dolphin M910001	White-sided Dolphin M910002	White-sided Dolphin M910004
Body length (m)	2.2	2.2	2.2
Volume (m^3)	0.141	0.131	0.148
Mass (kg)	N/A	N/A	N/A
Estimated mass (kg)	145	134	152
Surface area (m^2)	1.85	1.75	1.86
Fluke area (m^2)	0.0578	0.0496	0.0612
Fluke aspect ratio	2.82	2.90	3.19
Sweep angle (°)	40.8	42.0	40.8
C_v	13.2	12.3	13.9
C_p	0.52	0.48	0.52
Fineness ratio	5.5	5.5	5.5
Position of maximum girth (/body length)	0.36	0.36	0.36

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2m. Summary of geometric parameters for long-finned pilot whales, (*Globicephala melas*).

Parameter	Identification number		
	Pilot Whale M910001	Pilot Whale F910014	Pilot Whale F910016
Body length (m)	3.05	2.91	3.40
Volume (m^3)	0.475	N/A	N/A
Mass (kg)	N/A	N/A	N/A
Estimated mass (kg)	487	N/A	N/A
Surface area (m^2)	3.99	N/A	N/A
Fluke area (m^2)	N/A	0.093	0.109
Fluke aspect ratio	N/A	2.73	3.55
Sweep angle (°)	N/A	44.8	35.6
C_v	16.7	N/A	N/A
C_p	0.51	N/A	N/A
Fineness ratio	4.9	N/A	N/A
Position of maximum girth (/body length)	0.35	N/A	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table 2n. Summary of geometric parameters for a beluga whale (*Delphinapterus leucas*), a Sowerby's beaked whale (*Mesoploden bidens*), and a humpback whale (*Megaptera novaeangeliae*).

Parameter	Identification number		
	Beluga Whale M910001	Sowerby's Beaked Whale M900001	Humpback Whale M900001
Body length (m)	3.69	4.90	9.25
Volume (m^3)	0.856	1.33	12.1
Mass (kg)	N/A	N/A	N/A
Estimated mass (kg)	877	1400	12400
Surface area (m^2)	5.67	8.30	34.0
Fluke area (m^2)	0.173	0.238	1.46
Fluke aspect ratio	3.43	4.12	3.89
Sweep angle (°)	20.7	30.6	26.5
C_v	17.0	11.3	15.3
C_p	0.48	0.50	0.45
Fineness ratio	4.7	5.9	4.6
Position of maximum girth (/body length)	0.46	0.31	0.43

2.2.4. Methods

Differences in ratios between appropriate geometrical parameters within and between species may indicate real differences in their swimming performance characteristics (e.g. Bose *et al.*, 1990; Wu, 1977).

Within-species variation in parameters, including gender and age differences, were studied by using reduced major axis regressions (Rayner, 1985) and t-tests applied to the large sample of harbour porpoise (Table 4, Figures 4-9). Since the exact ages of the animals were unknown, body length was used in the regressions as an estimator of age (Lockyer, 1984).

The differences in geometric parameters between the harbour porpoise and Atlantic white-sided dolphin samples were statistically evaluated by using t-tests (Table 5). Ideally, only physically mature animals should be included in this type of analysis to eliminate possible biases arising from ontogenetic influences. However, lengths of both physical and sexual maturity vary between populations of cetaceans (e.g. Braham, 1984; Gaskin *et al.*, 1984; Stewart and Leatherwood, 1985), and are not well known for the Newfoundland/Labrador populations. Sexual maturity was assessed based on published standards. Female harbour porpoise exceeding 1.50 m and males exceeding 1.40 m were deemed sexually mature (Gaskin *et al.*, 1984); following these criteria, three females and seven males were included in the analysis. Male Atlantic white-sided dolphins are regarded as sexually mature upon attaining a length of 2.1 - 2.4 m, while females are considered mature at 1.94 - 2.22 m (Perrin and Reilly, 1984). Following these criteria, the three male Atlantic white-sided dolphins were included in the comparison.

The morphologies of mature harbour porpoise and Atlantic white-sided dolphins were compared with that of other cetaceans; data from Bose *et al.* (1990) were included in this section to provide more complete between-species comparisons (Figures 10-15). Cetacean species included in the comparison were: white-beaked dolphin, common dolphin, beluga whale, Sowerby's beaked whale, minke whale, humpback whale, fin whale and sperm whale. Within- and between-species means and standard deviations were calculated for several parameters (Table 6). In cases where more than one specimen per species was available, a species mean was computed and used in the calculation of the mean for all cetacean species.

Since measurements from only one animal were available for most of the species other than harbour porpoise and Atlantic white-sided dolphins, all specimens were included in the analysis regardless of maturity. Sexually mature animals included the common dolphin, the beluga whales, one pilot whale and the sperm whale, while the white-beaked dolphin, two pilot whales, two Sowerby's beaked whales, the minke whale, the humpback whale and the fin whale were sexually immature. Length criteria for sexual maturity for these species are summarized in Table 3.

2.3. Results and discussion

2.3.1. Harbour porpoise morphometrics

Measurements from a total of 35 harbour porpoise were available for analysis, including data for two specimens from Bose *et al.* (1990). Complete morphometrics were available for 29 of these animals, while fluke measurements only were available for the remaining six.

The sample of harbour porpoise displayed considerable variation in the values of many geometric parameters (Table 4).

Several geometric parameters were found to vary significantly with length, including C_v, fineness ratio, fluke aspect ratio, and the ratios of surface area : volume, and fluke area : surface area (Figures 4-9).

Figure 4 shows a significant decrease in volumetric coefficient with length ($n=29$, $r^2=0.455$, $p<0.01$). Figure 5 shows an increase in the fineness ratio with length ($n=29$, $r^2=0.451$, $p<0.01$). In general, at moderate and high Reynolds

Table 3. Lengths of sexual maturity for several cetacean species.

Species	Length, ♀ (m)	Length, ♂ (m)	Source
Common dolphin (*D. delphis*)	1.9	2.0	Perrin & Reilly, 1984
White-beaked dolphin (*L. albirostris*)	2.5	2.5	Perrin & Reilly, 1984
Beluga whale (*D. leucas*)	3.8	3.4	Brodie, 1989
Sowerby's beaked whale (*M. bidens*)	4.7 - 4.8	5.0	Lien and Barry, 1990; Lien *et al.*, 1990
Pilot whale (*G. melas*)	3 - 4	4 - 5	IWC, 1987
Minke whale (*B. acutostrata*)	7.2	6.8	Stewart & Leatherwood, 1985
Humpback whale (*M. novaeangeliae*)	12.1	11.6	Winn & Reichley, 1985
Sperm whale (*P. macrocephalus*)	8.3 - 9.2	11.0 - 12.0	Rice, 1989
Fin whale (*B. physalus*)	18.3	17.7	Gambell, 1985

Table 4. Means and standard deviations of several parameters for harbour porpoise (*Phocoena phocoena*) of all ages.

Parameter	n	mean	σ
Length (m)	35	1.31	0.17
C_v	29	17.6	2.6
C_p	29	0.49	0.03
Fineness ratio	29	4.73	0.31
Position of maximum girth (/body length)	29	0.39	0.05
Fluke area (m^2)	35	0.0200	0.0044
Aspect ratio	35	3.07	0.42
Sweep angle (°)	35	37.2	4.7
Fluke area $^{1/2}$: volume $^{1/3}$	29	0.42	0.03
Fluke area : surface area	29	0.028	0.004

Figure 4

Relationship between volumetric coefficient (C_v) and body length for harbour porpoise (*Phocoena phocoena*).

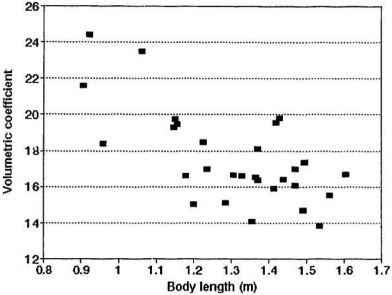
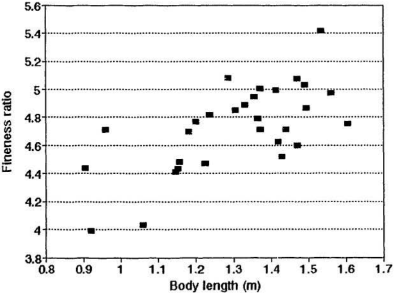

Volumetric coefficient
26
24
22
20
18
16
14
12
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
Body length (m)

Figure 5

Relationship between fineness ratio and body length for harbour porpoise (*Phocoena phocoena*).


Fineness ratio
5.6
5.4
5.2
5
4.8
4.6
4.4
4.2
4
3.8
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
Body length (m)

numbers, the drag coefficient of a body increases with its "fatness" (Vogel, 1981). These results indicate that young harbour porpoise have a relatively full-formed or "chunky" body, and suggest higher drag coefficients, compared with adult porpoise.

Figure 6 shows a significant increase in fluke aspect ratio with length ($n=35$, $r^2=0.498$, $p<0.01$), while Figure 7 shows a significant inverse relationship between fluke aspect ratio and sweep angle ($n=35$, $r^2=0.820$, $p<0.01$). The latter relationship is likely due to structural limitations (van Dam, 1987). In general, the efficiency of a hydrofoil increases with its aspect ratio (van Dam, 1987). However, theoretical studies of hydrofoils indicate that a high sweep angle may increase swimming efficiency for a given aspect ratio (van Dam, 1987), and may allow for restricted motion of the flukes, which decreases wake energy losses, without loss of thrust (Karpouzian *et al.*, 1990). Thus, the efficiency of juvenile harbour porpoise flukes relative to adults is uncertain.

The ratio of fluke area to surface area decreased significantly with length ($n=29$, $r^2=0.243$, $p<0.01$) (Figure 8). For a given speed, fluke motion and wetted-surface area, low ratios of fluke area : surface area suggest lower values of thrust and drag for a swimming animal (Bose *et al.*, 1990). This result indicates that young harbour porpoise are less efficient swimmers than their adult counterparts.

Juvenile whales and dolphins are often seen swimming in close company with adult animals in a position appropriate for riding the slipstream of the larger animals. In general, the position maintained by the younger animals is beside and above the midline of the adult, with the pectoral fin just below the adult's dorsal fin (Norris and Prescott, 1961). Young cetaceans seldom leave an adult's side during normal movements of the group until they are several months old (Norris and Prescott, 1961). This method of assisted locomotion aids smaller cetaceans in keeping up with faster moving animals, and may compensate for less efficient shape of the juvenile harbour porpoise.

Harbour porpoise live in cold coastal waters where thermoregulatory considerations may place constraints on hydrodynamic attributes. An individual animal's heat flux is partially determined by its surface area : volume ratio; some cetacean species may have reduced this ratio to compensate for their heat-conductive environment (Worthy and Edwards, 1990). A plot of the surface area : volume ratio vs. length for harbour porpoise is shown in Figure 9. The ratio was found to decrease significantly with length ($n=29$, $r^2=0.81$, $p<0.01$). Thus, the higher volumetric coefficients and lower fineness ratios displayed by juvenile harbour

<u>Figure 6</u>

Relationship between fluke aspect ratio and body length for harbour porpoise (*Phocoena phocoena*).

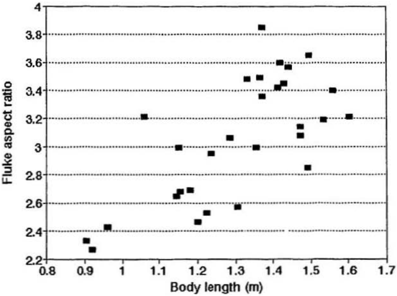

Fluke aspect ratio
4
3.8
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
Body length (m)

Figure 7

Relationship between fluke sweep angle and fluke aspect ratio for harbour porpoise (*Phocoena phocoena*).

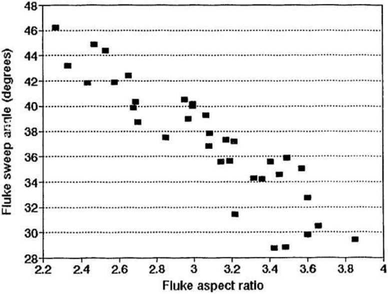
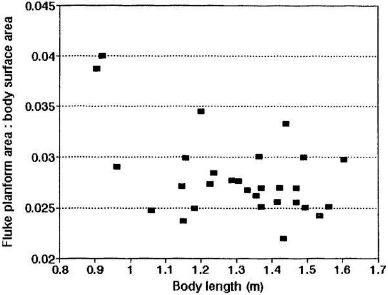

48
46
44
42
40
38
36
34
32
30
28
Fluke sweep angle (degrees)
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
3.8
4
Fluke aspect ratio

Figure 8

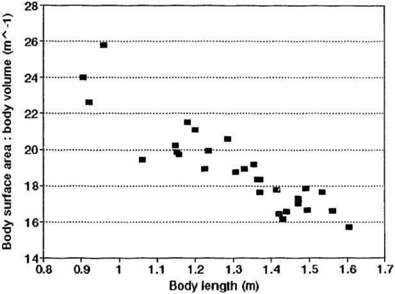
Relationship between the ratio of fluke planform area : body surface area and body length for harbour porpoise (*Phocoena phocoena*).



Fluke planform area : body surface area
0.045
0.04
0.035
0.03
0.025
0.02
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
Body length (m)

Figure 9

Relationship between the ratio of body surface area : body volume and body length for harbour porpoise (*Phocoena phocoena*).


Body surface area : body volume (m^-1)
28
26
24
22
20
18
16
14
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
Body length (m)

porpoise may be partly the results of thermoregulatory constraints.

Gender differences in derived parameters were also examined. No significant differences were found.

The finding that many derived parameters varied with length for the harbour porpoise suggests that the geometry of other cetacean species may also change with age. However, there are few data available to evaluate such relationships. Between-species comparisons of geometry should be made between similar age classes in other species.

2.3.2. Comparison of harbour porpoise and Atlantic white-sided dolphin morphology.

Nine parameters were analyzed for between-species differences using t-tests; specifically, these were volumetric coefficient, prismatic coefficient, fineness ratio, position of maximum girth, fluke area, fluke aspect ratio, fluke sweep angle, and the ratios of $(\text{fluke area})^{1/2}$: $(\text{volume})^{1/3}$, and (fluke area) : (surface area). Since the geometry of male and female harbour porpoise was not significantly different, harbour porpoise gender was ignored in this analysis. As described previously, only mature harbour porpoise and Atlantic white-sided dolphins were included in the analysis (Table 5).

Table 5. Comparison of geometric parameters for sexually mature harbour porpoise (*Phocoena phocoena*), and Atlantic white-sided dolphins (*Lagenorhynchus acutus*).

Parameter	Harbour Porpoise	White-sided Dolphins	t (df=12)	p
Body length (m)	$\mu=1.48$	$\mu=2.20$	-	-
C_p	$\mu=0.50$ $\sigma=0.03$	$\mu=0.50$ $\sigma=0.02$	-0.39	0.71
C_v	$\mu=16.8$ $\sigma=1.8$	$\mu=13.1$ $\sigma=0.8$	-3.35	<0.01
Fineness ratio	$\mu=4.70$ $\sigma=0.35$	$\mu=5.46$ $\sigma=0.12$	-3.63	<0.01
Position of maximum girth (/body length)	$\mu=0.39$ $\sigma=0.05$	$\mu=0.36$ $\sigma=0.0$	-1.13	0.28
Fluke area (m^2)	$\mu=0.0244$ $\sigma=0.0035$	$\mu=0.0562$ $\sigma=0.0060$	-11.96	<0.01
Fluke aspect ratio	$\mu=3.37$ $\sigma=0.20$	$\mu=2.97$ $\sigma=0.20$	-3.02	<0.05
Sweep angle (°)	$\mu=33.7$ $\sigma=2.6$	$\mu=41.2$ $\sigma=0.7$	-4.72	<0.01
Fluke area$^{1/2}$: volume$^{1/3}$	$\mu=0.41$ $\sigma=0.02$	$\mu=0.46$ $\sigma=0.02$	-3.30	<0.01
Fluke area: surface area	$\mu=0.0265$ $\sigma=0.0031$	$\mu=0.0307$ $\sigma=0.0025$	-2.11	0.06

Note: μ = mean, σ = standard deviation

Harbour porpoise were found to have a significantly higher volumetric coefficient and a significantly lower fineness ratio than the white-sided dolphins. This result quantifies the observation that harbour porpoise have a relatively full-formed body, and possibly a higher drag coefficient, in comparison with white-sided dolphins.

Harbour porpoise displayed a significantly lower ratio of (fluke area)$^{1/2}$: (volume)$^{1/3}$ than white-sided dolphins, indicating that harbour porpoise have a smaller amount of fluke area for a given body size. For a given speed, fluke motion and fluke shape, thrust is proportional to fluke area; at steady speeds, a low value of this ratio suggests a relatively low thrust and drag for the size of animal (Bose *et al.*, 1990).

The harbour porpoise sample displayed a significantly higher fluke aspect ratio and a significantly lower sweep angle than the white-sided dolphins. As mentioned previously, a high aspect ratio indicates a high hydrodynamic efficiency and a high lift production for thrust, while a high sweep angle may compensate for a low aspect ratio (Karpouzian *et al.*, 1990; van Dam, 1987). Flukes of high aspect ratio may not be able to support a high sweep angle due to structural limitations (van Dam, 1987).

Harbour porpoise maintain a coastal distribution and are often found in bays, rivers, estuaries and tidal channels; they are described as slow swimmers that usually do not jump clear of the surface (IUCN, 1991). Atlantic white-sided dolphins are considered a more pelagic, offshore form (Leatherwood, Reeves and Foster, 1983); offshore species of odontocetes are generally regarded as faster swimmers than inshore species (Lang and Pryor, 1966). The less streamlined body shape of harbour porpoise is consistent with slower movements, while the lower ratio of $(\text{fluke area})^{1/2} : (\text{volume})^{1/3}$ suggests a higher propulsive efficiency than white-sided dolphins. As described in section 2.3.1., the interaction between fluke sweep angle, fluke aspect ratio and swimming efficiency remains unclear.

2.3.3. Between-species geometric comparison: other cetaceans.

Derived parameters from adult harbour porpoise and Atlantic white-sided dolphins were compared to the parameters of other cetacean species. Relationships between derived parameters for all species were studied (Figures 10-15; Table 6). Logarithmic plots were used in several cases in order to consolidate the data points.

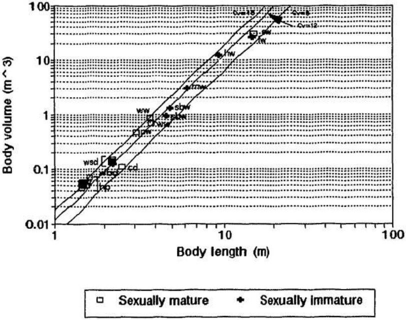
Table 6. Comparison of geometric parameters for harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and other cetacean species.

Parameter	Harbour Porpoise	White-sided Dolphins	All Species
Body length (m)	μ=1.48 σ=0.06	μ=2.20 σ=0	μ=5.88 σ=4.86
C_p	μ=0.50 σ=0.03	μ=0.50 σ=0.02	μ=0.47 σ=0.04
C_v	μ=16.8 σ= 1.8	μ=13.1 σ= 0.8	μ=12.4 σ= 3.4
Fineness ratio	μ=4.70 σ=0.35	μ=5.46 σ=0.12	μ=5.53 σ=0.72
Position of maximum girth (/body length)	μ=0.39 σ=0.05	μ=0.36 σ=0.0	μ=0.37 σ=0.06
Fluke aspect ratio	μ=3.37 σ=0.20	μ=2.97 σ=0.20	μ=3.88 σ=0.86
Sweep angle (°)	μ=33.7 σ= 2.6	μ=41.2 σ= 0.7	μ=32.6 σ= 5.5
Fluke area$^{1/2}$: volume$^{1/3}$	μ=0.41 σ=0.02	μ=0.46 σ=0.02	μ=0.44 σ=0.05
Fluke area: surface area	μ=0.0265 σ=0.0031	μ=0.0307 σ=0.0025	μ=0.0297 σ=0.0072

Note: μ = mean, σ = standard deviation

Figure 10

Relationship between body volume and body length for several cetacean species. Lines of constant volumetric coefficient (C_v) for values of 6, 12 and 18 are indicated. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).


Body volume (m ^ 3)
100
10
1
0.1
0.01
1
10
100
Body length (m)
cv=16
cv=8
cv=12
sw
fw
hw
mw
sbw
sbw
ww
ww
pw
wsd
wbd
cd
hp
Sexually mature
Sexually immature

Many of the relationships between parameters showed generally linear trends, although variation in the data existed both within- and between-species.

Figure 10 shows body volume vs. body length. As a guide, lines of constant volumetric coefficient, a measure of the stockiness of the body, are shown at values of 6, 12, and 18. Values of C_v ranged from 6.9 for the common dolphin to a mean of 16.8 (σ=1.8) for the harbour porpoise. The mean C_v for all species was 12.4 (σ=3.35). The means and standard deviations for harbour porpoise and white-sided dolphins were substantially different from those for all species: for the harbour porpoise, the mean was 35% higher and the standard deviation 46% lower than those for all species; for the white-sided dolphins, the mean was 6% higher and the standard deviation 76% lower than those for all species. This result, in addition to the fact that C_v was significantly different for harbour porpoise and white-sided dolphins (see Section 2.3.2), suggests that volumetric coefficients may be different between species. More specimens of each species could be examined to prove this.

Figure 11 shows $(\text{volume})^{1/3}$ vs. $(\text{fluke area})^{1/2}$, with lines of constant values of 0.01, 0.025 and 0.04 also plotted. Values of this ratio ranged from 0.37 for the fin whale to 0.53 for the humpback whale. The mean ratio for all species was 0.44 (σ=0.05). Both the harbour porpoise and the white-sided dolphins had mean values of this ratio within 7% of the mean value for all species, although the standard deviation for each differed from that for all species by 60%. The value of this ratio was significantly different for harbour porpoise and white-sided dolphins (see Section 2.3.2). More specimens may show that this ratio differs significantly between other cetacean species.

Figure 12 shows an increasing trend between fluke aspect ratio and fluke area. The values of aspect ratio ranged from 2.97 (σ=0.20) for the white sided dolphins, to 5.79 for the fin whale. The mean fluke aspect ratio between all species was 3.88 (σ=0.86), 13% greater than the mean for harbour porpoise and 23% greater than the mean for white-sided dolphins. These results indicate that fluke aspect ratio may vary significantly between cetacean species. Species known to be fast swimmers, such as fin whales, have a relatively high value of fluke aspect ratio (Bose and Lien, 1989).

Figure 13 is a plot of body wetted-surface area vs. fluke area, with lines of constant value indicated. For equal velocity, fluke motion parameters and thrust coefficient, thrust is proportional to fluke area, while drag is related to wetted-surface area through a drag coefficient (Blake, 1983). The mean value of this ratio for the harbour porpoise and white-sided dolphins was similar to

Figure 11

Relationship between (body volume)$^{1/3}$ and (fluke planform area)$^{1/2}$ for several cetacean species. Lines of constant values of the ratio are indicated. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).

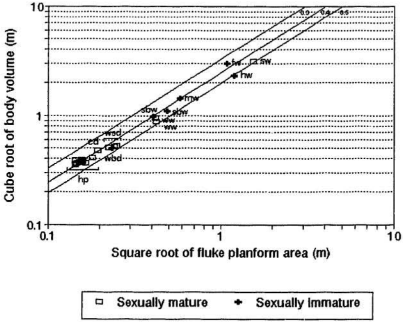

0.3
0.4
0.5
fw
sw
hw
mw
sbw
ww
wsd
cd
wbd
hp
10
1
0.1
Cube root of body volume (m)
0.1
1
10
Square root of fluke planform area (m)
□ Sexually mature
✚ Sexually immature

Figure 12

Relationship between fluke aspect ratio and fluke planform area for several cetacean species. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).

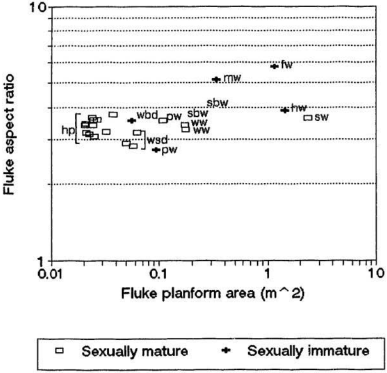
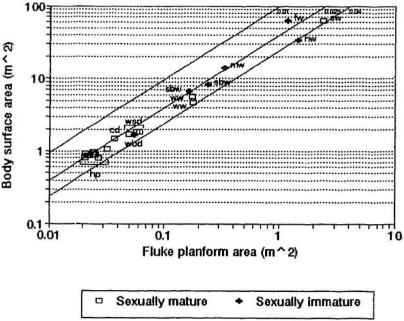

Fluke aspect ratio
10
1
0.01
0.1
1
10
Fluke planform area (m^2)
fw
mw
sbw
sbw
hw
sw
wbd
pw
ww
ww
hp
wsd
pw
Sexually mature
Sexually immature

Figure 13

Relationship between body surface area and fluke planform area for several cetacean species. Lines of constant values of the ratio are indicated. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).


0.01
0.025
0.04
fw
sw
hw
mw
sbw
sbw
ww
ww
wsd
cd
wbd
hp
100
10
1
0.1
0.01
0.1
1
10
Body surface area (m^2)
Fluke planform area (m^2)
□ Sexually mature
✦ Sexually immature

the mean for all species. However, the standard deviation for the harbour porpoise was 58% less than the standard deviation for all species, while the standard deviation for the white-sided dolphins was 65% less than that for all species. This suggests that the ratio of wetted-surface area : fluke area may be significantly different between cetacean species.

Figure 14 shows a decreasing trend between sweep angle and fluke aspect ratio. This result is similar to that found for the harbour porpoise (see Figure 10), although the relationship in this case is not linear. Cetacean flukes contain no bones for structural support; thus, as mentioned previously, the inverse relationship between sweep and aspect ratio is likely to be due to structural limitations (van Dam, 1987).

Figure 15 plots the position of maximum girth of the body vs. length. A decreasing trend is apparent; smaller species of cetaceans have their maximum girths placed farther back than larger species. A linear regression between the position of maximum girth and length for all cetaceans gave a correlation of -0.73 ($p<0.05$). For a swimming animal the size of a dolphin, the position of the maximum girth can influence the percentage of the surface area that will experience laminar flow; it is therefore a factor in determining the drag of the animal (Blake, 1983).

Again, considerable variation both within- and between-species was found.

Figure 14

Relationship between sweep angle and fluke aspect ratio for several cetacean species. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).

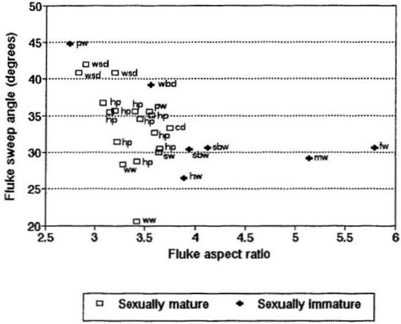
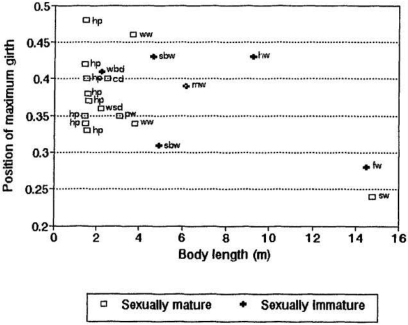

Fluke sweep angle (degrees)
50
45
40
35
30
25
20
2.5
3
3.5
4
4.5
5
5.5
6
Fluke aspect ratio
pw
wsd
wsd
wsd
wbd
hp
hp
hp
hp
pw
hp
hp
cd
hp
hp
hp
sbw
sbw
fw
sw
mw
hp
ww
hw
ww
□ Sexually mature
✚ Sexually immature

Figure 15

Relationship between the position of maximum girth and body length for several cetacean species. The key to the abbreviations is as follows: hp, harbour porpoise (*Phocoena phocoena*); wsd, Atlantic white-sided dolphin (*Lagenorhynchus acutus*); wbd, white-beaked dolphin (*Lagenorhynchus albirostris*); cd, common dolphin (*Delphinus delphis*); pw, long-finned pilot whale (*Globicephala melas*); bw, beluga whale (*Delphinapterus leucas*); sbw, Sowerby's beaked whale (*Mesoploden bidens*); mw, minke whale (*Balaenoptera acutostrata*); hw, humpback whale (*Megaptera novaeangeliae*); fw, fin whale (*Balaenoptera physalus*); sw, sperm whale (*Physeter macrocephalus*).


Position of maximum girth
0.5
0.45
0.4
0.35
0.3
0.25
0.2
Body length (m)
0
2
4
6
8
10
12
14
16
hp
ww
sbw
hw
hp
wbd
hp
cd
mw
hp
hp
wsd
hp
pw
hp
ww
hp
sbw
fw
sw
Sexually mature
Sexually immature

3. Cetacean swimming kinematics

3.1. Introduction to cetacean swimming kinematics

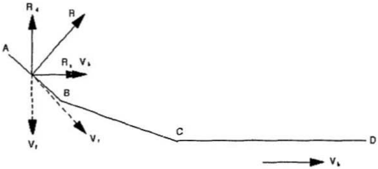
All members of the order Cetacea swim by moving their peduncle in a vertical plane. In addition, the flukes also move up and down in a vertical plane with their centre of rotation at the point of insertion in the peduncle. The flukes follow the motion of the peduncle such that they are approximately horizontal at the top and bottom of the peduncle's stroke, and bent at their maximum angle at the middle of the peduncle's stroke (Parry, 1949). It is easy to show qualitatively that this swimming movement will produce a forward thrust (Figure 16) (Parry, 1949).

Several geometrical parameters that may influence the propulsion of cetaceans were discussed in Chapter 2. However, how a species uses the shape it has evolved may be equally important in determining swimming ability. Detailed motions of the flukes, such as heave amplitude, pitch angle and oscillation frequency, significantly affect thrust and propulsive efficiency (Bose and Lien, 1989).

Little data exists on the swimming movements of dolphins and whales. The earliest record of cetacean swimming kinematics came from Parry (1949), who observed the swimming motions of a bottlenose dolphin (*Tursiops truncatus*) giving birth. Parry also reported that dolphins

Figure 16

The dynamics of cetacean swimming: production of thrust (from Parry, 1949). The flukes of the animal are represented by line AB; the peduncle and posterior portion of the animal are represented by line BC; and the relatively inflexible anterior portion of the body is shown as line CD. The animal is moving forward with velocity V_b; the true velocity of the fluke is represented by V_r, which is the sum of V_b and the downward velocity of the fluke, V_f. V_r produces the resultant R on the water; this resultant can be resolved into forward thrust, R_t, and drag, R_d.


R_d
R
A
R_h
V_h
B
V_f
V_r
C
D
V_h

observed swimming at a speed of 10 knots next to a ship had an oscillation frequency of 2 Hz. The movements of a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) were filmed during a study to determine power, speed and drag (Lang and Daybell, 1963), but detailed motions of the flukes were not examined thoroughly. Videler and Kamermans (1985) recorded and analyzed the swimming movements of two animals, a bottlenose dolphin and an estuary dolphin (*Sotalia guianensis*), in an effort to find evidence for asymmetry between upstrokes and downstrokes. Among the parameters examined were swimming velocities, frequencies of oscillation of the flukes, stride lengths (the number of body lengths travelled in the period of one fluke cycle), fluke angle of attack, and the forces generated during the upstroke and downstroke of the flukes. Some of the results from this analysis are included in the present discussion. One additional study of the kinematics, thrust and power production from a pair of bottlenose dolphins showed that the frequency of oscillation of the flukes increased with velocity, while the heave amplitude and maximum pitch angle of the flukes decreased with velocity (Fish, 1991).

There has been considerable debate on whether the upstroke and the downstroke of cetacean flukes produce equal power. Dissections of common dolphins, harbour porpoise, fin whales and blue whales revealed that the epaxial locomotor musculature was approximately double that of the hypaxial muscle mass, suggesting that the power of the upstroke is greater than the downstroke (Kermack, 1949; Pilleri *et al.*, 1976; Purves, 1963; Smith, Browne and Gaskin, 1976). Conversely, dissections of a franciscana (*Pontoporia blainvillei*), a short-finned pilot whale (*Globicephala macrorhynchus*), and an Indus dolphin (*Platanista indi*) implied that the thrust delivered in the upstroke and downstroke might be equal (Arkowitz and Rommel, 1985; Pilleri *et al.*, 1976; Strickler, 1980). A study of the architectural and histochemical characteristics of the axial musculature of a bottlenose dolphin suggested that the shorter, larger-diameter fibres of the ventral muscles give it a greater potential for force production for a given amount of muscle mass (Bello *et al.*, 1985). Finally, frame-by-frame analysis of a bottlenose dolphin swimming at a slow speed showed that the dolphin's forward velocity increased during the downstroke and decreased during the upstroke (Videler and Kamermans, 1985). Thus, controversy still exists about the power stroke of cetacean locomotion, and different species may use various power/thrust strategies.

To understand swimming dynamics, cetacean swimming has also been modelled theoretically. The thrust and efficiency of the flukes of an immature fin whale were computed, and the results compared with known characteristics of fin whale swimming (Bose and Lien, 1989). The thrust and efficiency of the flukes of a white-sided dolphin, a fin whale and a beluga whale were modelled and compared using a numerical method (Liu and Bose, 1992). Both models presented calculations over a range of parameters since details of the motions of the flukes of these species are unknown.

The purpose of this section was to measure and compare fluke motions at several swimming speeds of three cetacean species: harbour porpoise, Atlantic white-sided dolphin and long-finned pilot whale. The results were compared with similar data available for fish and other cetacean species.

3.2. Materials and methods

3.2.1. Materials

Underwater videotapes of three cetacean species filmed at the New England Aquarium were available for analysis. The first videotape, originally filmed in 1990 for promotional purposes, contained footage of a harbour porpoise and an Atlantic white-sided dolphin swimming within the confines of a small pool. The second videotape, filmed in June 1991, showed two long-finned pilot whales swimming together. At the times of filming, the animals were housed in a 12.8 m x 8.6 m outdoor pool at the aquarium, and were not on public display. In both cases, the camera was not mounted in a fixed position, but was held by an underwater diver. In general, the view of the camera was from slightly below the swimming plane of the animals, and the camera followed the movements of the animals.

Relatively complete morphometric data were available for both long-finned pilot whales and the Atlantic white-sided dolphin. Morphometric data for the harbour porpoise were not available.

3.2.2. Methods

The videotapes were analyzed frame-by-frame using a high quality video cassette player. Sequences of relatively steady swimming were selected for each animal for analysis. In all sequences, for the harbour porpoise and the white-sided dolphin, the animals were swimming alone (i.e. the other animal was out of view of the camera). The pilot whales, however, were swimming side-by-side for the duration of the video. Due to poor lighting conditions, the images of the animals were relatively fuzzy and ill-defined in several of the video sequences; thus, detailed motions of the flukes were not measurable for all sequences.

Swimming speed and the frequency of oscillation of the flukes were estimated for each steady swimming sequence for each animal. Additional measurements were possible for several of the clearer sequences. In these cases, measurements of the heave amplitude and the maximum pitch angle of the flukes were also taken.

Swimming speeds (v) of the animals were determined by observing sequences where the wall of the pool was visible behind the animal, and by estimating the distance travelled during a specific timed period. Each estimate of swimming speed was calculated at least six times; the average of the speeds was used in later analyses.

The frequency of oscillation of the flukes (f) for each steady swimming sequence was determined by a two-step process. First, a stopwatch was used to measure the time interval in seconds of a whole number of fluke cycles, where one fluke cycle was defined as the movement of the flukes from top of stroke to top of stroke, or bottom of stroke to bottom of stroke. Each time interval was measured at least six times. The average time interval was then used to calculate the frequency of oscillation of the flukes using the following relationship:

[7]
$$f=\frac{cycles}{time}\,Hz$$

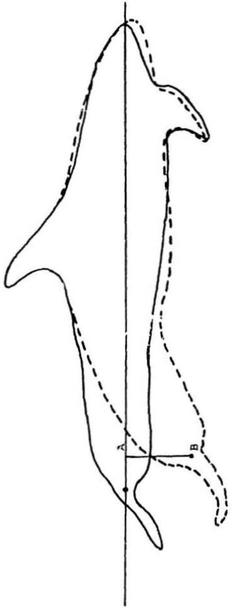
The clearest swimming sequences were further analyzed for heave amplitude (h) and pitch angle (θ) of the flukes. The "best" complete fluke cycle from each sequence, when the animal was swimming closest to perpendicular to the viewing angle of the camera, was chosen for analysis. This method was used as the camera view of the swimming animals usually followed the motion of animals, thus resulting in many images that were partly head-on or tail-on, and therefore unsuitable for heave and pitch measurements. The outline of the whole animal during the best fluke cycle of each sequence was traced onto transparent overhead sheets at intervals of 1/15 second (every second frame), resulting in 10 to 13 tracings for each cycle (see Figures 17 and 18). The top and bottom of the stroke were defined as the images which displayed the maximum fluke displacement above and below the midline of the animal. The midstrokes were defined as the images in which the animal's body appeared to be straight.

The transparencies for each sequence were then overlaid to provide measurements of the change in heave amplitude with time. Since the anterior end of the animals displayed pitching motions, the dorsal fin was used to align the transparencies. The upstroke and downstroke of each cycle were analyzed separately. Measurements of heave amplitude were obtained as follows. The midstroke of each half-cycle was used as the zero heave amplitude reference image for that half-cycle. Heave amplitudes were defined and measured as the perpendicular distance from the midpoint of the outline of the peduncle in the reference image to the midpoint of the outline of the peduncle in the other images (Figure 17). Since the camera view of animal was generally from below the midline, some distortion of the heave amplitude may be expected, and measured differences between the maximum heave of the upstroke and downstroke may not be real. The average of the maximum displacements was reported as the maximum heave amplitude.

The displacements measured on the transparencies were converted to real distances through multiplication by a scale factor. The Atlantic white-sided dolphin and long-finned pilot whale morphometrics included the straight-line distance from the tip of the snout to the tip of the dorsal fin. Since the anterior half of the dolphin showed relatively little flexibility, this measure was chosen as the basis for a conversion factor. As morphometrics were not available for the harbour porpoise, the length of the harbour porpoise from the snout to the tip of the dorsal fin and from the snout to the insertion of flukes were estimated from frames containing images of both the harbour porpoise and the white-sided dolphin. The calculated distance from

Figure 17

Sample measurement of fluke heave amplitude from videotapes (from Atlantic white-sided dolphin (*Lagenorhynchus acutus*) sequence #5). Fluke heave amplitude is shown as the line AB, the perpendicular distance from the animal's midline at midstroke to the centre of the peduncle.


A
B

snout to dorsal fin was used as the basis for a conversion factor for the harbour porpoise.

The maximum pitch angle of the flukes was assumed to occur at midstroke (Parry, 1949). This angle was measured from the midstroke transparency of the animals (Figure 18). The view of the camera did not permit an accurate measurement of the maximum pitch angle of the flukes for every midstroke image. In cases where two measurements were possible for a given fluke cycle, the average of the two measurements was used in later analyses in an attempt to compensate for error due to the viewing angle of the camera.

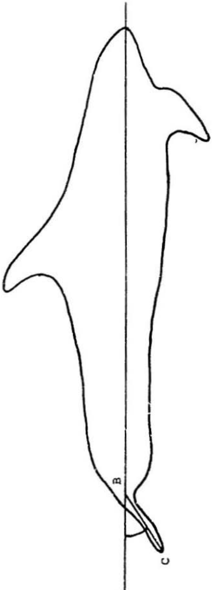
The measurements described above allowed for the calculation of the stride length of each animal. Stride length (*s*), a dimensionless expression of speed commonly reported in fish locomotion studies, is used to make interspecific comparisons of swimming performance (Videler and Kamermans, 1985). Stride length measures the number of body lengths travelled in the period of one fluke cycle, and is defined by:

[8]

$$s=\frac{speed*period}{bodylength}.$$

Figure 18

Sample measurement of maximum fluke pitch angle from videotapes (from Atlantic white-sided dolphin (*Lagenorhynchus acutus*) sequence #5). Pitch angle is shown as ∠ABC, the angle formed by the animal's midline and the line bisecting the profile of the fluke.


B
C
A

3.3. Results and discussion

3.3.1. Results

Measured morphometric data for the long-finned pilot whales and the Atlantic white-sided dolphin, and estimated data for the harbour porpoise, are shown in Table 7. Since the identities of pilot whales could not be determined from the video, the averages of their morphometric measurements were used in later analyses.

Steady swimming speeds and corresponding fluke oscillation frequencies were determined for six harbour porpoise sequences, six white-sided dolphin sequences, and two pilot whale sequences. One additional white-sided dolphin sequence showed the animal undergoing a relatively smooth acceleration, although the rate of acceleration was unknown. Table 8 shows the mean swimming speeds, frequencies and stride length for each sequence for each animal.

Maximum heave amplitude and maximum pitch angle measurements were possible for two harbour porpoise and three white-sided dolphin steady swimming sequences. These data are presented in Table 9.

Table 7. Morphometric data for a harbour porpoise (*Phocoena phocoena*), an Atlantic white-sided dolphin, (*Lagenorhynchus acutus*), and a long-finned pilot whale (*Globicephala melas*).

	Harbour porpoise	White-sided dolphin	Pilot whale
Sex	N/A	♂	♀
Mass (kg)	N/A	170	480
Length (m)	1.25	2.56	3.15
Length from beak to tip of dorsal fin (m)	0.7	1.33	-
Span of flukes (m)	N/A	0.68	0.73

Note: Data for the harbour porpoise was estimated from the videotapes; pilot whale data represents averages of measurements from two animals.

Table 8a. Summary of swimming kinematics data for a harbour porpoise, (*Phocoena phocoena*).

Sequence number	Swimming speed (m/s)	Swimming speed (lengths/s)	Oscillation frequency (Hz)	Stride length
1	2.6	2.1	2.0	1.0
2	2.1	1.7	1.8	0.9
3	1.8	1.4	1.4	1.0
4	1.6	1.3	1.4	0.9
5	1.8	1.4	1.4	1.0
6	2.3	1.8	1.8	1.0

Table 8b. Summary of swimming kinematics data for an Atlantic white-sided dolphin, (*Lagenorhynchus acutus*).

Sequence number	Swimming speed (m/s)	Swimming speed (lengths/s)	Oscillation frequency (Hz)	Stride length
1	1.8	0.7	1.0	0.7
2	1.8	0.7	1.1	0.6
3	2.1	0.8	1.1	0.8
4	1.8	0.7	1.1	0.6
5	2.9	1.1	1.6	0.7
6	2.6	1.0	1.3	0.8
7	4.5	1.8	2.6	0.7

Table 8c. Summary of swimming kinematics data for a long-finned pilot whale, (*Globicephala melas*).

Sequence number	Swimming speed (m/s)	Swimming speed (lengths/s)	Oscillation frequency (Hz)	Stride length
1	2.4	0.8	1.0	0.8
1	2.4	0.8	1.1	0.7
2	1.9	0.6	1.2	0.5

Note: Data was measurable for both pilot whales in the first sequence, but only one whale in the second sequence.

Table 9. Summary of fluke motion data for a harbour porpoise (*Phocoena phocoena*), and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*).

Sequence number	Swimming speed (m/s)	Heave amplitude (m)	Pitch angle (°)
		Harbour porpoise	
2	2.1	0.14	34
5	1.8	0.13	34
		White-sided dolphin	
1	1.8	0.21	31
5	2.9	0.34	33
6	2.6	0.30	34

3.3.2. Discussion

The methods described above include several sources of unavoidable error. Swimming speed measurements were probably in error due to the motion of the camera. The error in estimating the swimming speed during a timed period was dependent upon the distance of the animal from the wall of the pool, the distance travelled during the timed period, and the position of the photographer relative to the swimming animal (see Appendix B for detailed calculations). In general, the measured swimming speeds may have been underestimated by 15 - 30% as a result of the motion of the camera.

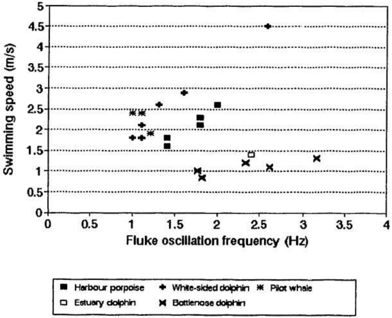
Errors in the measurement of heave amplitude and maximum pitch angle were a result of the position of the camera view in a different plane from the flukes of the animals. Ideally, the photographer should have been: (1) located at a large distance from the animal so that the oscillations of the peduncle did not carry the flukes significantly out of the plane of the view of the camera; and (2) located in the same plane as the body of the swimming animal. In the videotape, however, the camera was held within a few metres of the animals, and the view of the camera was from below the animals. In general, the view of the camera resulted in an underestimation of both the heave amplitude and the maximum pitch angle, but it was difficult to calculate the magnitude of this error.

Figure 19 shows the relationship between swimming speed and fluke oscillation frequency for five species. Kinematic data from Videler and Kamermans (1985) for a bottlenose dolphin and an estuary dolphin are included for interspecies comparisons. Swimming speed increased linearly with fluke oscillation frequency for the white-sided dolphin and the harbour porpoise (r^2=0.97, p<0.01; r^2=0.91, p<0.01 respectively). Swimming speed is known to increase linearly with tail beat frequency for fish (Bainbridge, 1958; Blake, 1983). Similar results have also been found for two bottlenose dolphins (Fish, 1991), although the bottlenose dolphin data displayed in Figure 19 showed no significant increase in speed with frequency (r^2=0.71, p=0.075).

The data points for the pilot whales did not show this trend. Unlike the white-sided dolphin and the harbour porpoise, the pilot whales swam together for the entire videotape. During sequence #1, the two whales swam side by side, and displayed similar fluke oscillation frequencies, with one whale showing a frequency of 1.0 s^{-1}, and the other whale showing a frequency of 1.1 s^{-1}. Although the magnitude of the heave amplitude was not measurable due to the position of the camera, both whales appeared to be exerting similar swimming effort. During sequence #2, one of the

Figure 19

Relationship between swimming speed (m/s) and fluke oscillation frequency for five cetacean species, including harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and long-finned pilot whale (*Globicephala melas*). Bottlenose dolphin (*Tursiops truncatus*) and estuary dolphin (*Sotalia guianensis*) data are taken from Videler and Kamermans (1985).


Swimming speed (m/s)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
3
3.5
4
Fluke oscillation frequency (Hz)
■ Harbour porpoise
✚ White-sided dolphin
✳ Pilot whale
□ Estuary dolphin
✖ Bottlenose dolphin

pilot whales swam slightly below and ahead of the other whale, which placed the upper whale in a position appropriate for obtaining energy from the flow around the lower whale. The upper whale was observed to swim actively for the first part of the sequence, and then coast beside the other whale for the remaining time. Although the heave amplitudes of the flukes of the whales were again not measurable, the whale in the lower position displayed noticeably larger heave amplitudes than the whale above it. Thus, it is possible that the swimming speed of the pilot whale observed in sequence #2 did not increase in response to a high fluke oscillation frequency because the other pilot whale was obtaining a "free ride". This behaviour is similar to that observed in young cetaceans which swim in comparable positions and obtain energy from the flow around their mothers (Norris and Prescott, 1961).

Figure 19 also shows that the white-sided dolphin swam faster than the smaller harbour porpoise at any given frequency. This dependence of speed upon the length of the animal has also been found for fish (Bainbridge, 1958; Blake, 1983). Data for the bottlenose dolphin and estuary dolphin did not show this trend.

Figure 20 shows the relationship between swimming speed, expressed in terms of body lengths/second, and frequency. Although the harbour porpoise travelled at a slower absolute speed than the white-sided dolphin for a given frequency, it swam at a higher speed relative to its body length. Within-species analyses of swimming data for fish have shown that different sizes of fish display similar speeds relative to their body lengths at given frequencies (Bainbridge, 1958). The different relative speeds shown by the harbour porpoise and white-sided dolphin may be morphological in origin (see Section 2.3.2), or due to other dynamic swimming differences such as heave amplitude, pitch angle or the flexibility of the flukes.

Figure 21 shows the relationship between swimming speed and stride length. A regression between the distance travelled per fluke cycle and swimming speed was not significant for the harbour porpoise, white-sided dolphin and bottlenose dolphin ($p=0.4$; $p=0.8$; $p=0.1$, respectively). Thus, the stride length appears to remain constant at all of the speeds measured for these species. This result is consistent with studies on fish swimming, where it was found that the distance travelled per beat was constant above frequencies of 5-6 Hz; below this frequency, the stride length slowly diminished (Bainbridge, 1958). A Neuman-Keuls Multiple Comparison (Hays, 1988) for all of the animals showed that the stride length was significantly different between all species ($p<0.05$) except the white-sided dolphin

Figure 20

Relationship between swimming speed (body lengths/s) and fluke oscillation frequency for five cetacean species, including harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and long-finned pilot whale (*Globicephala melas*). Bottlenose dolphin (*Tursiops truncatus*) and estuary dolphin (*Sotalia guianensis*) data are taken from Videler and Kamermans (1985).

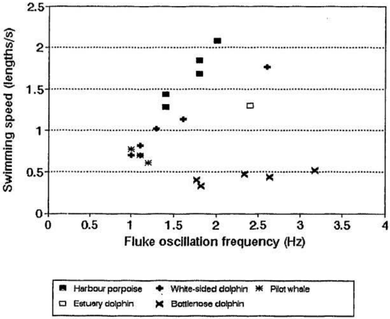

Swimming speed (lengths/s)
0
0.5
1
1.5
2
2.5
Fluke oscillation frequency (Hz)
0
0.5
1
1.5
2
2.5
3
3.5
4
Harbour porpoise
White-sided dolphin
Pilot whale
Estuary dolphin
Bottlenose dolphin

Figure 21

Relationship between swimming speed (m/s) and stride length for five cetacean species, including harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and long-finned pilot whale (*Globicephala melas*). Bottlenose dolphin (*Tursiops truncatus*) and estuary dolphin (*Sotalia guianensis*) data are taken from Videler and Kamermans (1985).

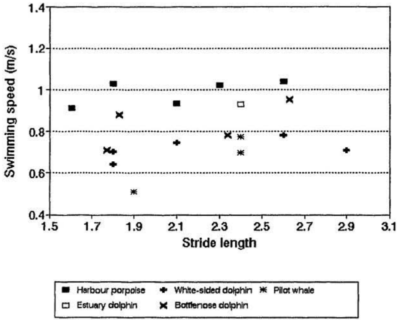
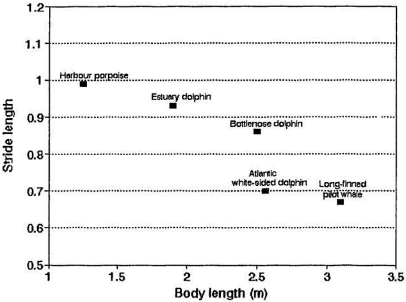

Swimming speed (m/s)
1.4
1.2
1
0.8
0.6
0.4
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
3.1
Stride length
Harbour porpoise
White-sided dolphin
Pilot whale
Estuary dolphin
Bottlenose dolphin

Figure 22

Relationship between stride length and body length for five cetacean species, including harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and long-finned pilot whale (*Globicephala melas*). Bottlenose dolphin (*Tursiops truncatus*) and estuary dolphin (*Sotalia guianensis*) data are taken from Videler and Kamermans (1985).


Stride length
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
Harbour porpoise
Estuary dolphin
Bottlenose dolphin
Atlantic
white-sided dolphin
Long-finned
pilot whale
1
1.5
2
2.5
3
3.5
Body length (m)

and the pilot whale, indicating species-specific stride lengths.

Figure 22 shows a decreasing trend between stride length and body length. A regression on this data yielded a statistically significant relationship ($r^2=0.85$, $p<0.05$). Thus, it appears that, for the species included in this study, larger cetaceans have shorter stride lengths than smaller cetaceans.

Detailed fluke motion measurements were possible for several of the harbour porpoise and white-sided dolphin sequences. The heave amplitude of the flukes throughout a complete fluke cycle was plotted against time for two harbour porpoise and three white-sided dolphin sequences (Figures 23-27). All of the plots showed an oscillatory pattern, with both the upstroke and downstroke equally long. This result agrees with data presented in Videler and Kamermans (1985). The heave amplitude varied between the upstroke and downstroke, but not consistently. This variation may be the result of the camera's view.

The relationship between the maximum heave amplitude and speed for the harbour porpoise and the white-sided dolphin is shown in Figure 28. Corresponding data for the bottlenose dolphin and the estuary dolphin were not included in Videler and Kamermans (1985). There were not enough data to perform meaningful statistics. However, the heave

Figure 23

Relationship between fluke heave amplitude and time for a harbour porpoise (*Phocoena phocoena*), sequence #2.

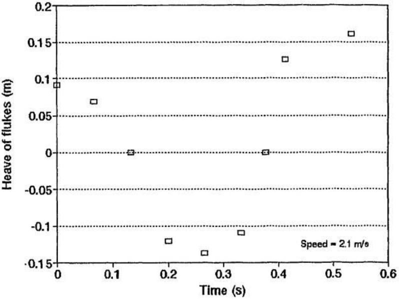
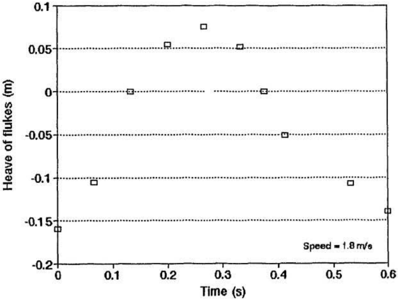

Heave of flukes (m)
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
Time (s)
0
0.1
0.2
0.3
0.4
0.5
0.6
Speed = 2.1 m/s

Figure 24

Relationship between fluke heave amplitude and time for a harbour porpoise (*Phocoena phocoena*), sequence #5.


0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
Heave of flukes (m)
0
0.1
0.2
0.3
0.4
0.5
0.6
Time (s)
Speed = 1.8 m/s

<u>Figure 25</u>

Relationship between fluke heave amplitude and time for an Atlantic white-sided dolphin (*Lagenorhynchus acutus*), sequence #1.

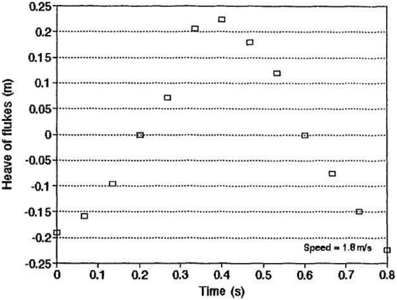
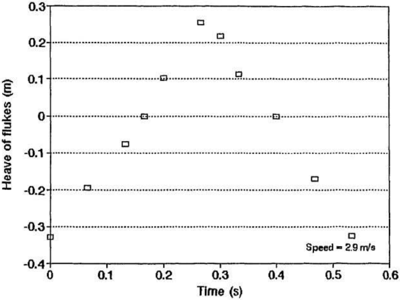

Heave of flukes (m)
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
-0.25
Time (s)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Speed = 1.8 m/s

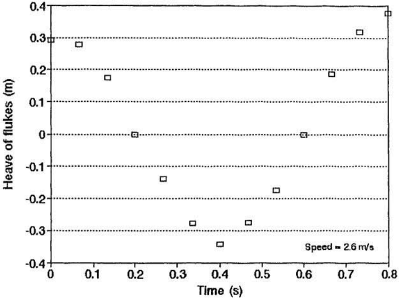
Figure 26

Relationship between fluke heave amplitude and time for an Atlantic white-sided dolphin (*Lagenorhynchus acutus*), sequence #5.


Heave of flukes (m)
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
Time (s)
0
0.1
0.2
0.3
0.4
0.5
0.6
Speed = 2.9 m/s

<u>Figure 27</u>

Relationship between fluke heave amplitude and time for an Atlantic white-sided dolphin (*Lagenorhynchus acutus*), sequence #6.


Heave of flukes (m)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
Time (s)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Speed = 2.6 m/s

amplitude of the white-sided dolphin appeared greater than that for the harbour porpoise, and there seemed to be an increasing trend between maximum heave and speed for both species. Fish locomotion studies have shown that the heave amplitude increases with speed for low speeds, and remains constant at high speeds (Bainbridge, 1958).

Figure 29 shows the maximum heave amplitude expressed as a fraction of body length vs. speed. Once again, statistical comparisons could not be made; however, it appears that the heave amplitudes of the harbour porpoise and the white-sided dolphin fall on the same upward-sloping line. The average amplitude for both animals was 0.1 body lengths. Fish (1991) found that the heave amplitude of bottlenose dolphins remained constant at a value of 0.1 body lengths for all measured speeds.

Maximum pitch angle vs. swimming speed is shown in Figure 30. Pitch angle values from Videler and Kamermans (1985) were not included in this plot since their values were averaged over each fluke half-cycle, and thus did not represent the maximum pitch. The average pitch angle for the harbour porpoise was 34 degrees, and the average for the white-sided dolphin was 33 degrees. Numerical modelling of the flukes of a white-sided dolphin found that the highest efficiencies were obtained at a pitch angle amplitude of between 20-30 degrees (Liu and Bose, 1992). The white-sided

Figure 28

Relationship between maximum fluke heave amplitude (m) and swimming speed (m/s) for a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*).

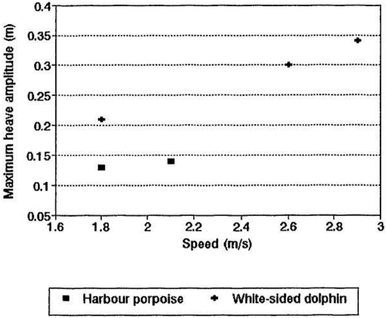

Maximum heave amplitude (m)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
1.6
1.8
2
2.2
2.4
2.6
2.8
3
Speed (m/s)
■ Harbour porpoise
✚ White-sided dolphin

Figure 29

Relationship between maximum fluke heave amplitude (% body length) and swimming speed (m/s) for a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*).

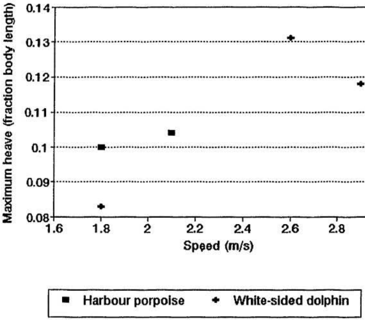
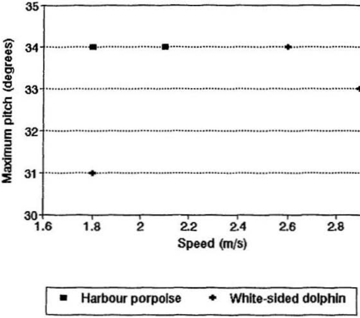

Maximum heave (fraction body length)
0.14
0.13
0.12
0.11
0.1
0.09
0.08
1.6
1.8
2
2.2
2.4
2.6
2.8
3
Speed (m/s)
■ Harbour porpoise
✚ White-sided dolphin

Figure 30

Relationship between maximum fluke pitch angle and swimming speed (m/s) for a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*).


Maximum pitch (degrees)
35
34
33
32
31
30
1.6
1.8
2
2.2
2.4
2.6
2.8
3
Speed (m/s)
■ Harbour porpoise
+ White-sided dolphin

dolphin appeared to display a slight increasing trend between pitch angle and speed. Fish (1991) found that the maximum pitch angle decreased with swimming speed for bottlenose dolphins.

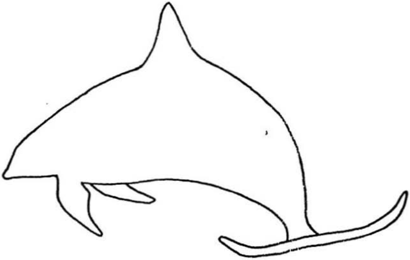
Figure 31 shows the tracings of the harbour porpoise and white-sided dolphin flukes as seen from behind when the animals were actively swimming at an unknown speed. These tracings showed that the spanwise flexibility of the white-sided dolphin was noticeably greater than that of the harbour porpoise. This may be due to the high sweep angle typical of the flukes of white-sided dolphins (see Chapter 2). At least one attempt has been made to model a hydrofoil in an inviscid fluid with a flexible span using lifting line theory (Ahmadi and Widnall, 1985); however, the effect of spanwise flexibility on the swimming performance of cetaceans is unclear.

Figure 32 shows tracings of the harbour porpoise and white-sided dolphin as seen from the side. These tracings showed that the chordwise flexibility of the white-sided dolphin was greater than that of the harbour porpoise. This result may also be due to the high sweep angle of the fluke of the white-sided dolphin. Chordwise flexibility of a two-dimensional hydrofoil in an inviscid fluid was modelled theoretically, and found to provide a moderate gain in efficiency with a decrease in thrust (Katz and Weihs, 1978).

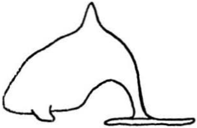
Tracings of the two species from the front showed that the harbour porpoise held its pectoral fins in a different orientation from the white-sided dolphin. Figure 33 displays this variation. The angle formed by the pectoral fins of the harbour porpoise was approximately 89 degrees, while the angle of the white-sided dolphin's pectoral fins was 39 degrees.

Figure 31

Comparison of spanwise fluke flexibility between a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*) at the bottom of a stroke. Animals are shown at different scales.



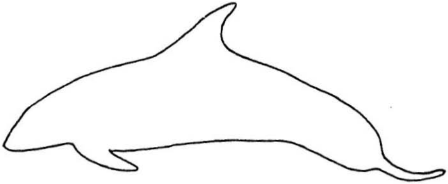
Atlantic White-sided dolphin



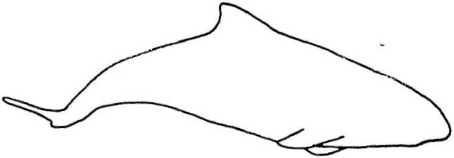
Harbour porpoise

<u>Figure 32</u>

Comparison of chordwise fluke flexibility between a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*) at the bottom of a stroke. Animals are shown at different scales.



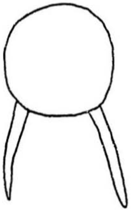
Atlantic white-sided dolphin



Harbour porpoise

Figure 33

Comparison of orientation of pectoral fins between a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*). Animals are shown at different scales.



Atlantic white-sided dolphin

Harbour porpoise

4. Wave-assisted cetacean propulsion

4.1. Introduction to wave-assisted cetacean propulsion

Cetaceans are known to make use of "free rides" by swimming in the bow wave of ocean-going vessels or other whales, or by planing within storm or surf waves (e.g. Fejer and Backus, 1960; Hayes, 1953; Norris and Prescott, 1961; Williams *et al.*, 1992). Bose and Lien (1990) used hydrodynamic theory to show that the flukes of large cetaceans are capable of absorbing energy from ocean waves for propulsion. This energy absorption was demonstrated by using the flukes of an immature fin whale as a model; the whale was estimated to make a propulsive power saving of around 25% in head seas and 33% in following seas in a fully developed seaway with a wind speed of around 20 knots. In seas corresponding to a wind speed of 30 knots, the calculated power saving increased to 30% in head seas and 40% in following seas. Theoretically, wave energy absorption by the flukes of cetaceans is substantial and may contribute significantly to the energy budget of large whales.

Fluid particles under moving waves travel in roughly circular orbits, completing one revolution in each wave period (Vogel, 1981). The orbits of these particles are not actually closed, but display a mean horizontal velocity known as Stokes drift (Newman, 1981, p. 252). The effect of this drift on a swimming whale is small, but will result in a slight increase in drag in head seas, and a decrease in drag in following seas (Bose and Lien, 1990).

A whale swimming near the surface of the ocean is subject to the orbital motions of waves, and will move with them. If the wave length is much longer than the whale, the action of the waves will cause the entire body of the whale to move up and down with the wave. However, if the wave length is short enough, the whale's body may move in such a way that the flukes are in water oscillating vertically out of phase with the body. In this way, the differential vertical velocity of the flukes enables the whale to absorb energy from ocean waves (Bose and Lien, 1990).

Direct evidence is needed to ascertain whether whales receive energetic savings from wave propulsion. One method of determining whether whales exploit this source of energy is by analysis of the movements of tagged whales in combination with known sea conditions. The purpose of this section was to devise a method to test the hypothesis of wave energy absorption for propulsion, and to analyze the track of a tagged long-finned pilot whale.

4.2. A method to test the theory of wave energy absorption

The amount of wave energy that a whale absorbs depends on environmental conditions and the behaviour of the whale.

Environmental conditions that will affect energy absorption include:

1) Wind speed. Wave energy is proportional to the square of the wave amplitude (Kinsman, 1965, p. 289). For this analysis, it was assumed that the energy savings potential was small at wind speeds less than 5 m/s since the power saved by a fin whale swimming in seas corresponding to this wind speed averaged 3% (Bose and Lien, 1990).

2) The ratio of whale length : wave length. As very long waves will move the entire length of the whale's body as a whole, the ability of the whale to absorb wave energy will decrease as the ratio of whale length : wave length decreases. The model assumed that wave energy absorption drops to zero in waves equal to and longer than four times the length of the whale (Bose and Lien, 1990).

Behavioural conditions that will affect energy absorption include:

1) The orientation of the whale to the direction of the wind. Since particle motion will vary the most over the length of the whale when it is swimming in head or following seas, energy savings potential is greatest when the whale is swimming in one of these orientations. Thus, although a whale may absorb energy while swimming at any orientation to the direction of the waves, it is expected to make the

largest energy savings when swimming in head or following seas (Bose and Lien, 1990).

2) The whale's swimming depth. In deep water, the particle motion produced by the wave decreases exponentially with depth (Kinsman, 1965, p. 16). Deep diving whales will therefore receive little benefit from the action of waves.

If a whale does absorb energy from ocean waves, it may either swim faster at the same energy cost, or it may swim at its normal speed at a reduced energy cost. Thus, there are four combinations of behavioural conditions and modes of energy utilization:

1) When environmental conditions are favourable, the whale may alter its behaviour to take advantage of wave energy absorption potential and swim faster than its normal speed (i.e. a higher speed than when environmental conditions are not favourable). A whale exhibiting this behaviour is expected to display shallower swimming depths and a higher swimming speed at a favourable heading during periods of high wind speeds.

2) When environmental conditions are favourable, the whale may alter its behaviour to take advantage of wave energy absorption potential, but swim at its normal rate at a reduced energy cost. Thus, the whale is expected to display shallower swimming depths at a favourable heading.

3) When environmental conditions are favourable, the whale may opportunistically absorb wave energy and swim faster than when environmental conditions are not favourable, but not alter its heading or its swimming depth. Thus, the whale is expected to display faster swimming speeds only.

4) When environmental conditions are favourable, the whale may opportunistically absorb wave energy and swim at a normal rate at a reduced energy cost, but not alter its heading or swimming depth. Wave energy absorption by a whale following this strategy will not be detectable through the analysis of tracking data.

4.3. Materials and methods

4.3.1. Materials

Three juvenile male long-finned pilot whales were temporarily brought into captivity and rehabilitated at the New England Aquarium following a mass stranding in December 1986 (Krieger, 1987). When the whales were released in June 1987 near Cape Cod, one of the whales was fitted with a UHF radio transmitter and tracked by polar orbit satellite for 95 days (Mate, Geraci & Prescott, unpublished report). Satellite data from the track of the pilot whale was provided by B. Mate, and included the latitude and longitude position of the whale, and the corresponding date and time of sighting. The satellite received data from the radio tag several times per day. The track of the pilot whale is shown in Figure 34.

Wave buoy data from four buoys in the Gulf of Maine/Georges Bank area were made available by the United States National Marine Fisheries Service (NOAA). Wave data from these records included the identification number of the buoy, the date and time of the record, latitude and longitude of the buoy, air temperature, sea level air pressure, wind speed, wind direction, wave height, sea surface temperature, dominant wave period and peak gusts of wind. These data were recorded over intervals of six hours. The positions of the four buoys in relation to the track of the pilot whale are also shown in Figure 34.

4.3.2. Satellite track and wave data analysis

The pilot whale satellite data was analyzed by using several FORTRAN programs as follows:

The latitude and longitude of each pair of consecutive sighting positions were combined, and the spherical distance between them computed. This value was then divided by the number of seconds between the sightings to give the minimum swimming speed of the pilot whale during that period. Several of the periods displayed corresponding speeds well outside the range of a pilot whale (e.g. 22 m/s); these

Figure 34

Satellite track of a tagged long-finned pilot whale (*Globicephala melas*) with positions of wave buoys indicated.

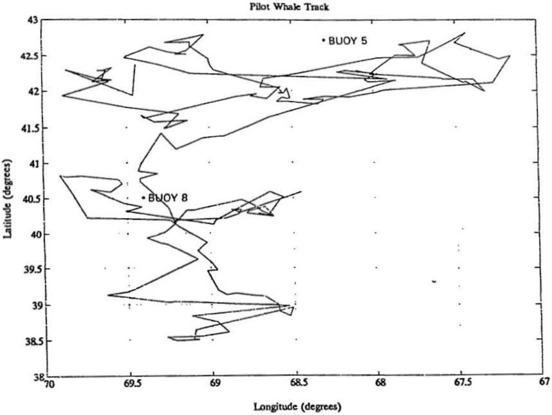
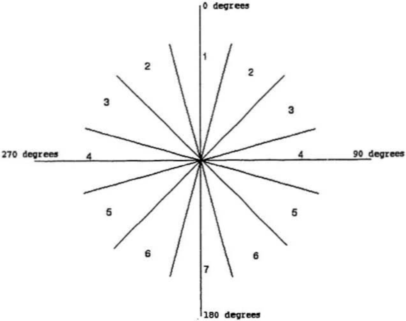

Pilot Whale Track
• BUOY 5
• BUOY 8
Latitude (degrees)
43
42.5
42
41.5
41
40.5
40
39.5
39
38.5
38
Longitude (degrees)
70
69.5
69
68.5
68
67.5
67

Figure 35

Swimming orientation bins for a tagged long-finned pilot whale (*Globicephala melas*). Each category spans an angle of 30 degrees. Bins represent the difference between wind direction and swimming direction, such that bin 1 represents following seas, bin 7 represents head seas, and bin 4 represents beam seas.


0 degrees
1
2
2
3
3
270 degrees
4
4
90 degrees
5
5
6
6
7
180 degrees

speeds were attributed to position errors, and the points were removed from the database.

The average heading of the whale during each period was calculated from the pairs of latitude and longitude positions. The absolute value of the difference between the whale's heading and the direction of the wind for each period was calculated. These values were then "binned" into one of seven categories, each spanning 30 degrees, including head seas, following seas, beam seas and four intermediate headings (see Figure 35). Bins 1 and 7, corresponding to the whale swimming in head and following seas were considered "favourable" headings, as expected energy savings potential was greatest for these two directions (Bose and Lien, 1990).

The initial position of the pilot whale for each period was compared with the positions of the four wave buoys to determine which buoy was nearest to the whale. Wave data from this buoy for the time period closest to the time of the starting point in the pair of whale sighting positions were used as the appropriate wave conditions. "Favourable" environmental conditions were judged to be periods when the wind speed exceeded 5 m/s.

4.3.3. Statistical tests

Three statistical tests were performed to determine whether the pilot whale made use of wave energy absorption.

(1) The average swimming speeds of the whale for periods when wind speeds exceeded 5 m/s were compared with periods of low wind speed regardless of the whale's heading through an analysis of variance (e.g. Keppel and Saufley, 1983). A positive result (i.e. a higher average swimming speed corresponding to favourable wind conditions) from this test would indicate that the whale swam faster during periods when the wind speed exceeded 5 m/s.

(2) The average swimming speed of the whale for periods when wind speeds exceeded 5 m/s and the whale's heading corresponded to either head or following seas was compared with its average swimming speed during periods of low wind speeds and unfavourable headings through an analysis of variance. As above, a positive result would indicate that the whale swam faster during periods of high wind speeds when the whale was aligned at a favourable heading. This test should be more sensitive than the previous one since it differentiates between more and less favourable headings. However, it may not yield a positive result for a whale absorbing wave energy opportunistically unless the whale found itself in head or following seas.

(3) The frequencies of points in the seven heading bins when wind speeds exceeded 5 m/s were compared using a chi-square test (e.g. Keppel and Saufley, 1983). If the whale adjusted its heading to the wind in response to high wind

speeds, this test would show a non-random distribution of points.

4.4. Results

Two hundred and three data points, including wind speeds greater than 5 m/s (n=153) and wind speeds less than this speed (n=50), were available for analysis. The mean swimming speed of the whale at all wind speeds was 0.68 m/s.

The average swimming speed of the pilot whale during periods when wind speeds exceeded 5 m/s was 0.63 m/s; during periods when wind speeds were less than 5 m/s, the whale's average swimming speed was 0.83 m/s. An analysis of variance of swimming speed by favourable or unfavourable wind speed showed this difference to be significant (F=5.35, d.f.=201, p<0.05). Thus, the pilot whale appeared to maintain a lower average speed during periods of high winds.

Of the 203 points available for analysis, 28 points corresponded to periods when the wind speed exceeded 5 m/s and the whale maintained a favourable heading. The average speed of the pilot whale swimming under these favourable conditions was 0.61 m/s, while its average speed during unfavourable conditions was 0.69 m/s. An analysis of variance of swimming speed by favourable or unfavourable wind speed showed this difference to be insignificant (F=0.706, d.f.=201, p>0.05). Thus, the pilot whale showed no

Table 10. Observed and expected distribution of data points during favourable wind conditions (≥ 5m/s) for a tagged long-finned pilot whale (*Globicephala melas*) in seven swimming orientations.

Bin number	1	2	3	4	5	6	7
Observed n	15	23	28	23	21	30	13
Expected n	13	25.5	25.5	25.5	25.5	25.5	13
Total n = 153							

Note: Bins 1 and 7 correspond to a whale swimming in following and head seas respectively; bin 4 corresponds to a whale swimming in beam seas (Figure 35).

difference in swimming speed in response to high wind speeds and favourable headings.

The distribution of the data points in the seven bins is shown in Table 10. A chi-square test performed on this frequency data was not significant ($\chi^2=2.7$, d.f.=6, $p>0.05$). Thus, the pilot whale showed no preference for any particular heading.

4.5. Discussion

The results presented above suggest that the pilot whale did not make use of wave energy absorption. The first test demonstrated that the whale swam more slowly during periods of high wind speeds (> 5 m/s) than during periods of low wind speeds. If the whale had been absorbing energy from ocean waves, its speed was expected to have increased or to have remained the same. The second, more sensitive, test showed that the whale's swimming speed during periods of favourable environmental and behavioural conditions was the same as that during other periods. The third test demonstrated that the whale showed no preference for favourable headings during periods of favourable wind speeds.

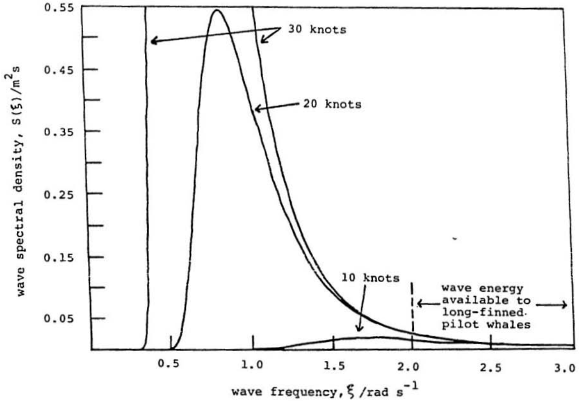
There are several possible explanations for these results. As discussed previously, one of the behavioural conditions that will affect the absorption of energy from ocean waves is the swimming depth of the whale since wave energy decreases exponentially with depth. Thus, deep diving whales will receive little or no benefit from the action of ocean waves. A whale whose primary activities are diving and foraging will show few energetic savings. Diving data were not available for this data set.

It is possible that the pilot whale absorbed wave energy opportunistically but did not increase its swimming speed in response to high wind speeds. Wave energy absorption by a whale following this strategy will not be detectable through analysis of tracking data.

Long whales potentially gain more energy from ocean waves than smaller whales because they can utilize the energy of larger waves. Figure 36 shows the Pierson-Moskowitz spectrum (e.g. Newman, 1977, p. 315-318) of wave energy vs. wave frequency for three different wind speeds. This distribution of waves describes a fully developed wave spectra, and was assumed valid for the derivation of the theory developed in Bose and Lien (1990). The wave frequency corresponding to four times the length of an average sexually mature pilot whale (4 m (IWC, 1987)) is indicated on the graph; animals of this length cannot utilize the energy of waves of frequencies less than this value. Thus, the amount of energy available to an animal of this size is small and probably insignificant to its energy budget.

Figure 36

Pierson-Moskowitz spectra of wave energy for three different wind speeds.


0.55
0.45
0.35
0.25
0.15
0.05
wave spectral density, S(ξ)/m²s
0.5
1.0
1.5
2.0
2.5
3.0
wave frequency, ξ /rad s⁻¹
30 knots
20 knots
10 knots
wave energy available to long-finned pilot whales

5. Conclusions

5.1. Conclusions from morphometrics studies

Several morphometric parameters were determined for a sample of ten sexually mature harbour porpoise. The average fineness ratio of the harbour porpoise was 4.70 ($\sigma=0.35$), the average position of maximum girth as a fraction of body length was 0.39 ($\sigma=0.05$), the average fluke aspect ratio was 3.37 ($\sigma=0.20$), and the average sweep angle of the flukes was 33.7 degrees ($\sigma=2.6$).

Harbour porpoise morphology displayed significant ontogenetic variation. Both volumetric coefficient and fineness ratio changed with body length (and therefore with age) such that the animals became more streamlined as they grew. Harbour porpoise fluke aspect ratios increased both with length and fluke area. These results may indicate a higher propulsive efficiency for adults than for juveniles, suggesting that mature harbour porpoise are more efficient hydrodynamically than immature porpoise.

No gender variation in any parameter was found for the sample of sexually mature harbour porpoise.

That harbour porpoise morphology changed with age suggests that the morphologies of other species may display similar variation. This result indicates that between-species geometric comparisons should be made between similar age classes where possible.

Harbour porpoise morphology was statistically compared with that of a sample of three Atlantic white-sided dolphins. The average fineness ratio of the white-sided dolphins was 5.5 (σ=0.12), the average position of maximum girth as a fraction of body length was 0.36 (σ=0.0), the average fluke aspect ratio was 2.97 (σ=0.20), and the average sweep angle of the flukes was 41.2 degrees (σ=0.7).

The harbour porpoise sample had higher volumetric coefficients and lower fineness ratios than Atlantic white-sided dolphins, showing that harbour porpoise have a "fatter" body and suggesting a higher drag coefficient. On the other hand, harbour porpoise had higher fluke aspect ratios and lower ratios of fluke area : body volume than white-sided dolphins. These results suggest that harbour porpoise flukes may have a higher propulsive efficiency than white-sided dolphins, although the high sweep angle of the latter may compensate for the lower aspect ratio. White-sided dolphins are regarded as a faster swimming and more pelagic species than harbour porpoises; further study of species-typical swimming dynamics and physiology, and a better understanding of the effects of fluke sweep angle on propulsion through theoretical models, may shed light on the adaptive significance of fluke morphology.

Morphometric parameters were compared qualitatively between harbour porpoise, Atlantic white-sided dolphins and several other cetacean species. Low sample sizes and different age groups of specimens did not permit statistical evaluation of observed differences. The comparisons suggested that differences in volumetric coefficient, the ratio of (body volume)$^{1/3}$: (fluke area)$^{1/2}$, the ratio of body surface area : fluke area, fluke aspect ratio and position of maximum girth between species may reflect differences in relative swimming ability, with values of volumetric coefficient, fluke aspect ratio and the ratio of body surface area : fluke area showing the largest between-species differences. More specimens from each species are needed to statistically evaluate these differences.

5.2. Conclusions from swimming kinematics study

Fluke oscillation frequencies were determined from videotapes for several steady swimming speeds for a harbour porpoise, an Atlantic white-sided dolphin and two long-finned pilot whales. Detailed fluke motions, including heave amplitude and maximum pitch angle, were measured for several swimming speeds for the harbour porpoise and the white-sided dolphin.

Swimming speed was found to increase with fluke oscillation frequency for both the harbour porpoise and the white-sided dolphin. These results correspond to those found for many species of fish. This trend was not observed for the pilot whales, because the pilot whales swam very near to one another with the upper whale in a position appropriate for the absorption of energy from the lower whale.

The larger white-sided dolphin travelled at a faster absolute speed than the smaller harbour porpoise at any given frequency. This dependence of speed upon body size has also been found for fish. The harbour porpoise, however, swam at a higher speed, measured relative to its body length, than the white-sided dolphin at any given frequency.

Stride length was computed for all three species, and compared with the stride lengths reported in the literature for other species. Stride lengths were found to remain constant within each species for all of the speeds measured. The stride lengths were significantly different between species; this result suggests that cetaceans have species-specific values of this parameter. These differences may be partly a function of differing morphologies, or varied fluke motions such as heave amplitude, pitch angle or fluke flexibility. Stride lengths were also found to decrease with body length.

The heave amplitudes of the flukes were measured for several swimming speeds for the harbour porpoise and white-sided dolphin. The upstroke and downstroke of each animal were found to be equally long at all speeds measured. The absolute heave amplitude of the white-sided dolphin was greater than that for the harbour porpoise, but the average amplitude for both animals was 0.1 body lengths. There were insufficient data points to perform meaningful statistical comparisons between species or at different speeds.

The average maximum pitch angle for the harbour porpoise was 34 degrees, and the average for the white-sided dolphin was 33 degrees.

Both the spanwise and chordwise flexibilities of the flukes of the white-sided dolphin were noticeably greater than those of the harbour porpoise. This may be partly due to high sweep angle of the white-sided dolphin's flukes. Chordwise flexibility has been found to increase swimming efficiency in theoretical studies, while the effect of spanwise flexibility on swimming performance is unclear.

Further theoretical studies are needed to quantify the effects of morphological and dynamical variation on cetacean propulsion. Specifically, the interaction between fluke aspect ratio and fluke sweep angle, and the effects of fluke chordwise and spanwise flexibility are poorly understood. The morphological and dynamical parameters reported here will be valuable for these types of studies.

While body morphology, fluke design and dynamics of motion are important to the locomotion of cetaceans, physiological differences will also affect swimming performance. Significant intra- and inter-specific haematological variations, for example, have been reported and related to differences in behavioural ecology (Duffield *et al.*, 1983; Hedrick and Duffield, 1991; Ridgway and Johnston, 1966). Further study of physiological parameters in conjunction with morphology and swimming dynamics may yield correlations with ecology and behaviour.

5.3. Conclusions from wave energy absorption study

Theoretical analyses using the measured morphology of a fin whale indicate that large cetaceans may absorb energy from ocean waves. In this thesis, a method was devised to test this hypothesis by using satellite track data and corresponding wave conditions. The method was applied to the satellite track of a long-finned pilot whale swimming in the vicinity of Cape Cod when wave conditions were known.

Statistical tests can indicate whether a whale is absorbing wave energy if: (i) the whale orients itself such that it is swimming in either head or following seas, swims at a relatively shallow depth and increases its speed in response to absorbing wave energy when wave conditions are favourable; (ii) the whale adjusts its heading to head or following seas and swims at relatively shallow depths but does not increase its speed when wave conditions are favourable; or (iii) the whale increases its swimming speed in response to opportunistically absorbing wave energy but does not adjust its heading. Favourable wave conditions were considered to be periods when the wind speed was greater than 5 m/s. Wave energy absorption would not be detectable if a whale opportunistically absorbs wave energy but did not increase its speed in response to this absorption.

The analysis of the satellite track of the pilot whale showed that the pilot whale did not increase its speed nor did it swim at a favourable heading when wave conditions were favourable for wave energy absorption. These results indicate that the pilot whale did not alter its swimming behaviour to increase its wave energy absorption potential, and that it did not increase its speed in response to opportunistic wave energy absorption.

It is possible that the pilot whale opportunistically extracted energy from ocean waves and swam at decreased energy cost during the period of analysis. As mentioned previously, wave energy absorption by a whale swimming by this strategy will not be detectable through the analysis of satellite data.

It is also possible that wave energy absorption potential may be unimportant to the energy budget of pilot whales. Deep diving whales will receive little or no benefit from the action of ocean waves; thus, a whale whose primary activities are diving and foraging will not make use of the energy available in ocean waves.

Finally, it is possible that the potential for wave energy absorption is not important to the energy budget of pilot whales because of their size. Large whales can utilize the energy in long waves, while the amount of wave energy available to an animal the size of a pilot whale is relatively small. Similar analyses of the tracks of larger whales may yield positive results.

Swimming is the only mode of locomotion available to cetaceans; it is therefore important to every other aspect of cetacean behavioural ecology, including thermoregulation, feeding, avoiding predation and reproduction. The morphology and swimming dynamics of a species will affect the production of thrust and drag during locomotion, while physical and thermal constraints will influence the range of possible adaptations to the aquatic environment. Knowledge of cetacean swimming is essential to an understanding of cetacean biology and behavioural ecology.

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Appendix A.

Table A1a. Whole girth measurements in metres.

Station from head	Harbour Porpoise F900871	Harbour Porpoise F900872	Harbour Porpoise M910710	Harbour Porpoise F910711
1	0.00	0.00	0.00	0.00
2	0.51	0.41	0.53	0.39
3	0.71	0.55	0.69	0.60
4	0.80	0.60	0.78	0.70
5	0.86	0.64	0.86	0.73
6	0.91	0.61	0.89	0.67
7	0.93	0.48	0.91	0.54
8	0.84	0.32	0.87	0.38
9	0.77	0.20	0.79	0.24
10	0.67	0.15	0.66	0.00
11	0.53	0.00	0.51	-
12	0.42	-	0.33	-
13	0.30	-	0.23	-
14	0.23	-	0.00	-
15	0.00	-	-	-
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.49	0.96	1.37	0.92
Mass (kg)	48	14	45	19.5

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1b. Whole girth measurements in metres.

Station from head	Harbour Porpoise F910712	Harbour Porpoise F910740	Harbour Porpoise M910741	Harbour Porpoise F910742
1	0.00	0.00	0.00	0.00
2	0.50	0.47	0.51	0.49
3	0.70	0.69	0.69	0.70
4	0.79	0.79	0.77	0.79
5	0.91	0.83	0.84	0.84
6	0.95	0.79	0.86	0.85
7	1.00	0.69	0.85	0.80
8	0.93	0.53	0.80	0.73
9	0.82	0.38	0.72	0.58
10	0.67	0.22	0.60	0.48
11	0.50	0.00	0.45	0.34
12	0.31	-	0.33	0.25
13	0.24	-	0.23	0.00
14	0.18	-	0.00	-
15	0.00	-	-	-
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.43	1.06	1.37	1.31
Mass (kg)	55	27	39	36

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1c. Whole girth measurements in metres.

Station from head	Harbour Porpoise F910743	Harbour Porpoise M910744	Harbour Porpoise M910745	Harbour Porpoise F910746
1	0.00	0.00	0.00	0.00
2	0.49	0.48	0.50	0.44
3	0.69	0.70	0.70	0.70
4	0.79	0.84	0.76	0.86
5	0.83	0.89	0.81	0.98
6	0.89	0.95	0.80	1.01
7	0.89	0.97	0.74	1.06
8	0.87	0.95	0.64	1.02
9	0.80	0.89	0.50	0.96
10	0.72	0.79	0.39	0.88
11	0.62	0.68	0.28	0.79
12	0.50	0.46	0.19	0.65
13	0.37	0.32	0.00	0.53
14	0.28	0.22	-	0.40
15	0.00	0.00	-	0.33
16	-	-	-	0.22
17	-	-	-	0.00
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.54	1.42	1.24	1.61
Mass (kg)	50	58	32	71

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1d. Whole girth measurements in metres.

Station from head	Harbour Porpoise F910747	Harbour Porpoise F910748	Harbour Porpoise M910755	Harbour Porpoise F910757
1	0.00	0.00	0.00	0.00
2	0.46	0.51	0.47	0.45
3	0.68	0.69	0.68	0.55
4	0.76	0.77	0.76	0.73
5	0.84	0.83	0.85	0.82
6	0.86	0.86	0.91	0.82
7	0.83	0.80	0.94	0.79
8	0.72	0.70	0.92	0.65
9	0.59	0.53	0.87	0.48
10	0.37	0.40	0.79	0.31
11	0.28	0.30	0.62	0.20
12	0.00	0.23	0.43	0.00
13	-	0.00	0.30	-
14	-	-	0.22	-
15	-	-	0.00	-
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.23	1.36	1.47	1.15
Mass (kg)	31	36	48	25

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1e. Whole girth measurements in metres.

Station from head	Harbour Porpoise M910758	Harbour Porpoise M910759	Harbour Porpoise F910760	Harbour Porpoise M910761
1	0.00	0.00	0.00	0.00
2	0.50	0.46	0.52	0.38
3	0.67	0.56	0.72	0.69
4	0.78	0.77	0.87	0.84
5	0.83	0.83	0.92	0.93
6	0.89	0.86	0.97	0.96
7	0.89	0.83	0.99	0.95
8	0.84	0.78	0.96	0.90
9	0.78	0.60	0.87	0.83
10	0.68	0.44	0.78	0.70
11	0.41	0.29	0.67	0.37
12	0.36	0.17	0.55	0.28
13	0.26	0.00	0.40	0.23
14	0.00	-	0.30	0.00
15	-	-	0.18	-
16	-	-	0.00	-
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.42	1.33	1.56	1.44
Mass (kg)	45	38	57	52

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1f. Whole girth measurements in metres.

Station from head	Harbour Porpoise M910762	Harbour Porpoise M910763	Harbour Porpoise M910764	Harbour Porpoise F910765
1	0.00	0.00	0.00	0.00
2	0.50	0.52	0.44	0.49
3	0.73	0.68	0.56	0.66
4	0.86	0.76	0.79	0.74
5	0.91	0.81	0.86	0.80
6	0.94	0.81	0.90	0.81
7	0.97	0.70	0.90	0.75
8	0.94	0.60	0.85	0.66
9	0.88	0.43	0.77	0.54
10	0.81	0.32	0.54	0.40
11	0.68	0.21	0.48	0.29
12	0.57	0.00	0.33	0.23
13	0.32	-	0.25	0.18
14	0.27	-	0.00	0.00
15	0.19	-	-	-
16	0.00	-	-	-
Station spacing (m)	0.1	0.1	0.1	0.1
Length (m)	1.50	1.16	1.37	1.29
Mass (kg)	54	26	41	29

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1g. Whole girth measurements in metres.

Station from head	Harbour Porpoise M910766	Harbour Porpoise F910768	Harbour Porpoise M910820	Atlantic White-sided Dolphin M910001
1	0.00	0.00	0.00	0.00
2	0.53	0.52	0.50	0.65
3	0.68	0.70	0.62	1.00
4	0.73	0.80	0.64	1.16
5	0.79	0.82	0.63	1.25
6	0.72	0.80	0.55	1.19
7	0.62	0.70	0.40	1.13
8	0.51	0.55	0.26	0.99
9	0.38	0.42	0.17	0.78
10	0.27	0.31	0.00	0.57
11	0.19	0.25	-	0.41
12	0.00	0.00	-	0.00
Station spacing (m)	0.1	0.1	0.1	0.2
Length (m)	1.20	1.15	0.91	2.20
Mass (kg)	28	27	14	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A1h. Whole girth measurements in metres.

Station from head	Atlantic White-sided Dolphin M910002	Atlantic White-sided Dolphin M910004	Pilot Whale M910001	Beluga Whale M910001
1	0.00	0.00	0.00	0.00
2	0.59	0.61	1.29	1.61
3	0.94	0.98	1.63	2.20
4	1.19	1.23	1.85	2.38
5	1.25	1.30	1.96	2.30
6	1.18	1.26	1.95	1.65
7	1.08	1.19	1.77	0.95
8	0.90	0.98	1.44	0.00
9	0.71	0.75	1.16	-
10	0.55	0.62	0.98	-
11	0.28	0.29	0.81	-
12	0.00	0.00	0.61	-
13	-	-	0.00	-
Station spacing (m)	0.2	0.2	0.28/ 0.25	0.5
Length (m)	2.20	2.20	3.05	3.69
Mass (kg)	N/A	N/A	483	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number. For the pilot whale, the station spacing for the first three girth measurements was 0.28, and 0.25 for the remaining measurements.

Table A1i. Whole girth measurements in metres.

Station from head	Sowerby's Beaked Whale M900001	Humpback Whale M900001
1	0.00	0.00
2	0.98	3.77
3	1.69	4.85
4	2.61	5.70
5	2.53	6.30
6	2.40	4.80
7	2.27	3.70
8	1.91	2.60
9	1.24	1.80
10	0.69	0.00
11	0.00	-
Station spacing (m)	0.5	1.0
Length (m)	4.90	9.25
Mass (kg)	N/A	N/A

Note: The sex of the specimen is indicated by the first letter of the identification number.

Table A2a. <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise F910734		Harbour porpoise M910735	
Station	t.e.	chord	t.e.	chord
LHS tip 11	38	-	17	-
10	2	78	1	57
9	6	92	9	73
8	21	94	19	79
7	31	98	27	83
6	38	102	31	89
5	44	104	35	94
4	50	105	36	100
3	53	111	36	109
2	54	120	37	119
1	56	-	36	-
0	68	-	51	-
Half span (mm)	155		161	
Station spacing (mm)	14.1		14.6	
0	68	-	51	-
1	55	-	39	-
2	53	126	35	121
3	51	117	34	112
4	48	111	34	100
5	45	105	31	94
6	39	100	27	88
7	33	94	24	82
8	26	88	16	76
9	10	87	8	67
10	1	76	2	51
RHS tip 11	25	-	16	-
Half span (mm)	157		151	
Station spacing (mm)	14.3		13.7	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2b. <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise F910736		Harbour porpoise M910737	
Station	t.e.	chord	t.e.	chord
LHS tip 11	21	-	17	-
10	1	60	4	48
9	10	71	10	69
8	26	71	16	80
7	33	77	22	88
6	37	80	26	95
5	40	91	29	102
4	43	99	34	108
3	45	106	35	116
2	45	119	37	127
1	48	-	41	-
0	60	-	52	-
Half span (mm)	150		175	
Station spacing (mm)	13.6		15.9	
0	60	-	52	-
1	51	-	39	-
2	48	114	35	133
3	48	103	34	119
4	47	95	31	111
5	44	89	27	106
6	40	90	24	99
7	35	80	19	93
8	28	74	13	83
9	12	75	8	71
10	1	63	3	54
RHS tip 11	27	-	17	-
Half span (mm)	143		165	
Station spacing (mm)	13.0		15.0	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2c. Fluke planform offsets in millimetres.

	Harbour porpoise M910738		Harbour porpoise M910739	
Station	t.e.	chord	t.e.	chord
LHS tip 11	18	-	16	-
10	3	52	2	49
9	8	65	8	62
8	16	72	14	68
7	22	80	19	74
6	26	88	22	81
5	30	90	23	87
4	32	98	24	93
3	36	102	24	101
2	35	114	23	113
1	38	-	25	-
0	57	-	42	-
Half span (mm)	160		168	
Station spacing (mm)	14.5		15.3	
0	57	-	42	-
1	36	-	24	-
2	34	121	23	116
3	32	109	25	103
4	29	103	26	96
5	26	97	25	88
6	23	89	25	81
7	18	84	21	76
8	14	75	17	70
9	9	65	9	62
10	3	54	2	49
RHS tip 11	17	-	17	-
Half span (mm)	162		165	
Station spacing (mm)	14.7		15.0	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2d <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise M910740		Harbour porpoise M910741	
Station	t.e.	chord	t.e.	chord
LHS tip 11	17	-	25	-
10	2	47	3	50
9	9	55	8	61
8	19	61	12	70
7	25	64	16	77
6	28	69	21	84
5	31	73	24	91
4	32	78	29	94
3	33	85	31	100
2	35	95	32	109
1	37	-	35	-
0	50	-	48	-
Half span (mm)	127		154	
Station spacing (mm)	11.5		14.0	
0	50	-	48	-
1	36	-	33	-
2	34	97	30	111
3	34	85	29	103
4	31	78	27	96
5	29	74	28	85
6	27	69	24	80
7	24	64	19	75
8	20	57	13	69
9	11	55	7	61
10	3	45	3	48
RHS tip 11	17	-	16	-
Half span (mm)	128		157	
Station spacing (mm)	11.6		14.3	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2e <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise F910742		Harbour porpoise F910743	
Station	t.e.	chord	t.e.	chord
LHS tip 11	31	-	21	-
10	6	66	7	48
9	9	80	9	69
8	19	83	16	76
7	27	88	24	81
6	35	92	29	85
5	40	97	32	95
4	47	100	32	104
3	51	106	32	113
2	54	115	30	127
1	60	-	33	-
0	74	-	48	-
Half span (mm)	139		160	
Station spacing (mm)	12.6		14.5	
0	74	-	48	-
1	60	-	32	-
2	56	119	30	125
3	55	105	30	113
4	51	96	29	104
5	45	93	28	95
6	37	91	23	88
7	29	88	21	81
8	19	86	13	76
9	10	81	12	58
10	6	69	4	49
RHS tip 11	25	-	20	-
Half span (mm)	133		160	
Station spacing (mm)	12.1		14.5	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2f Fluke planform offsets in millimetres.

	Harbour porpoise M910744		Harbour porpoise M910745	
Station	t.e.	chord	t.e.	chord
LHS tip 11	12	-	14	-
10	4	42	1	53
9	9	60	14	60
8	13	71	24	69
7	16	82	30	76
6	18	93	35	80
5	20	100	38	88
4	23	107	42	92
3	22	117	43	103
2	26	123	44	117
1	32	-	44	-
0	48	-	61	-
Half span (mm)	184		145	
Station spacing (mm)	16.7		13.2	
0	48	-	61	-
1	25	-	46	-
2	22	129	45	117
3	23	114	46	103
4	24	106	45	93
5	21	101	43	88
6	19	94	39	83
7	15	85	34	79
8	10	76	27	77
9	4	66	13	72
10	1	47	1	64
RHS tip 11	15	-	16	-
Half span (mm)	182		138	
Station spacing (mm)	16.5		13.2	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2g Fluke planform offsets in millimetres.

	Harbour porpoise F910746		Harbour porpoise F910747	
Station	t.e.	chord	t.e.	chord
LHS tip 11	22	-	26	-
10	1	69	4	63
9	8	86	7	84
8	17	93	16	89
7	21	101	28	91
6	25	108	36	93
5	28	112	43	96
4	35	120	49	101
3	34	128	53	111
2	34	138	57	-
1	39	-	61	-
0	51	-	74	-
Half span (mm)	194		136	
Station spacing (mm)	17.6		12.4	
0	51	-	74	-
1	40	-	60	-
2	36	138	56	108
3	36	128	52	99
4	36	120	49	93
5	36	112	42	91
6	30	108	36	88
7	27	101	28	84
8	22	93	18	83
9	12	86	8	77
10	3	73	4	62
RHS tip 11	25	-	28	-
Half span (mm)	200		136	
Station spacing (mm)	18.2		12.4	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2h Fluke planform offsets in millimetres.

	Harbour porpoise F910748		Harbour porpoise M910755	
Station	t.e.	chord	t.e.	chord
LHS tip 11	22	-	19	-
10	5	54	7	47
9	12	67	9	64
8	22	73	13	77
7	29	79	17	87
6	34	83	20	95
5	38	87	24	102
4	43	90	28	106
3	46	94	29	114
2	47	105	32	127
1	48	-	35	-
0	66	-	56	-
Half span (mm)	142		162	
Station spacing (mm)	12.9		14.7	
0	66	-	56	-
1	44	-	34	-
2	46	114	32	120
3	45	101	30	113
4	43	92	28	107
5	40	86	26	106
6	35	83	21	97
7	29	78	19	88
8	21	73	17	77
9	13	66	13	65
10	5	52	8	48
RHS tip 11	20	-	19	-
Half span (mm)	139		164	
Station spacing (mm)	12.6		14.9	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2i Fluke planform offsets in millimetres.

	Harbour porpoise F910757		Harbour porpoise M910758	
Station	t.e.	chord	t.e.	chord
LHS tip 11	23	-	20	-
10	1	55	6	41
9	6	69	7	59
8	20	74	11	69
7	30	76	16	75
6	36	82	16	84
5	43	84	15	93
4	47	89	15	100
3	49	95	14	108
2	52	105	13	120
1	55	-	15	-
0	67	-	35	-
Half span (mm)	129		164	
Station spacing (mm)	11.7		14.9	
0	67	-	35	-
1	56	-	18	-
2	53	98	16	115
3	51	89	16	107
4	47	86	16	98
5	43	84	16	92
6	37	84	15	86
7	30	82	13	78
8	17	82	11	69
9	5	81	7	60
10	1	67	6	46
RHS tip 11	25	-	20	-
Half span (mm)	122		159	
Station spacing (mm)	11.1		14.5	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2j <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise M910759		Harbour porpoise F910760	
Station	t.e.	chord	t.e.	chord
LHS tip 11	17	-	16	-
10	6	42	2	58
9	10	57	11	70
8	15	66	20	79
7	17	74	25	88
6	18	82	30	94
5	19	89	35	99
4	18	98	35	106
3	17	105	36	115
2	18	114	38	123
1	21	-	44	-
0	37	-	62	-
Half span (mm)	159		172	
Station spacing (mm)	14.5		15.6	
0	37	-	62	-
1	20	-	43	-
2	17	111	40	118
3	17	103	39	110
4	18	96	36	105
5	18	91	33	99
6	18	83	30	92
7	17	74	25	84
8	14	67	16	79
9	11	58	9	67
10	7	46	3	50
RHS tip 11	18	-	18	-
Half span (mm)	161		181	
Station spacing (mm)	14.6		16.5	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2k Fluke planform offsets in millimetres.

	Harbour porpoise M910761		Harbour porpoise M910762	
Station	t.e.	chord	t.e.	chord
LHS tip 11	22	-	10	-
10	3	58	1	45
9	9	73	7	59
8	21	79	12	72
7	26	88	15	83
6	33	97	19	90
5	35	104	20	100
4	38	111	18	110
3	40	118	18	118
2	43	133	18	127
1	48	-	24	-
0	75	-	46	-
Half span (mm)	187		182	
Station spacing (mm)	17.0		16.5	
0	75	-	46	-
1	49	-	23	-
2	44	126	21	122
3	43	115	22	112
4	44	104	24	102
5	42	97	24	94
6	38	91	21	83
7	32	86	18	80
8	24	78	15	71
9	14	70	10	62
10	3	57	4	49
RHS tip 11	20	-	13	-
Half span (mm)	193		182	
Station spacing (mm)	17.5		16.5	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A21 <u>Fluke planform offsets in millimetres.</u>

	Harbour porpoise M910763		Harbour porpoise M910764	
Station	t.e.	chord	t.e.	chord
LHS tip 11	18	-	18	-
10	5	53	2	51
9	7	71	9	63
8	9	79	17	73
7	20	83	28	76
6	25	89	27	88
5	29	94	31	95
4	33	99	33	104
3	35	103	34	115
2	37	110	36	124
1	40	-	40	-
0	57	-	65	-
Half span (mm)	131		174	
Station spacing (mm)	11.9		15.8	
0	57	-	65	-
1	40	-	42	-
2	37	116	36	126
3	36	103	33	113
4	32	98	32	102
5	28	94	32	95
6	23	91	28	86
7	18	85	25	79
8	13	78	20	70
9	6	71	12	65
10	5	50	3	53
RHS tip 11	21	-	15	-
Half span (mm)	135		174	
Station spacing (mm)	12.3		15.8	

<u>Note</u>: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2m Fluke planform offsets in millimetres.

	Harbour porpoise F910765		Harbour porpoise M910766	
Station	t.e.	chord	t.e.	chord
LHS tip 11	24	-	17	-
10	4	50	1	58
9	9	67	4	80
8	16	75	12	90
7	22	82	21	96
6	27	86	30	98
5	31	94	35	104
4	34	98	39	110
3	37	103	41	119
2	40	109	43	-
1	44	-	45	-
0	62	-	51	-
Half span (mm)	141		147	
Station spacing (mm)	12.8		13.4	
0	62	-	51	-
1	46	-	47	-
2	41	105	44	-
3	38	99	42	118
4	37	92	36	112
5	32	87	31	107
6	28	83	25	102
7	23	78	18	94
8	17	70	9	86
9	9	61	3	76
10	4	49	2	56
RHS tip 11	21	-	20	-
Half span (mm)	148		150	
Station spacing (mm)	13.5		13.6	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2n Fluke planform offsets in millimetres.

	Harbour porpoise F910768		Harbour porpoise M910820	
Station	t.e.	chord	t.e.	chord
LHS tip 11	23	-	29	-
10	5	53	3	60
9	15	61	3	79
8	24	65	11	83
7	32	70	23	81
6	38	75	30	83
5	42	79	34	87
4	45	85	33	90
3	46	92	39	104
2	47	-	41	-
1	50	-	42	-
0	66	-	51	-
Half span (mm)	142		112	
Station spacing (mm)	12.9		10.2	
0	66	-	51	-
1	49	-	42	-
2	47	-	40	111
3	47	95	38	100
4	44	87	35	94
5	42	80	31	89
6	37	76	26	86
7	31	73	20	82
8	25	68	12	78
9	16	64	5	71
10	6	55	2	57
RHS tip 11	23	-	25	-
Half span (mm)	141		115	
Station spacing (mm)	12.8		10.5	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2o Fluke planform offsets in millimetres.

	Atlantic White-sided dolphin M910001		Atlantic White-sided dolphin M910002	
Station	t.e.	chord	t.e.	chord
LHS tip 11	53	-	53	-
10	1	125	3	118
9	30	132	30	124
8	58	133	55	125
7	73	140	71	130
6	83	146	83	135
5	90	153	94	137
4	96	159	102	141
3	100	171	106	151
2	99	186	108	135
1	102	-	110	-
0	116	-	123	-
Half span (mm)	246		227	
Station spacing (mm)	22.4		20.6	
0	116	-	123	-
1	100	-	111	-
2	97	191	107	176
3	93	177	105	158
4	89	165	101	148
5	82	160	93	143
6	73	154	83	138
7	62	147	71	135
8	45	142	54	129
9	25	132	32	124
10	2	120	4	115
RHS tip 11	45	-	40	-
Half span (mm)	246		237	
Station spacing (mm)	22.4		21.5	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2p Fluke planform offsets in millimetres.

	Atlantic White-sided dolphin M910004		Beluga Whale M910001	
Station	t.e.	chord	t.e.	chord
LHS tip 11	37	-	109	-
10	16	97	75	99
9	41	112	65	139
8	59	128	56	175
7	73	140	46	211
6	86	148	35	244
5	96	155	23	274
4	105	159	14	302
3	109	168	9	326
2	113	184	18	359
1	118	-	32	-
0	141	-	89	-
Half span (mm)	273		466	
Station spacing (mm)	24.8		42.4	
0	141	-	89	-
1	116	-	39	-
2	111	183	21	355
3	105	171	14	342
4	100	165	15	319
5	94	159	21	291
6	87	152	32	262
7	75	144	47	225
8	61	134	62	188
9	37	126	73	152
10	6	118	79	115
RHS tip 11	48	-	96	-
Half span (mm)	265		473	
Station spacing (mm)	24.1		43.0	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2q Fluke planform offsets in millimetres.

	Pilot Whale F910002		Pilot Whale F910003	
Station	t.e.	chord	t.e.	chord
LHS tip 11	46	-	19	-
10	5	137	1	85
9	28	155	12	112
8	53	170	24	144
7	70	188	31	170
6	80	228	37	199
5	89	267	41	220
4	95	323	44	240
3	96	-	45	267
2	96	-	46	294
1	100	-	49	-
0	123	-	97	-
Half span (mm)	341		385	
Station spacing (mm)	31.0		35.0	
0	123	-	97	-
1	95	-	55	-
2	89	300	51	295
3	88	257	51	260
4	84	226	50	237
5	80	209	47	213
6	74	189	42	187
7	64	172	37	162
8	47	159	29	137
9	25	143	19	114
10	5	117	7	88
RHS tip 11	38	-	30	-
Half span (mm)	347		378	
Station spacing (mm)	31.5		34.4	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Table A2r Fluke planform offsets in millimetres.

	Sowerby's Beaked Whale M900001		Humpback Whale M900001	
Station	t.e.	chord	t.e.	chord
LHS tip 11	36	-	152	-
10	22	150	59	434
9	53	187	140	479
8	81	208	134	580
7	92	239	123	668
6	103	262	125	742
5	114	281	162	769
4	123	298	208	798
3	123	323	266	807
2	117	351	306	850
1	112	-	363	-
0	112	-	473	-
Half span (mm)	605		1540	
Station spacing (mm)	55.0		140.0	
0	112	-	473	-
1	114	-	370	-
2	120	357	334	-
3	121	331	296	795
4	123	306	237	763
5	117	289	194	733
6	114	265	160	686
7	105	242	156	620
8	93	212	170	534
9	62	194	176	450
10	18	158	91	416
RHS tip 11	40	-	155	-
Half span (mm)	605		1540	
Station spacing (mm)	55.0		140.0	

Note: The sex of the specimen is indicated by the first letter of the identification number. t.e. denotes the distance of the trailing edge from the datum line; see Figure 2 for method of measurement.

Appendix B - Error analysis of videotapes

The camera was held by a stationary diver, and the view of the camera followed the motion of the swimming animals. This motion of the camera introduced error into the estimation of the distance travelled by a swimming animal during a timed period. Figure B1 shows the geometry of the pool. Table B1 summarizes the magnitudes of the lines indicated in the figure.

Two estimates of error were calculated. In each case, the photographer was assumed to be located at the center of the pool (position O), and the animal assumed to swim 70% of the length or width of the pool at a distance of 1 m from the background wall. These values were judged to be typical for the sequences used in the analysis in Chapter 3.

The first case corresponds to the animal swimming along the length of the pool. The actual distance travelled was 8.96 m (line eh). The apparent distance travelled (line di) was calculated by simple geometry as follows.

$$\begin{aligned} \tan(\angle Ohe) &= \frac{\overline{Oq}}{\overline{qh}} \\ &= \frac{3.3}{4.48} \\ &= 0.74 \\ \therefore \quad \angle(Ohe) &= 36.4^\circ \end{aligned}$$

By subtraction,

$$\angle(ihg) = 54.6^\circ .$$

Then,

$$\begin{aligned} \overline{ig} &= \tan[\angle(ihg)] \times \overline{gh} \\ &= \tan[54.6^\circ] \times (1\,m) \\ \therefore\ \overline{ig} &= 1.36\,m \end{aligned}$$

and, by symmetry,

$$\overline{di} = \overline{eh} + 2\overline{ig}.$$

The percentage error in the estimate of distance travelled is:

$$\begin{aligned} e &= \frac{|\overline{eh} - \overline{di}|}{\overline{di}} \times 100\% \\ &= \frac{|8.96 - 11.68|}{8.96} \times 100\% \\ &= -30.4\%. \end{aligned}$$

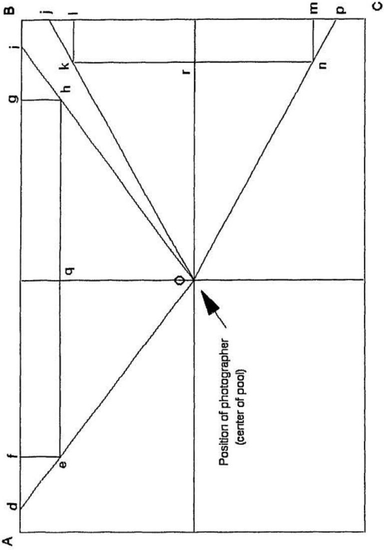
Similar calculations for an animal swimming along the width of the pool show that the actual distance travelled (line kn) was 6.02 m, the apparent distance travelled (line jp) was 7.14 m, and the error was -18.6%.

Table B1. <u>Summary of line magnitudes in Figure B1.</u>

Line	Magnitude (m)
AB	12.8
BC	8.6
eh	8.96
Oq	3.3
qh	4.48
[illegible]n	1
kn	6.02
Or	5.4
rn	3.01
lk	1

<u>Figure B1</u>

Geometry of cetacean pool, with lines marked as described in error analysis (see Table B1 for line magnitudes).



Position of photographer
(center of pool)