Morphological Specializations of Baleen Whales Associated With Hydrodynamic Performance and Ecological Niche

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ABSTRACT Feeding behavior, prey type, and habitat appear to be associated with the morphological design of body, fluke, and flippers in baleen whales. Morphometric data from whaling records and recent stranding events were compiled, and morphometric parameters describing the body length, and fluke and flipper dimensions for an "average" blue whale *Balaenoptera musculus*, humpback whale *Megaptera novaeangliae*, gray whale *Eschrichtius robustus,* and right whale *Eubalaena glacialis* were determined. Body mass, body volume, body surface area, and fluke and flipper surface areas were estimated. The resultant morphological configurations lent themselves to the following classifications based on hydrodynamic principles: fast cruiser, slow cruiser, fast maneuverer, and slow maneuverer. Blue whales have highly streamlined bodies with small, high aspect ratio flippers and flukes for fast efficient cruising in the open ocean. On the other hand, the rotund right whale has large, high aspect ratio flukes for efficient slow speed cruising that is optimal for their continuous filter feeding technique. Humpbacks have large, high aspect ratio flippers and a large, low aspect ratio tail for quick acceleration and high-speed maneuvering which would help them catch their elusive prey, while gray whales have large, low aspect ratio flippers and flukes for enhanced low-speed maneuvering in complex coastal water habitats. J. Morphol. 267:1284–1294, 2006. © 2006 Wiley-Liss, Inc.

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Cetaceans have evolved a smooth, streamlined, fusiform body that is propelled by flukes connected to the body by a narrow peduncle region. This body configuration maximizes swimming efficiency and is typical of vertebrates designed for steady swimming (Webb, 1984a). However, the morphology of body, fluke, and flipper vary widely among species within the general framework of the classic cetacean form.

Studies on fish have indicated that body form is directly correlated to foraging behavior and ecology (Webb, 1984a,b, 1988). Different body forms make some fish better suited for cruising, accelerating, or maneuvering based on thrust production capabilities and drag reduction mechanisms (Webb, 1984b).

Small, high aspect ratio tails and stiff, streamlined bodies reduce resistance and increase efficiency for steady swimming, but this design is poorly suited for rapid accelerations. On the other hand, large tail areas and flexible bodies are able to produce larger thrust forces for quick acceleration at the cost of increased drag and less efficient motion. Highly mobile fins and laterally compressed bodies are able to effect slow, precise swimming maneuvers in structurally complex habitats. Most fish occupy a median position between the three diverse body forms, balancing requirements for cruising efficiency, acceleration, and maneuvering based upon their feeding ecology.

The food particle size, dispersion, and evasiveness of prey dictate a fish's locomotion performance requirements (Webb, 1984a,b). Thus, it becomes possible to make predictions of optimum body, fin, and tail shape for a species based upon hydrodynamic models and the performance measures (speed, acceleration, and efficiency) required for it to occupy its ecological niche (Webb, 1988).

These same prediction models can be applied to examine potential associations between cetacean body form and species-specific performance requirements. Swim speeds and maneuverability requirements differ according to habitat, prey species, and feeding mechanisms. These performance attributes were proposed to be associated with variations in body flexibility and control surface (e.g., flukes, flippers, peduncle) design among odontocete cetaceans (Fish, 2002). However, limited data are available on the design of appendages in mysticete whales with regard to hydrodynamic performance (Benke, 1993;
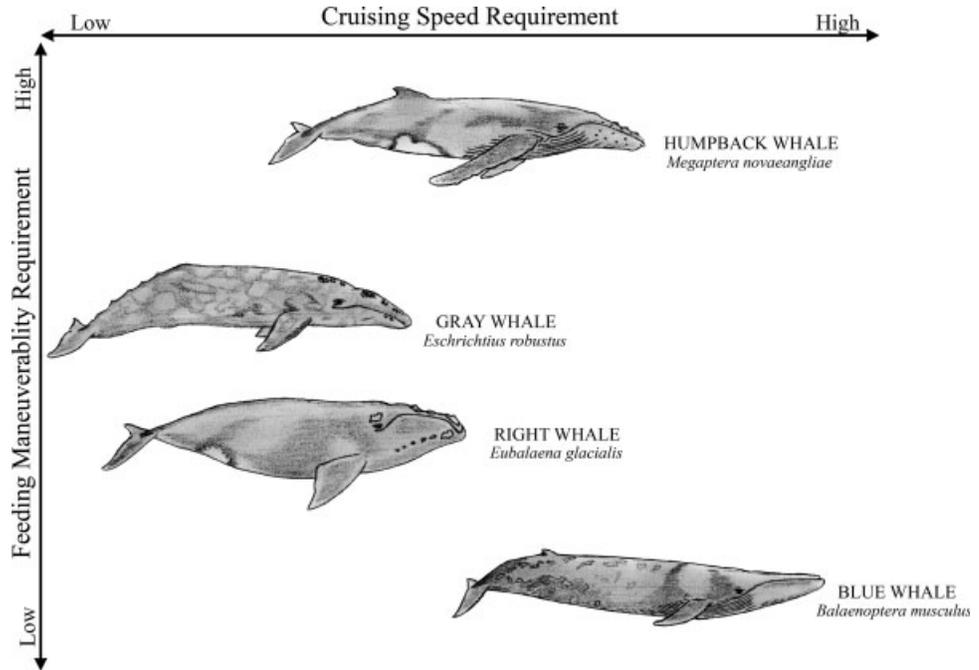
Fig. 1. Body form continuum for selected baleen whale species. Whales were ranked based on cruising speed and feeding maneuverability requirements.

Fish and Battle, 1995). Previous studies on swimming performance of small cetaceans have been performed in captivity. However, this option is not available for the larger species. Thus, the associations between morphological design and feeding ecology of the large whales have been theorized about but not fully explored (Webb, 1984a; Webb and de Buffrenil, 1990; Fish and Battle, 1995).

This study was undertaken to determine if the differences in mysticete morphology were associated with hydrodynamic performance and feeding ecology. A representative species for each of the major body shapes found among the mysticete whales was selected for comparison: the blue whale *Balaenoptera musculus* (*B. musculus*), humpback whale *Megaptera novaeangliae* (*M. novaeangliae*), gray whale *Eschrichtius robustus* (*E. robustus*) and right whale *Eubalaena glacialis* (*E. glacialis*). These species cover a wide range of habitats, feeding techniques, and morphological adaptations. It is hypothesized that a body form continuum exists among mysticetes to balance speed, acceleration, and maneuverability requirements according to their feeding ecology (Fig. 1).

To examine this hypothesis, the body form, fluke, and flipper morphology of these four representative species, blue, humpback, gray, and right whales, were analyzed. It was predicted that on the basis of these morphological parameters and their related hydrodynamic characteristics, an association could be made with the ecology of each species. Specific predictions from morphology were that the blue whale is a rapid rectilinear swimmer, the humpback whale uses rapid maneuvers, the gray whale uses slow maneuvers, and the right whale is a slow steady swimmer.

MATERIALS AND METHODS

A database of external morphometric measurements was compiled for *B. musculus*, *M. novaeangliae*, *E. robustus*, and *E. glacialis* to develop an "average" representative whale for each species. Data sources included whaling records (Holder, 1883; Struthers, 1889; True, 1904; Andrews, 1908, 1914; Lillie, 1915; Hinton, 1925; Mackintosh and Wheeler, 1929; Matthews, 1937, 1938; Nishiwaki and Oye, 1951; Omura, 1958; Tomilin, 1967; Scammon, 1968; Omura et al., 1969; Rice and Wolman, 1971; Mitchell, 1973) and recent stranding data (Moore et al., 2005; Right Whale Consortium, 2006; Cape Cod Stranding Network; Marine Mammal Center; Virginia Aquarium Stranding Program; Santa Barbara Museum of Natural History; Natural History Museum of Los Angeles County; Allied Whale; Memorial University in Newfoundland).

Morphometric data, measured in meters, included body length (L, straight line distance from the tip of the snout to the notch of the flukes), flipper length (FL, distance from the anterior insertion of the flipper to the flipper tip), flipper width (FW, maximum cranio-caudal width of the flipper), fluke span (FS, tip to tip spread of the flukes), fluke chord (FC, distance from the fluke notch to the anterior margin of the fluke); and max body girth (g_{max}, maximum body circumference) (Fig. 2). When present, dorsal fins represented only a minor control surface area for the large baleen whales. Thus, data on dorsal fin presence, size, and placement on the body were not included in the present study.

To avoid issues related to scaling in comparison of different sized animals, measurements were reduced to a proportion of body length for each individual whale and then averaged within a species to generate representative body, fluke, and flipper dimensions for the "average" whale for each species. The study sample was restricted to sexually mature animals (Table 1) to eliminate any potential differences in geometric proportions due to age class differences among animals (Curren et al., 1993).
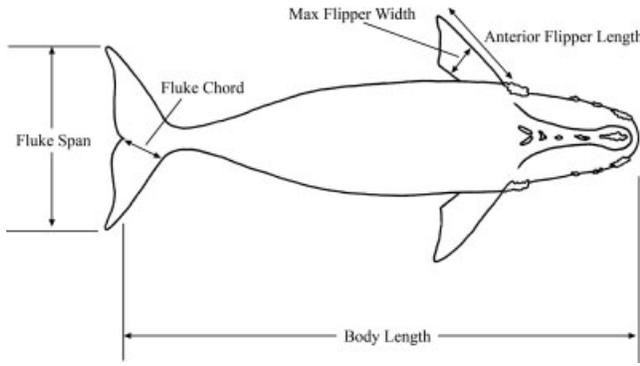
Fig. 2. Morphological measurement sites. Exact position of the girth measurement varied slightly according to species, ranging from the anterior insertion of the flipper to the tip of the flipper lying flat against the side of the body.

The reported average body length at sexual maturity for southern hemisphere blue whales was larger than that of northern hemisphere animals; however, when expressed as a percent of body length, the morphometric parameters were not significantly different between the two populations at the 0.05 level (Wilcox-Mann-Whitney rank sum test). For the purposes of this study, the two populations were pooled when determining the proportions of the average blue whale.

There was no significant difference ($P > 0.05$) between male and female flipper and fluke dimensions for blue and humpback whales. Male gray whales had longer and wider flippers and a greater fluke span than the females, and male right whales had longer and wider flippers than the females ($P < 0.05$, Wilcox-Mann-Whitney rank sum test). Although right and gray whales showed a significant difference in fluke and/or flipper length between the sexes, the overall difference between the sexes expressed as a percentage of body length was slight (1–2%) compared to differences among the species. For the purpose of this study, males and females were grouped together when determining the average representative whale for each species.

Using the dimensions of the "average" whale, a number of additional parameters were derived from the basic morphometric data set, including estimated body mass, body volume, body surface area, fineness ratio, volumetric coefficient, flipper and fluke planform areas, and flipper and fluke aspect ratios.

1. Body mass (M, kg) was estimated using Lockyer's (1976) formula to predict a whale's weight (W, tons) based upon its body length (L, m)

$$W = aL^b$$

where a and b are species specific coefficients. The following coefficient values have been corrected for blood and fluid loss: blue whale $a = 0.0029$, $b = 3.25$; humpback $a = 0.0165$, $b = 2.95$; gray whale $a = 0.0054$, $b = 3.28$; and right whale $a = 0.0132$, $b = 3.06$. Lockyer's formula provides a general estimate of weight for the average whale. True body mass varies seasonally as well as with the animal's condition, age, and reproductive status.

2. Body volume (V, m³) was calculated based upon the assumption that whales are nearly neutrally buoyant in seawater (Bose et al., 1990). The true buoyancy of a particular whale is dependent upon its body composition, particularly the relative quantities of muscle and blubber tissues. Balaenopterid whales have a higher proportion of muscle tissue and tend to be negatively buoyant while the opposite is true for right whales (Lockyer, 1976). Additionally, blubber thickness fluctuates on the individual level with seasonal fattening and with reproductive status (Rice and Wolman, 1971). For the purposes of this study, the simplified assumption of neutral buoyancy was deemed adequate for estimating body volume of the "average" whale. The estimated M was used in conjunction with the density of sea water, $\rho_{seawater}$ (1,025 kg/m³), according to the following:

$$V = M/\rho_{seawater}$$

3. Body surface area (SA, m²) was determined using a prediction equation (Fish, 1993b):

$$SA = 0.08 \, M^{0.65}$$

4. Max body diameter (d_{max}, m) was determined from the maximum body girth (g_{max}, m) assuming a circular cross-section of the body.

$$d_{max} = g_{max}/\pi$$

5. Fineness ratio (FR) represents a measure of the whale's streamlining and is associated with the drag on the body. FR was calculated as:

$$FR = L/d_{max}$$

6. Volumetric coefficient (C_v) is the ratio of body volume to length cubed and provides a measure of the stockiness of a body (Bose et al., 1990). Higher values denote stockier bodies.

$$C_v = V/(0.1 \times L)^3$$

7. Flipper and fluke surface area. A photograph of the lateral aspect of the flipper was used to outline the typical planform of the pectoral fin for each of the whale species. The image was scaled to match the flipper length of the "average" whale as determined by the morphometric data. ImageJ software (Abramoff et al., 2004) was then used to estimate the planar surface area of the flipper. This surface area was doubled to

TABLE 1. Reported average body length at sexual maturity for various whale species

	Body length (m)		
Species	Female	Male	Source
Blue whale – Northern/Southern (*Balaenoptera musculus*)	21.0/23.0	20.0/22.0	Yochem and Leatherwood (1985)
Humpback whale (*Megaptera novaeangliae*)	12.09	11.58	Winn and Reichley (1985)
Gray whale (*Eschrichtius robustus*)	11.7	11.1	Wolman (1985)
Right whale (*Eubalaena glacialis*)	13.2	13.2	Best et al. (2001), Kraus et al. (2001), and Moore et al. (2005)

For blue whales *Balaenoptera musculus*, reported lengths at sexual maturity were slightly larger for Southern versus Northern Hemisphere animals.

account for both sides of the flipper, and the resulting area was doubled again to include both flippers in the calculation of the total flipper surface area for the whale. Fluke surface area was similarly determined using fluke span as the scale factor for the image. The resulting planar area was then doubled to include both sides of the fluke for the total fluke surface area.

8. Aspect ratios (AR) for the flippers and flukes were determined according to the equation:

$$AR = Length^2/Planform\ Area$$

Flipper length was used in the calculation of flipper aspect ratio ($AR_{flipper}$), while fluke span was used when calculating fluke aspect ratio (AR_{fluke}). The planform area was taken as the planar surface area of a single side of the flipper or fluke.

The baleen whale morphometrics were plotted together with previously published odontocete morphometric data to examine trends in fluke and flipper size relative to body size. Fish et al. (2003) reported body length, body mass, fluke span, fluke area, flipper length, and flipper area for the following species: beluga *Delphinapterus leucas*, long-finned pilot whale *Globicephala melaena*, Pacific white-sided dolphin *Lagenorhynchus obliquidens*, killer whale *Orcinus orca*, false killer whale *Pseudorca crassidens*, Atlantic spotted dolphin *Stenella plagiodon*, and bottlenose dolphin *Tursiops truncatus*. Body surface area and body volume were estimated from the reported body mass using the same procedure as outlined earlier for the mysticete species. When data on multiple individuals of a particular species were available, morphometric parameters were averaged among the individuals to produce representative dimensions for the species. Regression lines were plotted assuming linear relationships on the plots. The standard errors of prediction were used to determine the 90 and 95% confidence intervals of the mysticete data points using the regression coefficients for the plots (Zar, 1996).

Accuracy of the Data

The morphometric data used in this study were compiled from a wide range of sources ranging from recent stranding data to whaling data from the early 1900s. Standard morphometric measurement techniques have only recently been established (Dierauf and Gulland, 2001). As a result, one must bear in mind that the measurements used in compiling the morphometric database were taken by a wide range of people in varying environmental conditions on specimens in various stages of decomposition. Girth measurements in particular are difficult to obtain for the large whales and are highly dependent upon the condition of the carcass at the time of measurement. Bloating of the carcass and/or distention of the throat grooves may affect the measurements taken.

Inevitably, some sources of error are introduced into the data. However, the average morphometric parameter values calculated from the large sample size of the amassed data should help to dissipate some of the error of individual whale measurements. Averages and standard errors of the mean (SEM) for the data are reported.

RESULTS
The "Average" Whale

Morphometric parameters and derived geometric data describing the "average" whale for each species are summarized in Tables 2 and 3. Average flipper length ranges from a minimum of 13.2% of the body length for the blue whale *B. musculus* to a maximum of 30.8% for the humpback whale

M. novaeangliae. Gray whale *E. robustus* (17.4%) and right whale *E. glacialis* (17.1%) flipper lengths are intermediate between the blue and humpback, but are not significantly different from one another ($P = 0.3$, Wilcox-Mann-Whitney rank sum test). Blue whales have the narrowest flippers (flipper width = 3.7%) and right whales have the widest (9.3%) with humpback whales (7.3%) and gray whales (6.6%) in between. The following trend in flipper aspect ratio is apparent: humpback whale (5.67) > blue whale (4.47) > gray whale (3.11) > right whale (2.35). Because of their flipper length, width, and planform shape, humpbacks have more surface area in their flippers than the other three species (Fig. 3A). Right whale flipper area is 75% of the humpback, followed by gray whales at 58% and blue whales at 23%.

Average fluke span as a percentage of body length is similar for the right whale (35%) and the humpback (34%) ($P = 0.7$). However, the gray whale (24.5%) and the blue whale (21.5%) have significantly smaller fluke spans ($P < 0.01$, Wilcox-Mann-Whitney rank sum test). Fluke aspect ratio is highest for the right whale (6.31) followed closely by the blue whale (6.16). Humpback (4.07) and gray whales (3.76) have lower aspect ratio flukes. The large fluke span and wide fluke chord of the humpback's tail give it the largest relative fluke area (Fig. 3B). Right whale flukes have 67% of the area of the humpback, gray whales have 56% and blue whales have 27%.

Few girth measurements are available ($n = 3$ for blue whales; $n = 5$ for gray whales). However, based upon the available data, blue whales have a higher fineness ratio (6.37) than the other three species. Gray whales have an intermediary fineness ratio (5.64), while humpback (4.21) and right whales (4.58) show similar low fineness ratio values. These fineness ratio values are consistent with previously reported values for baleen whales (Bose and Lien, 1989; Bose et al., 1990; Curren, 1992; Fish, 1993a).

The volumetric coefficient (C_v) provides an alternative measure of body stockiness that is dependent upon body length and volume rather than girth measurements. Blue whales have the lowest volumetric coefficient (5.72), and are the least stocky of the species studied. Although humpback and right whales have similar fineness ratios, the right whale has a higher volumetric coefficient (13.74) and a stockier body than the humpback (12.80).

General Cetacean Trends

To compare relative fluke and flipper size among cetaceans as a whole, data from this study were combined with Fish et al.'s (2003) odontocete data to provide a data set of cetacean morphometrics that encompasses body lengths ranging from 1.83 m (Atlantic spotted dolphin *Stenella plagiodon*) to 24.72 m

TABLE 2. *Summary of morphometric data from whaling and stranding records*

	Body length (L, m)	Ant. flipper length (FL/L)	Max flipper width (FW/L)	Fluke span (FS/L)	Fluke chord (FC/L)	Max girth (g_{max}/L)
Blue whale[a,e] (*Balaenoptera musculus*)						
Average	24.72	0.132	0.037	0.215	0.051	0.493
SEM	0.0703	0.0005	0.0002	0.0062	0.0002	0.0088
Median	24.80	0.132	0.037	0.210	0.051	0.498
Min	20.02	0.102	0.027	0.185	0.039	0.476
Max	28.96	0.164	0.049	0.256	0.061	0.505
Sample size	n = 448	n = 249	n = 292	n = 13	n = 366	n = 3
Humpback whale[b,f] (*Megaptera novaeangliae*)						
Average	13.50	0.308	0.073	0.341	0.080	0.747
SEM	0.0827	0.0023	0.0007	0.0096	0.0009	0.0169
Median	13.50	0.310	0.072	0.350	0.079	0.758
Min	11.58	0.265	0.058	0.283	0.067	0.521
Max	15.85	0.344	0.109	0.384	0.109	0.899
Sample size	n = 128	n = 60	n = 94	n = 14	n = 75	n = 29
Gray whale[c,g] (*Eschrichtius robustus*)						
Average	12.29	0.174	0.066	0.245	0.073	0.558
SEM	0.0373	0.0008	0.0003	0.0016	0.0003	0.0402
Median	12.22	0.175	0.066	0.247	0.073	0.531
Min	11.10	0.123	0.047	0.115	0.061	0.467
Max	14.62	0.208	0.081	0.328	0.098	0.704
Sample size	n = 288	n = 266	n = 270	n = 223	n = 238	n = 5
Right whale[d,h] (*Eubalaena glacialis*)						
Average	15.02	0.171	0.093	0.350	0.083	0.686
SEM	0.2181	0.0039	0.0019	0.0051	0.0015	0.0362
Median	14.70	0.182	0.099	0.335	0.083	0.681
Min	13.50	0.136	0.071	0.309	0.074	0.431
Max	17.80	0.209	0.115	0.399	0.099	0.847
Sample size	n = 30	n = 24	n = 29	n = 23	n = 18	n = 10

Average, standard error of the mean (SEM), median, minimum, maximum, and sample size (n) for each parameter are provided. Stranding data provided by Cape Cod Stranding Network, Right Whale Consortium, Marine Mammal Center, Virginia Aquarium Stranding Program, Santa Barbara Museum of Natural History, Natural History Museum of Los Angeles County, Allied Whale, and Memorial University in Newfoundland.
Position of girth measurement varied according to species:
[a]Tip of flipper lying flat along the side of the body.
[b]Axilla.
[c]"Max".
[d]Anterior insertion of the flipper.
[e]True (1904), Hinton (1925), Mackintosh and Wheeler (1929), Nishiwaki and Oye (1951).
[f]Struthers (1889), True (1904), Lillie (1915), Hinton (1925), Matthews (1937), Tomilin (1967), Scammon (1968), Mitchell (1973).
[g]Andrews (1914), Scammon (1968), Rice and Wolman (1971).
[h]Holder (1883), True (1904), Andrews (1914), Matthews (1938), Omura (1958), Omura et al. (1969), Moore et al. (2005).

(blue whale *B. musculus*). Plots of body length to flipper and fluke length, body volume$^{1/3}$ to fluke and flipper area$^{1/2}$, fluke area to flipper area, and body volume to body length are found in Figure 4.

When compared with other cetacean species, humpback whales had longer flippers than predicted based upon their body length at the 95% confidence interval. Their fluke area$^{1/2}$ was also larger than expected based upon their body volume$^{1/3}$ at the 90% confidence interval. Blue whales, on the other hand, tended toward small flippers and flukes for their body size. Gray whales and right whales followed the trend line well in regards to flipper length; however, both had slightly higher than predicted flipper area$^{1/2}$ to body volume$^{1/3}$ ratios. The right whale's fluke span fell above the trend line, although its fluke area$^{1/2}$ to body volume$^{1/3}$ ratio closely followed the trend (Fig. 4A–D). Right whales tended to have a larger flipper area than predicted based on fluke area, while both gray and humpback whales closely fol-

lowed the general cetacean trend. Blue whale flipper area, however, was smaller than expected based on the flipper area at the 90% confidence interval.

DISCUSSION

Although social, courtship and reproductive pressures also influence body morphology, this study focused on potential relationships between morphological adaptations and feeding performance. Prior to the morphological analysis, the four baleen whale species were ranked based on hydrodynamic principles and the performance requirements necessitated by their feeding ecology. Predicted and actual values for fluke and flipper design are listed in Table 4. Whales were classified as fast cruiser (blue whale *B. musculus*), fast maneuverer (humpback whale *M. novaeangliae*), slow maneuverer (gray whale *E. robustus*) and slow cruiser (right

TABLE 3. Derived morphometric parameters

	Blue whale (*Balaenoptera musculus*)	Humpback whale (*Megaptera novaeangliae*)	Gray whale (*Eschrichtius robustus*)	Right whale (*Eubalaena glacialis*)
Morphometric parameters				
Body length (m)	24.72	13.50	12.29	15.02
Body mass – estimated (kg)	88,587	32,278	18,361	47,736
Body volume (m^3)	86.43	31.49	17.91	46.57
Body surface area (m^2)	131.49	68.21	47.27	87.97
Max body diameter (m)	3.88	3.21	2.18	3.28
Fineness ratio (L/d_{max})	6.37	4.21	5.64	4.58
Fluke span tip to tip (m)	5.32	4.61	3.00	5.25
Fluke surface area – total (m^2)	9.19	10.43	4.79	8.73
Fluke aspect ratio (AR_{fluke})	6.16	4.07	3.76	6.31
Flipper length – anterior (m)	3.25	4.16	2.14	2.57
Flipper surface area – total (m^2)	9.44	12.20	5.89	11.26
Flipper aspect ratio ($AR_{flipper}$)	4.47	5.67	3.11	2.35
Volumetric coefficient $C_v = V/(0.1L)^3$	5.72	12.80	9.65	13.74
Comparisons				
Total flipper area:total fluke area	1.027	1.170	1.230	1.290
Total fluke area:body surface area	0.070	0.153	0.101	0.099
Total flipper area:body surface area	0.072	0.179	0.125	0.128
Total fluke + flipper area:body surface area	0.142	0.332	0.226	0.227
Body surface area$^{1/2}$:body volume$^{1/3}$	2.594	2.615	2.628	2.607
Total fluke area$^{1/2}$:body volume$^{1/3}$	0.686	1.023	0.837	0.821
Total flipper area$^{1/2}$:body volume$^{1/3}$	0.695	1.106	0.928	0.933

Morphometric parameters were derived based on the definition of the average whale for each species. Parameter calculation methodology is described in the text.

whale *E. glacialis*) according to the body form continuum (Fig. 1). Fluke aspect ratio was predicted based on swim speed with higher ranking assigned to fast swimmers. Higher aspect ratios were also predicted for cruisers than for maneuverers.

Fluke and flipper areas were ranked based upon maneuvering requirements. Whales with high maneuverability requirements were predicted to have higher fluke and flipper area$^{1/2}$ to body volume$^{1/3}$ ratios to generate larger thrust forces. Flippers were assumed to be primarily involved in maneuvering; however, swim speed affects the flipper's performance. Whales were separated into high- and low-speed swimmers (blue and humpback whales versus gray and right whales), with fast swimmers predicted to have higher aspect ratio flippers. Within the speed class, maneuverers were predicted to have higher aspect ratio flippers than cruisers.

Efficiency for Cruising

Efficiency of locomotion for cruising appears to be a key selection pressure for the pelagic blue whale. Since drag forces increase with the square of swim speed, the need for drag reduction has a significant impact on the morphological design of the fast swimming blue whale, who reaches speeds up to 8.3 m/s when cruising or migrating (Sears, 2002). Streamlining the body helps to increase swimming efficiency by reducing the drag on the whale. When compared with humpback, gray and

right whales, blue whales have the most elongate, streamlined body form with the highest fineness ratio and lowest volumetric coefficient of the four species. They also have high aspect ratio flukes, a hydrodynamic feature that improves their propulsive efficiency. A higher efficiency enables the whales to exert more thrust for their fluke area for a given speed, power input, and fluke motion while minimizing induced drag (Bose and Lien, 1989; Bose et al., 1990; Fish, 1998).

Drag is also produced by a whale's appendages (flippers, flukes, and dorsal fin) which can add substantially to the overall drag of the animal (Fish, 2004). In the case of the harbor porpoise *Phocoena phocoena*, the flippers contribute 18% of the overall drag on the animal yet only comprise 4.2% of the body area (Yasui, 1980). The blue whale has small flipper and fluke surface areas relative to the size of the body.

Blue whales feed almost exclusively on widely distributed patches of large zooplankton, primarily euphausiids, by engulfing large quantities of water using their highly expandable throat grooves and filtering out their prey (Yochem and Leatherwood, 1985; Pauly et al., 1998). Although their ability for quick starts and sharp turns is hampered by their relatively small fluke and flipper areas, their prey species are relatively nonevasive. As such, efficiency of travel from one prey patch to the next is more important in their foraging strategy than is a high degree of maneuverability. Overall, the blue whale's morphology is indicative of a species designed for steady, high speed, efficient cruising in

A

HUMPBACK WHALE   RIGHT WHALE   GRAY WHALE   BLUE WHALE

Megaptera   *Eubalaena*   *Eschrichtius*   *Balaenoptera*
novaeangliae   *glacialis*   *robustus*   *musculus*

Flippers

Relative Area   100%   75%   58%   23%

B

HUMPBACK WHALE   RIGHT WHALE   GRAY WHALE   BLUE WHALE

Megaptera   *Eubalaena*   *Eschrichtius*   *Balaenoptera*
novaeangliae   *glacialis*   *robustus*   *musculus*

Flukes

Relative Area   100%   67%   56%   27%
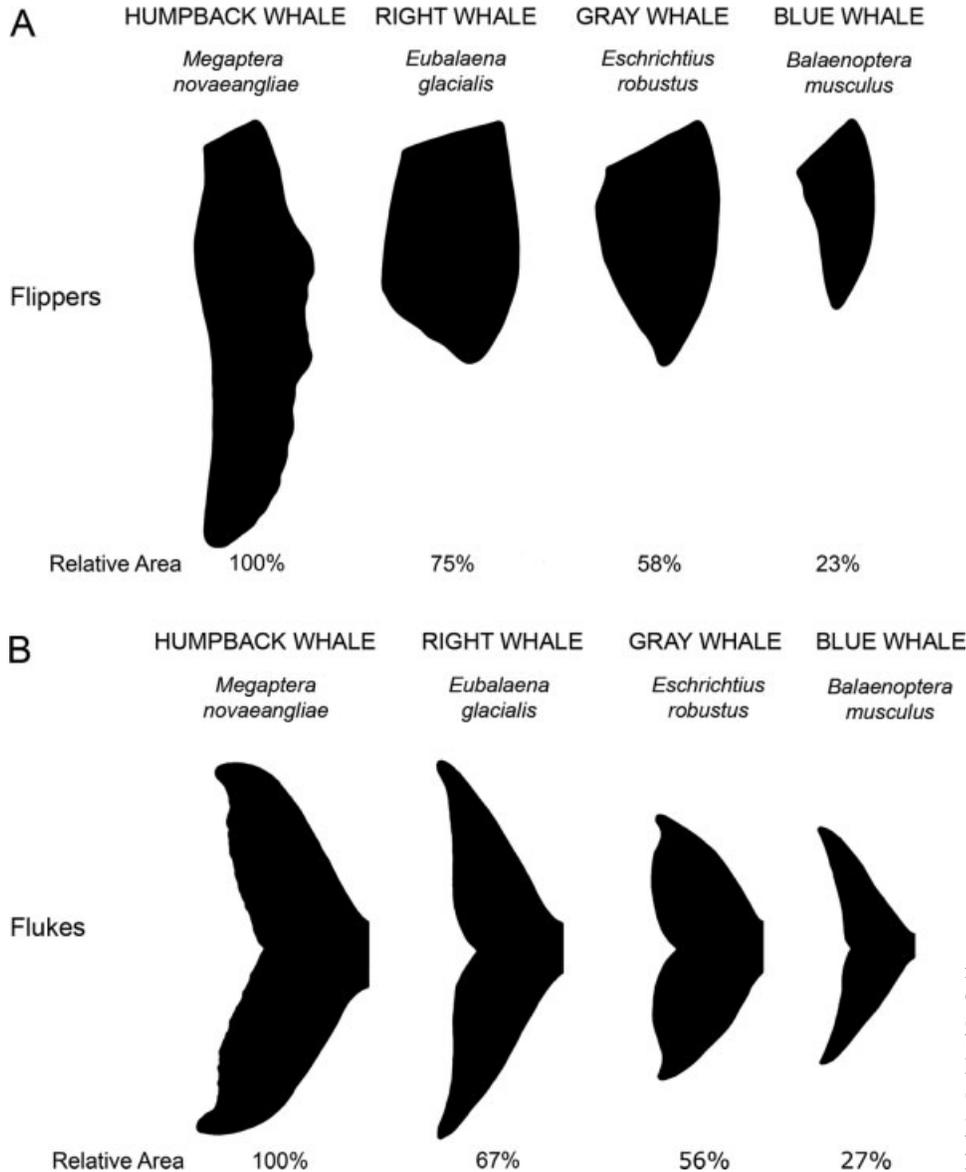
Fig. 3. Relative size and planform shape for flippers and flukes of the four species. (**A**) Flippers scaled according to flipper length/body length for the species. (**B**) Flukes scaled according to fluke span/body length for the species. Relative flipper and fluke area is provided using the planform area of the humpback as the reference.

a pelagic environment with low maneuvering requirements.

The right whale also has a morphological design for efficient cruising, but for slower swim speeds [1.8 m/s when cruising (Tomilin, 1967)] and with several design constraints imposed by its head size and skim feeding technique. The right whale uses a continuous filtration process to skim its prey from the water (Pivorunas, 1979; Cummings, 1985; Werth, 2004; Lambertson et al., 2005). These whales have large heads (1/4–1/3 of their body length) with large cavernous mouths containing baleen plates up to 2.8 m in length (Cummings, 1985). The large head enables right whales to filter large volumes of water, but results in a substantially less streamlined and more rotund body than that of the sleek elongate blue whale. To help compensate for its reduced streamlining, the right whale has a larger relative fluke area

than the blue whale. The increased surface area of the tail generates a larger thrust force per fluke stroke (Fish, 1998) which would help to overcome the resistance associated with the right whale's shape. Since drag increases with velocity squared, the right whale's slower swim speed would help to mitigate the energetic cost of moving its large area propulsor through the water.

Right whale flukes not only have a large surface area, but they also have a high aspect ratio. In general, high aspect ratio flukes are associated with fast swim speeds and high efficiency (Fish, 1993a, 1998), yet the results of this study indicate that the right whale, a slow swimmer, has a higher aspect ratio fluke than the fast swimming blue whale. The right whale's feeding mechanism requires nearly continual propulsion to push the open mouth through the water for extended peri-
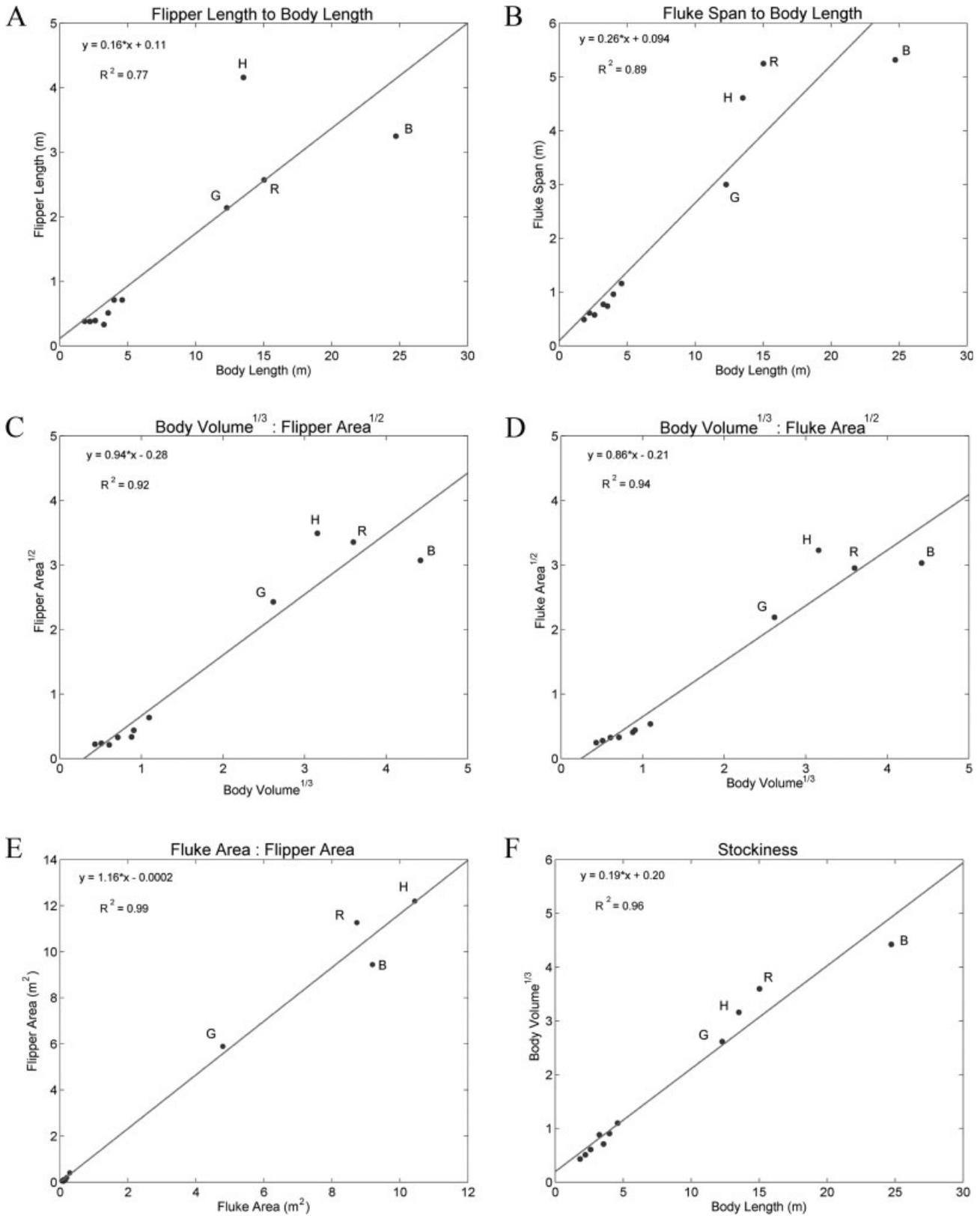
Fig. 4. Plots of fluke, flipper, and body data for a variety of cetaceans species. Data points are coded as follows: G, gray whale *Eschrichtius robustus*; H, humpback whale *Megaptera novaeangliae*; R, right whale *Eubalaena glacialis*; B, blue whale *Balaenoptera musculus*. Remaining data points are from Fish et al.'s (2003) odontocete data. Equations for regression lines are provided.

TABLE 4. Relative ranking (predicted/actual) of morphological characteristics

	Fluke design		Flipper design	
Species	Fluke area$^{1/2}$: body volume$^{1/3}$	Fluke aspect ratio	Flipper area$^{1/2}$: body volume$^{1/3}$	Flipper aspect ratio
Blue whale (*Balaenoptera musculus*)	4/4	1/2	4/4	2/2
Humpback whale (*Megaptera novaeangliae*)	1/1	2/3	1/1	1/1
Gray whale (*Eschrichtius robustus*)	2/2	4/4	2/3	3/3
Right whale (*Eubalaena glacialis*)	3/3	3/1	3/2	4/4

Whales were ranked on a 1–4 scale (1 = high). Predicted values were based upon foraging habitat, feeding mechanism, and primary prey species for each of the whale species. Actual values were based upon the "average" whale for each species calculated from the morphological data.

ods of time, and the drag associated with this method of feeding is expected to be high (Fish, 1993a; Werth, 2004). It follows that high efficiency propulsion associated with a high aspect ratio tail would therefore be helpful in overcoming the drag inherent in the skim feeding behavior. In effect, the right whale's large, high aspect ratio fluke provides an optimally efficient means of propulsion to maintain high thrust production for slow steady cruising associated with its feeding activities.

Right whales also possess large, low aspect ratio flippers (Tomilin, 1967; Cummings, 1985; Kenney, 2002). While skim feeding, the drag generated by the open mouth has the potential to create a variable pitching moment about the whale's center of gravity. The large surface area of the flippers may be used to generate lift forces to counteract these pitching moments and help the whale maintain its horizontal trajectory while feeding.

It is also possible that the large flippers play a role in the social activities of the whale. Right whales regularly engage in surface active groups, a courtship or social behavior in which a group of whales aggregate near the surface, rolling and competing for position next to a focal animal (Kraus and Hatch, 2001; Best et al., 2003). A large flipper area would generate large forces for drag-based sculling and rowing maneuvers to turn and position the body when forward velocity is essentially zero.

Maneuverability

In contrast to the cruising blue and right whales, maneuverability requirements are high for both humpback and gray whales. Humpback whales are reported to be the most acrobatic of the whale species (Jurasz and Jurasz, 1979; Winn and Reichley, 1985; Fish and Battle, 1995; Fish, 2004). Field observations indicate that sharp, high speed, banked turns are regularly employed within the humpback's wide repertoire of feeding techniques. When bubble netting, these whales often blow a ring of bubbles 1.5–50 m in diameter to surround their prey. Once the ring is complete, they pivot sharply using their flippers, banking to the inside and turn into the center of the net

(Jurasz and Jurasz, 1979). Another feeding maneuver, the inside loop, involves the whale swimming rapidly away from its prey, performing a 180 degree roll, with a lunge back toward the prey (Hain et al., 1982). This maneuver is executed in 1–2 body lengths.

The humpback's large, high aspect ratio flippers can produce lift for tight turning maneuvers (Fish and Battle, 1995). In addition, the scalloped leading edge serves to delay stall angles, increase lift and decrease drag (Miklosovic et al., 2004). The humpback also has a large fluke area for its body size. The low aspect ratio and large surface area enable the humpback whale to generate large acceleration reaction forces suitable for quick maneuvers (Webb, 1984b). The body form of the humpback whale with its large anterior cross-section may serve to reduce recoil motions of the head due to the large thrust generated by the flukes during quick maneuvers (Fish et al., 2003). Thus, the humpback's flippers, flukes, and body form all contribute to the quick maneuverability necessary for its more elusive prey and unique feeding techniques.

The gray whale is also designed for maneuverability rather than cruising. But in contrast to the quick turns of the humpback, its body form is better suited for slow precise maneuvering. With its large, low aspect ratio flippers and flukes, small movements of the control surfaces affect large amounts of water and are able to generate large forces for maneuvering the body. The larger drag associated with the increased area has less of an energetic effect due to the slow swim speeds of the gray whale.

Gray whales use their rostrum to stir up the bottom sediments in shallow coastal waters and filter the free-swimming amphipods from the turbid waters (Rice and Wolman, 1971). They are also reported to feed in and around rocks and kelp beds where hyper-benthic mysids and other small crustaceans swarm (Dunham and Duffus, 2001). A tagging study in British Columbia revealed that more than half of the whales' bottom time on feeding dives was spent rolled at an angle greater than 45 degrees (Woodward and Winn, 2006). Similar rolling behavior was observed in two young captive gray whales, Gigi (Ray and Schevill, 1974) and

J.J.[1], rehabilitated at an aquarium in San Diego. These observations combined with the uneven baleen wear found in harvested specimens (Kasuya and Rice, 1970) suggest that this rolling behavior is a common strategy used in gray whale feeding. Skulling and rowing motions of the large area flippers and flukes may help the gray whale maintain precise positioning and control within coastal high-energy zones. In addition to maneuvers necessary for their benthic feeding, gray whales can turn tightly when opportunistically feeding on squid and bait fish (Nerini, 1984) and have been reported to surface repeatedly in the same spot (Tomilin, 1967). Like other slow moving cetaceans (i.e., river dolphin *Inia geoffrensis*, beluga *Delphinapterus leucas*) inhabiting shallow, structurally complex environments (Fish, 2002, 2004), the gray whale has traded speed for maneuverability that is more suited to its habitat and feeding mechanisms.

ACKNOWLEDGMENTS

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