**Title**

Swimming performance and propulsive efficiency of baleen whales

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**Abstract**

Baleen whales (Mysticeti) comprise some of the largest swimming animals that have ever evolved on earth and, as a result, present an ideal case study for examining how morphology and the kinematics of swimming scale up to the largest body sizes. We used data from whale-borne inertial sensors coupled with morphometric measurements from aerial drones to calculate the hydrodynamic performance of oscillatory swimming in three baleen whale species (minke whales, *Balaenoptera bonaerensis*; humpback whales, *Megaptera novaeangliae*; blue whales, *Balaenoptera musculus*) ranging in body length from ~9-25m. Our results suggest that mass-specific thrust increases with increasing swimming speed but is unaffected by body size or fluke area. Propulsive efficiency increased with increasing swim speed but decreased with increasing body size, contrary to previous estimates for smaller animals that propulsive efficiency should increase with increasing body size. Although our empirically-parameterized estimates for the drag of a swimming baleen whale was ~3-6 times higher than a simple gliding model, oscillatory locomotion at this scale exhibits high propulsive efficiency as in other adept swimmers.

**Introduction**

The repeated invasion of aquatic and marine environments by tetrapods over the last 250 million years has resulted in a host of convergent morphological adaptations that facilitate life in water (Kelley & Pyenson, 2015). Among these adaptations are the evolution of a fusiform body shape, flattened control surfaces, and sickle-shaped caudal fin to locomote more effectively through the water (Fish et al., 2008). These morphological adaptations are functionally analogous with other swimming animals such as thunniform fish, lamnid sharks, cetaceans, sirenians, and the extinct ichthyosaurs (Donley et al., 2004; Gleiss et al., 2011). The majority of these swimmers use an oscillatory swimming style that involves side-to-side or up-and-down movement of a hydrofoil-like tail to generate lift-based thrust and overcome drag (Fish, 1998). Cetaceans are unique among oscillatory swimmers because of their extreme body mass, exemplified in mysticetes, which evolved in the last five million years (Slater et al 2017). Although the swimming performance of large whales has long been of interest to researchers (Krogh, 1934; Kermack, 1948; Bose and Lien, 1989), direct measures of their swimming kinematics and morphology have been lacking.

Cetacean swimming performance has been studied to understand important morphological differences that affect swimming kinematics, behavior and ecology (Fish, 1993a; Curren et al. 1994, Fish 1998). However, these studies focused on unsteady maximum speed measurements of smaller and highly maneuverable odontocete species in captivity (Fish, 1993; Fish, 1998). In fact, most work on cetaceans and other swimming animals has historically been conducted in a laboratory setting due to the logistical and technological constraints of working in uncontrolled aquatic or marine environments (Edel and Winn, 1978; Fish, 2002; Fish, 2006; Potvin et al., 2009; Fish et al., 2018).

The lab based studies has helped to explain the locomotion and variations in swim performance for many smaller cetaceans. It has been found that cetaceans engage in lift-based propulsion through an oscillation of their fluke (Fish, 1996; & Woodward, 2006). They have a smooth and fusiformed body shape that moves up and down dorso-ventrally at a center of rotation near the backside of the dorsal fin. (Parry, 1948; Fish, 1993; Fish and Rohr, 1999; & Woodward, 2006). Forward movement is generated by a lift force produced perpendicular to the plane that the flukes and flippers are on, and through heaving (vertical motion of the peduncle) and pitching (angle of the flukes with respect to the penduncle) (Chopra and Kambe, 1977; Fish, 2004; & Woodward, 2006). Maneuverability is achieved through a combination of flipper activation, body curvature, motion of the peduncle, and rotation of the tail flukes (Smith et al., 1976; Fish, 2002; Fish 2004; & Woodward, 2006).

With all that’s known about smaller cetaceans, much is still a mystery when understanding the larger cetaceans, mysticetes. Obtaining accurate data in their natural environment is difficult and often inaccurate. Although, recent technological advances are finally allowing us to study the scale effects of locomotion from smaller cetaceans to the largest cetaceans in their natural context. In fact, remote sensing biologgers allow for the measurement of uncontrolled behavior, verification of locomotion characteristics, and information surrounding ecological context (Johnson, 2011; Goldbogen et al., 2017). Additionally, photographs obtained from unoccupied aerial systems (UAS) are especially useful for classifying the demographic and health status of marine mammals (Christiansen et al., 2016; Johnston, 2019). When used in concert, biologging devices and UAS can complement each other and allow us to answer a wide range of questions related to the fundamental biology of cryptic species such as marine mammals in their natural habitats (Jones et al., 2006; Chambot & Bird, 2015; Johnston, 2019)

Here, we use Custom Animal Tracking Solutions (CATS) tags and UAS measures to calculate thrust power, drag coefficients, Reynolds numbers, and propulsive efficiencies for free-swimming whales. Previous studies have estimated the propulsive efficiency of swimming for odontocetes and other swimming animals to be approximately ~75-90% (Fish, 1998), but the upper end of the body size range remains unstudied. This information on large whales will provide insight into the evolution of body shapes for whales and other oscillatory swimmers and will improve our understanding of baleen whale energetic efficiency (Gough et al., 2019; Goldbogen et al. 2019 Science scaling paper). Propulsive efficiency is typically defined as the percentage of locomotive energy that is successfully transferred into useful work and forward thrust (Chopra and Kambe, 1977; Fish, 1993). Estimating the propulsive efficiency for these large whales would fill in our knowledge gap for the extreme upper end of body size and support the idea of oscillatory swimming as one of the most energetically efficient swimming modes for animals required to swim rapidly or travel long distances.

**Methods**

*Focal Whales*

The whales that are the focus of the study include the Antarctic minke whale (*Balaenoptera bonaerensis*, Burmeister, 1867), humpback whale (*Megaptera novaeangliae*, Borowski, 1781), fin whale (*Balaenoptera physalus*, Linnaeus, 1758), bryde’s whale (*Balaenoptera* edeni, Anderson, 1879), sei whale (*Balaenoptera* borealis, Lesson, 1828), and blue whale (*Balaenoptera musculus*, Linnaeus, 1758). The six species are members of the family Baleanoptera, commonly referred to as rorquals, and tend to have similar life histories and behaviors. The three species ranged in size from ~9 m in length for the minke whale, ~ up to 19 m for the humpback whale, and up to ~25 m for an adult blue whale (Goldbogen et al., 2019). Distinct morphological differences are also present between these species, with the most prominent being the enlarged flukes and flippers of the humpback whale relative to body size (Fish and Battle, 1995).

Data on foraging and swimming was collected on humpback whales off of the coast of Monterey, CA and the Western Antarctic Peninsula, blue whales off the coast in California (Monterey Bay and Santa Barbara) and on the minke whale around Antarctica. **MAY NEED MORE ON THE LOCALITIES**

*CATS Tags and UAV Technology*

The CATS camera tags (Fig. 1s) integrate video (1280 x 720p resolution, 25-30 frames per second) with 800 Hz accelerometers and gyroscopes; 100 Hz magnetometers, pressure and temperature sensors; a 20 Hz internal temperature sensor; and 10 Hz light and GPS sensors. Videos were recorded in 1280 x 720p HD resolution at between 25 and 30 frames per second. Tags were deployed from 6 m rigid hull inflatable boats using a 6 m carbon-fiber pole. Tags were attached to the animal with four suction cups, detached after suction failed, floated to the surface and were recovered via VHF telemetry. Deployment lengths in this study ranged from 8 min to 26 hr (Cade et al., 2016). For more information on the tags used in this study, see Goldbogen et al. (2017).

UAS Operations and *Morphometric Measurements*

Photographs of all species were collected using Unoccupied Aerial Systems (UAS or drone) between 2017 and 2019. Specifically, two types of hexacopters were used, the FreeFly Alta 6 and a custom Mikrokopter-based LemHex-44. Both aircrafts were contained with a 2-axis gimbal fitted with a Lightware SF11/C laser altimeter and a Sony Alpha A5100 camera with an APS-C (23.5 mm by 15.6 mm) sensor, 6000 x 4000 pixel resolution and either a Sony SEL 50 mm or SEL 35 mm focal length low distortion lens.

ImageJ 1.5i (Schindelin et al., 2012) was used to measure the total length, maximum body diameter, fluke chord length, and fluke area (Fig. 2). Measurements in pixels were multiplied by the ground sampling distance (GSD) to convert to meters following Fearnbach et al. (2012):

(1)

(2)

where *L is the length (m), npix* is the number of pixels, *a* is the altitude, *lfoc* is th focal length (mm), *Sw* is the sensor width (mm), and *Pw* is the image resolution width (px). The width of the sensor and image resolution was used since images of the whales were captured full frame widthwise (Gough et al., 2019). In ImageJ (NIH), the scale was set by creating a straight line from the notch in between the caudal flukes to the tip of the rostrum and entering the total length as the known distance. The combined planar surface area of the flukes (*Fa*; m2) was calculated by carefully drawing a polygonal outline of the flukes. Chord length of the flukes (C; m) was measured as the linear distance from the notch between the flukes to the anterior insertion of the flukes on the tail. Body mass (kg) was estimated from total body length using known regressions (Kahane-Rapport and Goldbogen 2018). The wetted surface area of the body (*Sa* ;m2) was estimated from total body length using data provided by Fish (1993).

*Thrust Force Modeling*

Our calculations of the fluking thrust are based on the model of lunate tail propulsion using unsteady wing lifting surface theory (Chopra and Kambe, 1977; Yates, 1983). The modeling first involved the estimation of two input parameters, namely the reduced frequency ( here defined as:

(3)

with *ω* as angular frequency of the fluking (with *ω =* 2π*f*, where *f* is the frequency in Hz), and *U* the swimming velocity (m s-1); and the feathering parameter () expressed as:

(4)

This parameter is expressed as the ratio of the maximum angle the fluke makes with the direction of motion and the maximum angle (*ωh1/U*) achieved by the trajectory of the pitching axis of the flukes (Yates, 1983) when reaching the heave amplitude *h1 (m)*. The Chopra-Kambe theory yield a series of parametric curves expressing the coefficient of thrust ( in terms of and (digitized from the graphs shown in Chopra and Kambe (1977). From the extrapolated C­T one obtains the total mean thrust force () (over a tail heave cycle),given the relationship:

(5)

with as the density of seawater, the fluke area, and ratio as the heaving amplitude. The theory also yields parametric curves for calculating the efficiency ( here defined given by:

(6)

with as the mean rate of oscillation (Chopra and Kambe, 1977, Yates, 1983, Fish, 1998).

We used a customized MATLAB script to detect flukebeats based upon methods defined by Gough et al. (2019). For each detected tailbeat, we combined values from the digitizing of Chopra and Kambe’s figures, kinematic variables from the tag data such as *U,* *f*, and UAV-measured morphometrics to calculate thrust power output, drag coefficient, and Reynolds number for the period of time corresponding to a single tailbeat. The (mechanical) thrust power output (*PT*) is given by:

(7)

and equating the propulsive mechanical power generated with the drag power dissipated by the body yields the (mean) drag force and its corresponding drag coefficient: (Fish 1993):

(8)

*Routine vs. Maximum Effort Swimming*

The relationship between routine and maximum effort swimming can be analyzed where routine effort swimming was defined as steady-state migratory swimming behaviors or swimming in between foraging events. Maximum effort swimming was defined as the period within 10 s before a lunge feeding event. This punctuality was chosen because at this point during the lunge, we can compare measurements of absolute performance by looking at the same swimming velocities and compare relative kinematics at that specific speed. Once identified, routine swimming kinematics and maximum swimming kinematics were sorted from one another to be individually analyzed and compared.

*Comparison to a Simple Rigid-Body Model*

Cetacean swimming involves body and tail heaving motions that are altogether absent with the motions of rigid bodies (such as submarines) and bound to significantly increase the drag (Fish 1993, 1998, Fish and Rohr 1999). We compared our drag coefficient data with that of airship models tested in wind tunnels in the late 1920’s (Hoerner, 1962) as summarized in the following correlation (Hoerner, 1962; Blevins, 1983, Webb 1975, Koyman 1989)

(10)

where is the maximum body diameter (m). This equation is expressed in terms of the Reynold’s number

(9)

where in which is the kinematic viscosity. In this case the drag force () sustained by the airship (or non-tail-heaving whale) is given by:

(11)

**Results**

*Statistical Analyses*

We investigated intra-and-interspecific relationships between and among 63 animals. We compared hydrodynamic performance variables (thrust power output, drag coefficient, and propulsive efficiency) with swim speed, Reynolds number and morphometric measurements using R and RStudio (Version 1.2.1335, packages: ggplot2, ggpubr, and tidyverse). Generalized linear mixed-effects models (GLMMs) were created using the mean mass-specific thrust for routine effort swimming speed (m s-1) (Fig. 3). Linear fit regressions were performed for the thrust figures (Fig. 3 - 5), drag figures (Fig. 6), and propulsive efficiency figure (Fig. 7). GLMMs for propulsive efficiency (Fig. 6) depending on *U* for routine effort and *Lbody* were constructed with identical details and parameters as Fig. 3.

The species-level means (± se) for each of our measured kinematics variables and morphometrics are given in Table 1. The species-level means (± se) for each of our measured hydrodynamic parameters are given in Table 2.

Figure 3 shows that mean mass-specific thrust is constant at increasing body size and increases linearly as swimming speed increases. Figure 4 shows mean mass-specific thrust against total body length at both **r**outine and maximum effort swimming, Both effort levels show slight increases with increasing body size, but only routine effort was found to be significant (Table 3). At any given body size, the mean-mass specific thrust increased with the transition from routine to maximum effort swimming. Figure 5 shows mean mass-specific thrust against the ratio of fluke area over total body length. There was substantial scatter around the linear fit and no significant relationship (Table 3).

Figure 6 shows our empirically-derived data for drag coefficient as a function of Reynolds number for swimming whales as well as the rigid-body model regression based on the Hoerner equation. While the Hoerner model predicts a slight decrease in drag coefficient with increasing Reynolds number, we found the opposite to be true for swimming animals, with larger animals having a significantly greater drag coefficient than smaller animals.

We regressed the propulsive efficiency against swimming speed (Fig 7A) and total body length (Fig. 7B) and found that propulsive efficiency increases significantly as swimming velocity increases and decreases significantly with increasing body size.

Comparing the mean propulsive efficiencies for our three studied species against other swimming animals showed that all oscillatory swimmers (mysticete cetaceans, odontocete cetaceans, tuna, manatee, pinnipeds) were highly efficient at ~80% or higher (Fig. 8). Other styles of swimming were lower, with subcarangiform undulatory swimmers averaging ~75% and drag-based paddling swimmers averaging ~25%.

**Discussion:**

Many previous studies that have quantified the kinematics and hydrodynamics of cetacean swimming have used captive animals that can be measured reliably from a stable reference position (Fish, 1993; Fish 1998; Rohr and Fish 2004). While our methods are less precise, they provide a first approximation for many of the same kinematic variables. Some, such as the amplitude of heave or angle of attack of the flukes relative to the body are still beyond our reach, except in rare circumstances (Gough et al., 2019), so we supplemented our empirical data with validated estimates for these unknown variables (Bainbridge, 1958; Fish, 1998). This approach allowed us to quantify hydrodynamic and kinematic aspects of mysticete swimming using many of the same methods derived by Chopra and Kambe (1977), which has also been validated for odontocetes by Fish (1998). The similarity between our methods and those of previous studies extends our ability to compare swimming performance across vast body size ranges.

*Mean mass-specific thrust*

Thrust generation is a fundamental aspect of any swimming mode and the achievable mass-specific thrust for a swimming animal has a direct impact on its maximum swimming speed and, subsequently, the types and quantities of prey that it can capture (Fish, 1998; Potvin et al., 2009; Cade et al., 2020). For cetaceans, high mass-specific thrust allows odontocetes to capture fast-moving, individual fish (Maresh et al., 2004) and allows mysticetes to achieve high speeds during feeding lunges to offset the deceleration during prey engulfment as well as the potential escape response of different prey types (Cade et al., 2016, 2020). Fish (1998) measured the swimming speed and estimated the thrust output for four odontocete species and found that thrust increased with increasing swimming speed for all species. Additional studies surrounding odontocete swimming speed and thrust have also found a similar relationship between increasing thrust and swimming speed (Weihs, 2002A; Fish et al., 2014). In this study, we found that the mass-specific thrust for routine fluking (at lower velocities of 1-3 m s-1) are very similar for all three species, and show similar relationships to Fish (1998) and Weihs (2002A) in that thrust increases as swimming velocity increases. The results presented here correspond to the trends of the hydrodynamics of rigid moving bodies as the thrust (= drag as constant velocity) increases with the square of the velocity (Vogel, 1994). Furthermore, the propulsive motions of dolphins and fishes incurs a further three to five times increase in thrust with swimming velocity (Lighthill, 1971; Liu et al., 1997; Anderson et al., 2001; Fish et al. 2014).

Our comparisons of speed-matched mass-specific thrust output between routine swimming and lunges suggest that whales may alter other kinematic variables in order to generate greater thrust during feeding. Thrust generation is more trivial at routine effort swimming because these animals are typically swimming at a speed that results in the lowest energetic cost (~1.5-2.5 m s-1) and larger animals have lower mass-specific power expenditures than smaller animals (Gough et al., 2019). The similarity of the increase (~two-fold) from routine to a higher-lunge feeding effort thrust generation across our range in body size suggests that all of the large whales studied are preparing for a lunge in dissimilar ways. All of the species included in our study are lunge feeders that feed by opening their mouth and engulfing a large volume of water into a highly expansible throat pouch (Cade et al., 2016; Cade et al., 2020). Empirical data (Cade et al., 2019) and hydrodynamic models (Potvin et al. 2009) suggest that the whales begin these lunges at high speeds (3.5-5 m s-1) in order to overcome heightened drag during engulfment and move through the prey patch entirely on momentum (Potvin et al., 2009; Cade et al., 2016, 2020). Our results give an approximation for how much thrust may be required for whales of different sizes to generate the momentum necessary to complete their feeding lunges effectively.

Focusing more heavily on the relationship between mass-specific thrust generation and body size, our results diverge slightly from previous estimates. Fish (1998) determined that mass-specific thrust and body size have no relationship. Hill (1950) considered that for similar animals, the maximum power generated during a steady effort would increase not directly with the weight (W), but rather with W0.73. Therefore it was expected that power output would decrease proportionately with increasing body size. We found that mass-specific thrust increases as body length increases (Fig. 4). This relationship was significant for routine effort swimming, but was found to be non-significant for swimming just prior to lunge feeding. The large amount of data in our dataset for routine effort swimming relative to feeding effort could explain why the relationship was significant for the former and not the latter. We expected that the humpback whale might exhibit a larger mass-specific thrust than the other two species in the study, because of their very large fluke area relative to body size and less streamlined body. In addition, humpback whales will make tight turning maneuvers using the elongate flippers to catch prey that both increase the drag and energetics of foraging (Fish and Battle, 1995).

For lift-based oscillatory swimmers, thrust is produced as the forward component of the hydrodynamically-derived lift produced by motion of the tail flukes (Goldbogen et al., 2016). Maximum thrust and high propulsive efficiency are typically achieved with a broad, semi-lunate fluke area that is attached to the body through a constricted peduncle region (Fish, 2004). There are morphological variations in rorquals across scale (Woodward et al. 2006; Kahane-Rapport & Goldbogen, 2018), but there has been minimal work relating fine-scale morphology of the control surfaces to hydrodynamic performance in large whales. Interestingly, we found that the scaled fluke length has no effect on thrust production and was very similar for all species (Fig. 5). We believe that the large flukes of the humpback whale are offset by their enlarged flippers and rotund body shape, which are both adaptations for increased maneuverability at the potential expense of higher thrust generation (Fish, 1999; Weihs, 2002B). Overall, our results show that thrust production on a mass-specific basis is greatest in the largest animals and scales with body size and not necessarily appendage size or shape.

Drag coefficient vs. Reynolds number

In comparison to our tagged animals, Hoerner’s R-100 airship models used for computational analysis did not include control surfaces (flippers or flukes). Instead, the approximated environment around the airship was determined using wind tunnel test data (Hoerner 1965; Blevins, 1993). These modeled values suggest that for a minke whale (~9m), the drag coefficients for fluking should be roughly three times as high than non-fluking and gliding. But the difference between these coefficients should increase for larger animals, culminating in a six-fold difference for a blue whale (~22m) (Fig. 6). (Hope to get more of Jean’s input here) (Lighthill, 1971 indicated this increase as did Fish, 1993, 1998).

*Propulsive efficiency*

*Swimming velocity (m s-1)*

Findings from Fish (1998) show that the propulsive efficiency of swimming odontocetes in captivity are ~80-90% (Fish, 1998). Our goal was to determine if body size, especially at the extreme upper limits, significantly impacts this efficiency. Figure 7 shows the propulsive efficiencies of the three species in our study. We found each species follows the same trend. Namely that velocities < 1.5 m s-1 result in an efficiency less than 83%, while velocities > 1.5 m s-1 results in an efficiency between 84% and 95% with the average close to 91%. This suggests that there is an optimum velocity to swim at that maximizes propulsion.

Optimal locomotor speeds have been demonstrated for runners, flyers, and swimmers (e.g., Tucker, 1968; Webb, 1975; Hoyt and Taylor, 1981). The cost of transport (CT) has been used as the metabolic proxy that is inversely related to the propulsive efficiency (Fish, 2000). Williams et al. (1993) and Yazdi et al. (1999) found that the minimum CT for the bottlenose dolphin (*Tursiops truncatus*) occurred at swimming speeds of 2.1 and 2.5 m s-1, respectively. These speeds coincided with the routine swimming speeds in wild populations. Similarly, gray whales (*Eschrichtius robustus*) and minke whales cruise at the speed of the lowest CT (Sumich, 1983; Blix and Folkow, 1995). The minimum CT for the gray whale corresponded to the swimming velocity (2.0-2.5 m s-1) of migrations (Wyrick, 1954; Williamson, 1972; Sumich, 1983), which was similar to the velocity of maximum efficiency for whales in the present study. Minke whales, however, were determined to have a minimum CT at the maximum cruising velocity of 3.25 m s-1 (Blix and Folkow, 1995), which was 37% higher than the optimal velocity for maximum efficiency in the present study. However, the velocity of maximum propulsive efficiency (2.37 m s-1) was within the range of swimming velocites (1.5-2.6 m s-1) for migrating minke whales (Williamson, 1972). Correspondingly, the swimming velocity for maximum propulsive efficiency of the blue whale (2.02 m s-1) and the humpback whale (2.00 m s-1) were within the ranges of migratory velocities of 1.5-3.1 m s-1 (Williamson, 1972) and 1.1-4.0 m s-1 (Chittleborough, 1953; Williamson, 1972), respectively.

Lunge feeding by balaenopterids involves high accelerations to attain velocities greater than the velocities for maximum propulsive efficiency (Cade et al., 2016). A reduced propulsive efficiency would increase the energetic expenditure when foraging. Such an increase would have consequences to the whale’s energy budget and limit dive duration and associated feeding efficiency. Compared to the Balaenopteridae, the Balaenidae (i.e., right whales, bowhead whale) swim slowly through the water while maintaining a steady speed (Burns et al., 1993). The foraging strategy of the rorquals places greater energetic demands on these whales than the balaenids (Dolphin, 1987).

*Total body length (m)*

In this study, propulsive efficiency directly relates to the amount of work the animal does to propel itself forward. We predicted that the blue whalewould have the greatest propulsive efficiency because of its streamlined body shape and high fineness ratio, while we predict that the minke whale has a lower propulsive efficiency due to its similar shape but lower fineness ratio. We hypothesized that the humpback whale and its rotund body shape, large flippers, and low fineness ratio would have the lowest propulsive efficiency. However, we found that propulsive efficiency decreases with increasing body size among rorquals but is unaffected by other morphological parameters (See Fig. 7B). We can understand this relationship by referencing Figures 4 and 6; a larger animal will have a slightly increased thrust generation but a greatly increased drag coefficient, thus resulting in a lower propulsive efficiency, because they expend more energy to overcome drag and achieve equivalent locomotor performance.

Our finding showed that size does matter in regard to swimming performance, regardless of the conservation of body shape within a defined cetacean lineage. The Balaenopteridae extends in size from the minke whale to the enormous blue whale. The scale of these ocean giants necessitates the use of oscillatory lift-based swimming as an effective propulsive mechanism for high-speed swimming at high Reynolds numbers (Webb and De Buffrénil, 1990; Fish, 2020). A major conclusion of the study was that the high propulsive efficiency decreased with increasing body size despite the similarity of body shape from small to large balaenopterid whales. Interestingly in parallel with the trend of propulsive efficiency found for whales, another locomotor performance variable, maximum speed, was also found to decrease above an optimal size (Hirt et al., 2017). Locomotion and its associated energetics for whales are thus constrained at large body sizes. Furthermore, the high burst velocities and accelerations attained by the whales during lunges would incur reduced propulsive efficiencies compared to routine and migratory velocities. The reduced propulsive efficiency would place increased energetic demands during active foraging using a lunge feeding strategy for the balaenopterids.

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**Competing Interests:**

We have no competing interests to report.

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**Tables/Figures/Legends**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | |  | ***Kinematics*** | | | | ***Morphometrics*** | | | | | | |
| ***Species*** | ***Number of Individuals*** | ***Swim Speed (Norm) (m s-1)*** | | ***Oscillatory Frequency (Norm) (Hz)*** | ***Swim Speed (Max) (m s-1)*** | ***Oscillatory Frequency (Hz)*** | ***Total Length (m)*** | ***Maximum Diameter (m)*** | ***Fineness Ratio*** | ***Wetted Surface Area (m2)*** | ***Body Mass (kg)*** | ***Chord Length (m)*** | ***Fluke Area (m2)*** |
| ***Minke*** | 14 | 2.37 ± 0.003 | | 0.40 ± 0.001 | 3.03 ± 0.01 | 0.50 ± 0.002 | 7.30 ± 0.34 | 1.24 ± 0.06 | 5.37 ± 0.06 | 25.54 ± 1.21 | 6020.75 ± 284.60 | 0.55 ± 0.40 | 0.77 ± 0.06 |
| ***Humpback*** | 31 | 2.00 ± 0.002 | | 0.23 ± 0.0003 | 2.27 ± 0.01 | 0.32 ± 0.002 | 11.09 ± 0.33 | 2.29 ± 0.08 | 4.84 ± 0.08 | 61.50 ± 1.80 | 25761.42 ± 755.40 | 1.05 ± 0.03 | 3.14 ± 0.18 |
| ***Blue*** | 18 | 2.02 ± 0.005 | | 0.18 ± 0.0003 | 2.83 ± 0.01 | 0.25 ± 0.001 | 22.50 ± 0.32 | 2.83 ± 0.06 | 8.01 ± 0.13 | 152.50 ± 2.20 | 82347.35 ± 1185.94 | 1.29 ± 0.03 | 4.71 ± 0.18 |

Table 1. Kinematic and morphometric variables used for modeling of hydrodynamic properties for all (n=63) individual whales in our dataset. Those with an asterisk were modeled using available data and methods in the literature. All values are given as the mean ± the standard error.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | ***Hydrodynamic Calculations*** | | | |
| ***Species*** | ***Mass-Specific Thrust (N kg-1)*** | ***Drag Coefficient*** | ***Reynolds Number*** | ***Propulsive Efficiency*** |
| ***Minke*** | 0.336  ±  1.3 x 10-3 | 0.011  ±  3.8 x 10-5 | 1.71 x 107  ±  2.3 x 104 | 0.920  ±  1.4 x 10-4 |
| ***Humpback*** | 0.237  ±  1.3 x 10-3 | 0.023  ±  9.9 x 10-5 | 2.23 x 107  ±  2.7 x 104 | 0.901  ±  1.8 x 10-4 |
| ***Blue*** | 0.365  ±  2.7 x 10-3 | 0.048  ±  2.9 x10-4 | 4.64 x 107  ±  1.1 x 105 | 0.851  ±  3.1 x 10-4 |

Table 2. Results from hydrodynamic and morphometric calculations for all individuals (n=63) from each species. All values are given as the mean of all tailbeats in a deployment ± the standard error. The drag coefficient, Reynolds number, and propulsive efficiency are dimensionless. The mean fluke area is shown in m2 and the chord length and total lengthare shown in meters.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | ***GLMM equation*** | ***Estimate*** | ***P - value*** | ***R2*** |
| ***Mean Mass-Specific Thrust Power*** |  |  |  |  |
| Figure 3: Speed (m s-1) | y = 0.834x – 2.872 | 0.834 | < 0.001 | 0.79 |
| Figure 5: Fluke Area / Total Length (m) | y = 1.513x – 1.080 | 1.513 | 0.219 | 0.15 |
|  |  |  |  |  |
| ***Mean Mass-Specific Thrust Power vs. Total Length (Figure 4)*** |  |  |  |  |
| Routine Effort Swimming | y = 0.025x – 0.637 | 0.025 | 0.016 | 0.11 |
| Maximum Effort Swimming | y = 0.030x – 1.571 | 0.03 | 0.201 | 0.33 |
|  |  |  |  |  |
| ***Drag Coefficient vs. Reynolds Number***  ***(Figure 6)*** |  |  |  |  |
| Empirical Calculations | y = (-1.47e-09)x + (6.84e-02) | -1.47e-09 | <0.001 | 0.88 |
| Hoerner Model Calculations | y = (-3.36e-11)x – (3.62e-03) | -3.36e-11 | <0.001 | 0.88 |
|  |  |  |  |  |
| ***Propulsive Efficiency***  ***(Figure 7)*** |  |  |  |  |
| Speed (m s-1) | y = 0.057x + 0.766 | 0.057 | <0.001 | 0.8 |
| Total Length (m) | y = -0.005x + 0.954 | -0.005 | <0.001 | 0.51 |

Table 3. This table contains equations, estimates, R2 values, and p values from generalized linear mixed models for sequential figures 3-7.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Species*** | ***Swim Speed (m s-1) or (bl s-1)\**** | ***Total Length (m)*** | ***Propulsive Efficiency*** | ***Source(s)*** |
| ***Homo sapien***  *Human (Female)* | 0.95 | 2.38 | 0.29 | von Loebbecke et al., 2009 |
| ***Ondatra zibethicus***  *Muskrat* | 0.75 | 0.44 | 0.33 | Fish, 1984 |
| ***Pterophyllum eimekei***  *Freshwater Angelfish* | 0.04 | 0.08 | 0.16 | Blake, 1979; Blake, 1980 |
| ***Danio rerio***  *Zebra Danio* | Multiple | 0.0315 | 0.80 | McCutchen, 1975 |
| ***Cymatogaster aggregata***  *Shiner Perch* | 0.57 | 0.143 | 0.65 | Webb, 1975 |
| ***Oncorhynchus mykiss***  *Rainbow Trout* | Ucrit | 0.293 | 0.75 | Webb, 1975 |
| ***Euthynnus affinis***  *Mackerel Tuna (Kawakawa)* | 1.52 | 0.40 | 0.90 | Magnuson, 1978 |
| ***Pusa hispida***  *Ringed Seal* | 0.75 | 1.03 | 0.88 | Fish et al., 1988 |
| ***Pagophilus groenlandicus***  *Harp Seal* | 1.04 | 1.43 | 0.87 | Fish et al., 1988 |
| ***Trichechus manatus***  *American Manatee* | 0.30\* | 3.23 | 0.83 | Kojeszewski and Fish, 2007 |
| ***Delphinapterus leucas***  *Beluga Whale* | 3.00 | 3.64 | 0.84 | Fish 1998 |
| ***Lagenorhynchus obliquidens***  *Pacific White-Sided Dolphin* | 5.30 | 2.00 | 0.89 | Webb, 1975; Yates, 1983; Blickhan and Cheng, 1994 |
| ***Orcinus orca***  *Killer Whale* | 6.50 | 4.74 | 0.88 | Fish, 1998 |
| ***Pseudorca crassidens***  *False Killer Whale* | 3.80 | 3.75 | 0.90 | Fish, 1998 |
| ***Sotalia guianensis***  *Guiana Dolphin* | 2.40 | 1.90 | 0.83 | Blickhan and Cheng, 1994 |
| ***Tursiops truncatus***  *Common Bottlenose Dolphin* | 2.401, 3.802 | 2.501, 2.612 | 0.781, 0.862 | Blickhan and Cheng, 19941; Fish, 19982 |
| ***Balaenoptera physalus***  *Fin Whale* | 8.00 | 14.5 | 0.87 | Bose and Lien, 1989 |
| ***Balaenoptera bonaerensis***  *Antarctic Minke Whale* | See Table 1 (Routine Effort Swimming) | See Table 1 | See Table 2 | Current Study |
| ***Megaptera Novaeangliae***  *Humpback Whale* | See Table 1 (Routine Effort Swimming) | See Table 1 | See Table 2 | Current Study |
| ***Balaenoptera musculus***  *Blue Whale* | See Table 1 (Routine Effort Swimming) | See Table 1 | See Table 2 | Current Study |

Table 4. Propulsive efficiency and metadata collected from various sources for the creation of figure 8.

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Figure 1. Adaptation from Shadwick (2005) showing the forces acting on the tail of a thunniform swimmer such as a blue whale during active oscillatory fluking of the tail. The heaving motion of the tail creates a pressure imbalance between the top and bottom faces of the fluke that results in the generation of a lift force perpendicular to the path of the flukes and a thrust force in the forward direction of travel of the animal.

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Figure 2. Representative UAS drone image of a humpback whale showing the morphometric measurements taken from each animal. The orange line corresponds to the total length (in meters) from the tip of the lower jaw to the caudal midpoint of the tail. The chord length of the fluke (in meters) is denoted by the red line running from the cranial insertion of the fluke onto the peduncle to the caudal midpoint of the tail. The green shaded region corresponds to the tail area (in m2) comprising the entirety of the flukes and the peduncle region caudal to the cranial fluke insertions.

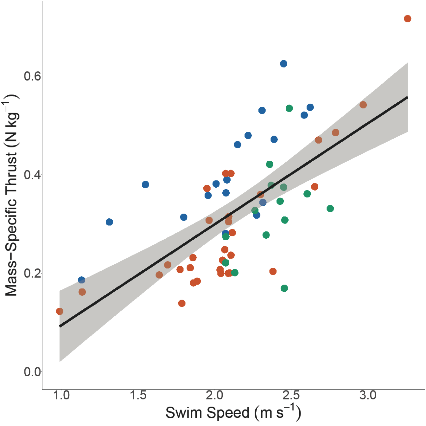


Figure 3. Linear regression of mass-specific thrust (N kg-1) versus swimming speed (m s-1). Each point corresponds to the averaged value for a single individual whale. Green points are minke whales, orange points are humpback whales, and blue points are blue whales.

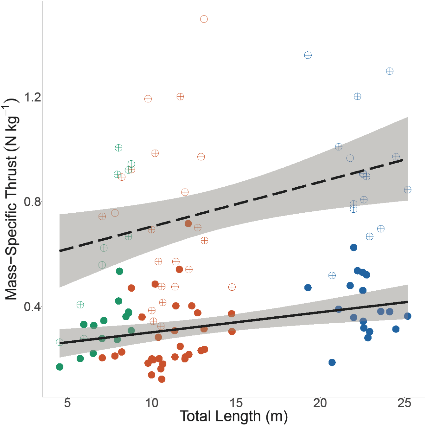


Figure 4. Linear regressions of mass-specific thrust (N kg-1) versus total body length (m) for both routine effort swimming (solid points and solid line) and maximum effort swimming (open crossed points and dotted line). Green, orange, and blue points correspond to minke, humpback, and blue whales.

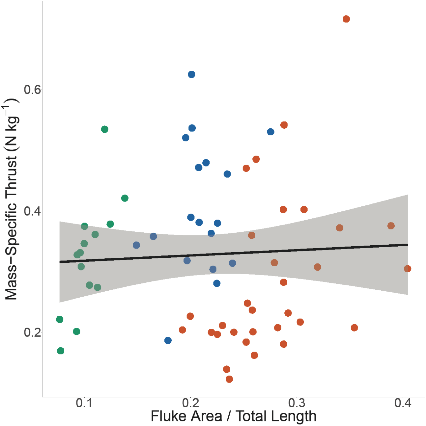


Figure 5. Linear regression of mass-specific thrust (N kg-1) versus the ratio of fluke area over total body length. Green, orange, and blue points correspond to minke, humpback, and blue whales.

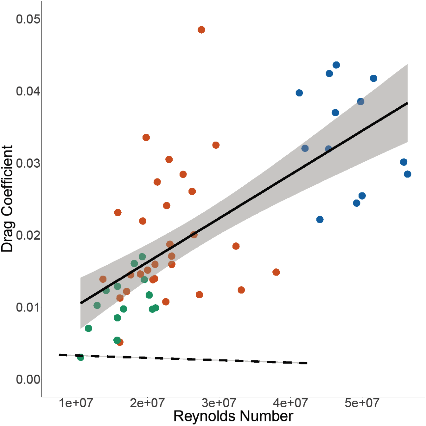


Figure 6. Linear regressions of drag coefficient versus Reynolds number for empirically-derived tag data (points and solid line) and a simple rigid-body model comparison using equations derived from Hoerner (1962) (dotted line). Green, orange, and blue points correspond to minke, humpback, and blue whales.

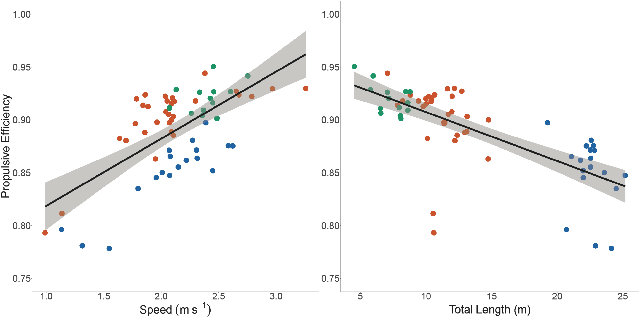
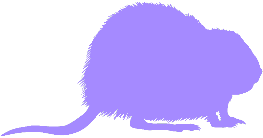
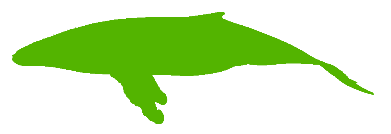
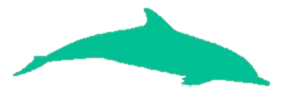
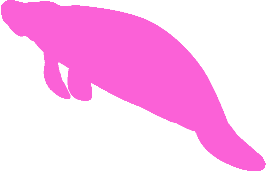
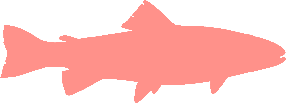


Figure 7. Linear regressions of propulsive efficiency versus swimming speed (m s-1) (left) and total body length (m) (right). Green, orange, and blue points correspond to minke, humpback, and blue whales.



* Mysticete Cetaceans
* Odontocete Cetaceans
* Pinnipeds
* Sirenians (Manatee)
* Fish
* Rodents (Muskrat)
* Humans
* Oscillatory Swimming
* Undulatory Swimming
* Drag-Based Paddling

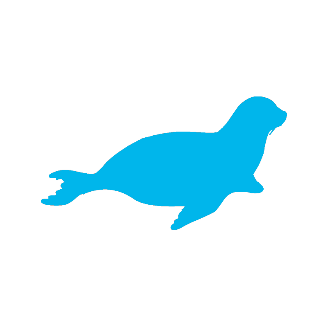


Figure 8. Propulsive efficiency versus total body length (m) for species from different morphological and taxonomic groups and which use different swimming modes. Three of the four mysticete cetaceans are the averaged species-level minke whale, humpback whale, and blue whale data from the present study. Silhouettes correspond to each group by rough position and color.