**Title**

Swimming Scaling of oscillatory kinematics and propulsive efficiency in baleen whales

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**Abstract**

High efficiency lunate-tail swimming with high-aspect-ratio lifting surfaces has evolved in many vertebrate lineages. Baleen whales (Mysticeti) are the largest swimming animals that exhibit this locomotor strategy and present an ideal case study for examining how morphology and the kinematics of swimming scale 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 six baleen whale species (fin whale, *Balaenoptera physalus*;, Bryde’s whale, *Balaenoptera* edeni; sei whale, *Balaenoptera* borealis; Antarctic minke whales, *Balaenoptera bonaerensis*; humpback whales, *Megaptera novaeangliae*; and blue whales, *Balaenoptera musculus*) ranging in body length from ~5-25m. We find that mass-specific thrust increases with increasing swimming speed but is unaffected by body size. Propulsive efficiency, defined as: the amount of work the animal does to propel itself forward, increased with swimming speed but decreased with body size. This finding is contrary to previous data for smaller animals that propulsive efficiency is positively related to body size. Although our empirically-parameterized estimates for the drag of a swimming baleen whale was higher than a simple gliding model, oscillatory locomotion at this scale exhibits high propulsive efficiency as in other adept swimmers. Our results are some of the first to quantify the fine-scale hydrodynamics that underlie these energetic differences between routine and energetically expensive swimming modes and include some of the largest absolute body sizes as well as a larger body size range than any previous study on swimming animals.

**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 achieve high performance locomotion (Fish et al., 2008). These morphological adaptations are functionally analogous with other swimming animals such as thunniform fish, lamnid sharks, cetaceans, and the extinct ichthyosaurs (Motani, 2002; 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 modern baleen whales (Mysticeti), which evolved massive body sizes within 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 difficult to obtain. Studies of cetacean swimming kinematics have typically focused on smaller and highly maneuverable odontocete species in captivity (Fish, 1993; Curren et al. 1994, Fish 1998). Attempts to study mysticetes have been constrained to breathing events at the water’s surface. Energetic assumptions (Sumich, 1983; Parry, 1949; Blix and Folkow, 1995) and morphological measurements were limited to deceased animals that had stranded on beaches or been captured by whaling operations (Lockyer, 1976; Kahane-Rapport and Goldbogen, 2018). The recent development of high-resolution biologging methods now allows researchers to quantify the kinematics of free-swimming cetaceans in their natural habitats (Johnson, 2011; Cade et al., 2016; Goldbogen et al., 2017; Gough et al., 2019). In addition, unoccupied aircraft systems (UAS, or drone) technology has enhanced our ability to obtain precise morphological data, thereby enabling comparative and scaling analyses of form and function (Kahane-Rapport et al. in review; Gough et al., 2019).

Understanding the size-dependent kinematics of swimming cetaceans is critical to analyze their swimming performance and energetics. The dorso-ventral oscillation of the flukes produces lift that is resolved into a forward thrust vector (Fig. 1; Lighthill, 1971; Chopra and Kambe, 1977; Vogel, 1994; Fish, 1998). This lift-based thrust power is equal to the drag power of the animal when swimming at a constant velocity (Lighthill, 1971; Fish, 1998). This mechanism is considered to be highly efficient (>75%; Triantafyllou et al., 1991; Rohr and Fish, 2004). Previous attempts to estimate the thrust power of actively swimming large whales have been made based on a number of assumptions without reliable kinematic data (Parry, 1949; Chopra and Kambe, 1977; Yates, 1983; Bose and Lien, 1989). Thrust power generation is modulated through the adjustment of basic kinematic parameters of the oscillatory tailbeat cycle, and new biologging tags make these empirical measurements possible for large, free-swimming animals.

Kinematic studies performed on cetaceans have focused on the three fundamental parameters of an oscillatory tailbeat cycle: amplitude of heave, swimming speed, and oscillatory frequency. Among these, speed has been studied most extensively. Using various methods, researchers have found that many different species of cetaceans are able to swim over an extended range of speeds. High speeds in excess of 8 m/s have been achieved by rorqual mysticetes (Fish and Rohr, 1999; Hirt et al., 2017; Segre et al., 2020). A recent study by Gough et al. (2019) has shown that mysticetes tend to swim around ~2 m/s when they are not feeding. In order to swim at different speeds within this wide range, mysticetes must adjust either their oscillatory frequency or the amplitude of heave (Lighthill, 1971; Chopra and Kambe, 1977). For small odontocetes, Fish (1998) found that oscillatory frequency increased with increasing swimming speed but decreased roughly with body length while amplitude of heave remained constant at ~0.2 of an animal’s body length. These findings were recently confirmed for mysticetes by Gough et al. (2019).

Measuring the fundamental kinematic parameters of the oscillatory tailbeat cycle has allowed researchers to estimate propulsive efficiency, or the percentage of mechanical energy that is successfully transferred into forward thrust (Vogel, 1994; Fish, 1998). The dimensionless Strouhal number has typically been used as a rough way to describe how the amplitude of heave, swimming speed, and oscillatory frequency are modulated and interact to provide a maximally efficient pattern of vorticity around the tail during swimming (Triantafyllou et al., 1991; Fish, 1998; Taylor et al., 2003; Rohr and Fish, 2004; Gough et al., 2019). The generally accepted rule is that highly-efficient oscillatory swimming falls within a Strouhal range from 0.25-0.35 (Triantafyllou et al., 1991). Both Rohr and Fish (2004) and Gough et al. (2019) found that cetaceans fall within this range, but a more detailed analysis of the kinematics and hydrodynamic parameters, such as the thrust power output and drag, has only been performed previously by Fish (1998) for much smaller odontocetes

Here, our goal is to move beyond the Strouhal number and use a combination of whale-borne tags and UAS morphological measurements to calculate the kinematics, thrust power output, and propulsive efficiencies for free-swimming mysticete whales using similar methods to Fish (1998). Apart from Gough et al. (2019), we have a very limited understanding of how kinematics affect swimming performance at the upper extremes of body size. Previous studies have estimated the propulsive efficiency of swimming for odontocetes and other oscillatory swimming animals to be approximately ~75-90% (Fish, 1998), but the only estimate for a mysticete before our study came from a single fin whale (*Balaenoptera physalus*) of unknown body size swimming at ~8 m/s (Bose and Lien, 1989). Our current data set goes far beyond any previous analyses and includes six species and a ~20m range in body size. We hypothesize that the kinematic and hydrodynamic parameters of swimming scale similarly between small and large cetaceans and will lead to high (>75%) propulsive efficiencies for even the largest animals. Our study will lead to a more complete scaling-based understanding of oscillatory swimming in mysticetes and the kinematic, hydrodynamic, and morphological factors that impact swimming performance in the world’s largest animals.

**Methods**

*Study species and locations*

The whales included in this study are 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. These species range in size from ~5 m in length for the minke whale 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; Woodward et a., 2006).

Data on foraging and swimming was collected on humpback whales off of the coast of Monterey, CA and the Western Antarctic Peninsula, blue whales of California (Monterey Bay and Southern California Bight), minke whales off the western Antarctic Peninsula, fin whales in Monterey Bay and the fjords of southeastern Greenland, Bryde’s whales off the southern coast of South Africa, and sei whales near the Falkland Islands**.**

*CATS Tags and UAS Technology*

The Customized Animal Tracking Solutions (CATS) tags 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. Tags were deployed from rigid-hull inflatable boats using a 6 m carbon-fiber pole. Tag 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 mins to 26 hrs. For more information on the tags used in this study, see Goldbogen et al. (2017).

UAS Operations and *Morphometric Measurements*

Images of each species were collected using UAS between 2017 and 2019. Specifically, two types of hexacopters were used, the FreeFly Alta 6 and a custom Mikrokopter-based LemHex-44. Both aircrafts contained a 2-axis gimbal fitted with a Lightware SF11/C laser altimeter and a Sony Alpha A5100 camera with an APS-C sensor (23.5 mm by 15.6 mm), 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 the 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)

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. Lunge-Associated Swimming*

The relationship between routine and lunge-associated effort swimming can be analyzed where routine effort swimming was defined as steady-state migratory swimming behaviors or swimming in between foraging events. Lunge-associated swimming was defined as the period within 10 s before a lunge feeding event. Once identified, routine swimming kinematics and lunge-associated 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 (e.g., submarines) and significantly increase 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)

*Statistical Analyses*

We compared hydrodynamic performance variables (thrust power output, drag coefficient, and propulsive efficiency) with swim speed, Reynolds number and morphometric measurements using R v. 3.6 and RStudio (Version 1.2.1335, packages: ggpubr, and tidyverse). Generalized linear mixed-effects models (GLMMs) were fit to assess relationships with species as a random effect using package lme4 in R (Bates et al., 2015; Wickham et al., 2019; Kassambara, 2020).

**Results**

*Kinematic and Morphometric Summary*

We investigated interspecific relationships between 68 animals. For both the oscillatory frequency (Hz) and the swimming speed (m s-1), we found that the mean (± se) values for all species increased when transitioning from routine to lunge-associated swimming. The mean increase in swimming speed between the two modes was 0.695 ± 0.152 m s-1 and the mean increase in oscillatory frequency was 0.09 ± 0.02 Hz.

We found that the mean oscillatory frequency for the three species with the most data (humpback, blue, minke) decreased with increasing body length with the minke whale having the highest values (routine: 0.40 ± 0.010 Hz; lunge-associated: 0.49 ± 0.008 Hz), followed by the humpback whale (routine: 0.24 ± 0.006 Hz; lunge-associated: 0.34 ± 0.011 Hz) and the blue whale (routine: 0.19 ± 0.004 Hz; lunge-associated: 0.24 ± 0.004 Hz). We found the Bryde’s and fin whales to have similar routine oscillatory frequencies to the humpback whale while having longer average body lengths (Bryde’s: 12.04 ± 2.07 m; fin: 18.90 ± 0.43 m) than the humpback whale (11.09 ± 0.33 m). Both of the oscillatory frequency values for the lone sei whale (routine: 0.22 Hz; lunge-associated: 0.30 Hz) fell approximately halfway between the values for the humpback and blue whales, which aligns with the sei whale’s body length (16.62 m) being approximately halfway between the mean humpback and blue whale (22.50 ± 0.32 m) body lengths. We found that the oscillatory frequency decreases as the total length increases. We found significant negative relationships between oscillatory frequency and body size during both routine and lunge-associated swimming (routine: *ŷ* = -0.478x – 0.135; *R2* = 0.88; *p* < 0.001; lunge-associated: *ŷ* = -0.471x + 0.147; R2 =0.81; p < 0.001; Fig. 3A).

The mean values for both routine and lunge-associated swimming speeds were similar for the humpback (routine: 2.15 ± 0.066 m s-1; lunge-associated: 2.85 ± 0.100 m s-1), blue (routine: 2.27 ± 0.063 m s-1; lunge-associated: 3.05 ± 0.056 m s-1), and minke whales (routine: 2.44 ± 0.053 m s-1; lunge-associated: 2.96 ± 0.117 m s-1). Despite low sample sizes, the average routine and lunge-associated swimming speeds for the Bryde’s whale (routine: 1.76 ± 0.51 m s-1; lunge-associated: 3.11 ± 0.629 m s-1) and the routine swimming speed for the sei whale (2.23 m s-1) aligned with the humpback, blue, and minke whales, while the lunge-associated swimming speed for the sei whale (2.46 m s-1) was lower than other values and both swimming speeds were higher for the fin whale (routine: 3.02 ± 0.125 m s-1; lunge-associated: 3.61 ± 0.900 m s-1). We found that swim speed stays fairly constant as the total length increases. Our statistical analysis found no effect of body size on swim speed for both routine and lunge-associated swimming (routine: *ŷ* = 0.081x – 0.605; *R2* = 0.56; *p* = 0.415; lunge-associated: *ŷ* = 0.082x – 0.869; R2 =0.08; p = 0.253; Fig. 3B). All species-level means (± se) for each of our measured kinematic and morphometric variables are given in Table 1.

*Mass-Specific Thrust Power Output*

Among the three species with a large amount of data in our dataset (humpback, blue, and minke whales), the humpback whale had the lowest mean mass-specific thrust power output (0.30 ± 0.023 Watts kg-1), with the minke whale having a slightly higher value (0.36 ± 0.028 Watts kg-1) and the blue whale having the highest value (0.48 ± 0.025 Watts kg-1). The Bryde’s (0.50 ± 0.213 Watts kg-1), sei (0.51), and fin whale (0.74 ± 0.130 Watts kg-1).

We found that mean mass-specific thrust power output increased with the transition from routine to lunge-associated swimming modes (Fig. 4A-B). There was a positive effect of swimming speed on mass-specific thrust power output during both routine and lunge-associated swimming (routine: *ŷ* = 0.693x – 2.445; *R2* = 0.72; *p* < 0.001; lunge-associated: *ŷ* = 0.601x – 1.841; R2 =0.79; p < 0.001) (Fig 4A). We also found that mean mass-specific thrust power output increases with body length for both routine (*ŷ* = 0.055x – 1.661; *R2* = 0.66; *p* = 0.006) and lunge-associated swimming (*ŷ* = 0.062x – 0.939; *R2* = 0.71; *p* = 0.013) (Fig. 4B). The species-level means (± se) for each of our measured hydrodynamic parameters are given in Table 2. The equations and statistics pertaining our models is given in Table 3.

*Drag Coefficient*

Among humpback, blue, and minke whales, the minke whale had the lowest mean drag coefficient (0.01 ± 0.001), with the humpback whale slightly higher (0.02 ± 0.002) and the blue whale having the highest value (0.04 ± 0.006). We found that the drag coefficient for both routine and lunge-associated swimming decreases with increasing swim speed (routine: *ŷ* = -0.603x – 2.452; *R2* = 0.63; *p* = 0.001; lunge-associated: *ŷ* = -0.331x – 2.819; R2 = 0.62; p = 0.001) (Fig 5A). Conversely, we found that the drag coefficient increased for both routine and lunge-associated swimming with increasing total body length (routine: *ŷ* = 0.166x – 6.256; *R2* = 0.93; *p* < 0.001; lunge-associated: *ŷ* = 0.132x – 5.724; R2 = 0.90; p < 0.001) (Fig 5B).

We found that the drag coefficient for both routine and lunge-associated swimming was not significantly related to Reynolds number and showed significant variability at the species-averaged level, especially for lunge-associated swimming.In comparison to the R-100 rigid-hulled airship model, all species displayed higher drag coefficients for both swimming modes.

*Propulsive Efficiency*

Of the three species with a large quantity of data in our dataset (humpback, blue, and minke whale), the minke whale had the highest mean propulsive efficiency (0.920 ± 0.004), with the humpback having a lower mean value (0.908 ± 0.003) and the blue whale having the lowest mean value (0.860 ± 0.006). The mean values for the Bryde’s (0.868 ± 0.022), sei (0.876), and fin whales (0.889 ± 0.018) were all near the low end of the range.

We found that mean propulsive efficiency increases with increasing swimming speed (routine: *ŷ* = 0.041x + 0.213; *R2* = 0.75; *p* < 0.001; lunge associated: *ŷ* = 0.024x – 0.196; R2 = 0.73, p < 0.001) (Fig. 6A). On the other hand, we uncovered a trend of mean propulsive efficiency decreasing with increasing body length; however, this relationship was not statistically significant (routine: *ŷ* = -0.005x + 0.046; *R2* = 0.72; *p* = 0.325; lunge-associated: *ŷ* = -0.004x – 0.065; *R2* = 0.58; *p* = 0.200) (Fig. 6B). As compared to prior studies, our results demonstrate that, regardless of body size, rorqual whales fall with the range for high efficiency (>75%) oscillatory swimmers (Fig. 7). Sub-carangiform, undulatory swimmers such as the rainbow trout (*Oncorhynchus mykiss*) are slightly lower (~60-80%) and drag-based swimmers, such as the muskrat and human, have much lower propulsive efficiencies (~20-35%) (Fig. 7). Table 4 gives additional information about each literature-based mean propulsive efficiency value.

**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). By comparison, the present study is a first approximation for many of the same kinematic variables of much larger species in their natural environment. Several parameters, such as the amplitude of heave or angle of attack of the flukes relative to the body are still generally unknown (except in rare circumstances, see 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.

*Oscillatory Frequency and Swimming Speed*

Our results illustrate that the transition from routine to lunge-associated swimming predictably results in increased oscillatory frequencies and swimming speeds as the animal prepares for a lunge (Fig. 3)(Goldbogen et al., 2011; Cade et al., 2016). Gough et al. (2019) found that the oscillatory frequency decreases with increasing body size to the power of -0.53, and with a more robust data set we have found a similar scaling exponent of -0.48. For swimming speed, we again found similar results to Gough et al. (2019) with swimming speed remaining consistent at ~2 m s-1. For both oscillatory frequency and swimming speed, the scaling exponents for routine and lunge-associated swim efforts were nearly identical, with a difference of 0.006 for oscillatory frequency and a difference of 0.001 for swimming speed. These results suggest that, regardless of body size, mysticetes prepare for a feeding lunge through similar kinematic pathways which include a consistent increase in both oscillatory frequency and swimming speed. These results for oscillatory frequency and swimming speed align with previous results for fish and odontocetes that have shown that swimming speed is heavily modulated by oscillatory frequency (Bainbridge, 1958; Fish, 1998; Gough et al., 2019).

*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 well-sampled species (Fig. 4A), 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 similar 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). Field 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).

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. As a result, we expected that power output would decrease proportionately with increasing body size. Instead, we found that mass-specific thrust increases as body length increases (Fig. 4).

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 (~5m), 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). Other studies predicted similar increases in the drag coefficient, with Lighthill (1971) first noticing a discrepancy between the expected drag coefficient based on Hoerner’s model and the observed values for swimming fish, but his conclusions did not account for changing Reynolds numbers and were based upon animals swimming at Reynolds numbers of ~105 whereas large cetaceans are routinely swimming at values of ~107. Fish (1993) included a variety of species and groups and found higher drag coefficient values for swimming animals as compared to model estimates, but they did not find an increase with increasing Reynolds number like we have for larger cetaceans. Fish (1998) analysed how the drag coefficient might vary with Reynolds number among four species of odontocetes and found that the drag coefficient should decrease with increasing Reynolds number.

For mysticetes, we did not find a significant relationship between drag coefficient and Reynolds number, but we did find a negative relationship between the drag coefficient and the swimming speed as well as a positive relationship between the drag coefficient and body length. Reynolds number is affected by both the swimming speed and the body length of an animal, so we believe that the competing impacts of swimming speed within individuals and body length between individuals are resulting in a net neutral impact of Reynolds number on drag coefficient. The effects of swimming speed on drag coefficient have been determined previously by Fish (1998) for a group of odontocetes, but ours is the first study that includes a large enough body size range to be able to parse out the effect of body size on both Reynolds number and drag coefficient.

*Propulsive efficiency vs. Swimming Velocity (m s-1)*

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 velocities (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 rorquals 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 (references here.. Croll et al. ;Acevedo-Guitteriez et al. ). Compared to the Balaenopteridae, the Balaenidae (i.e., right whales, bowhead whale) swim slowly through the water and maintain a steady speed during ram filter feeding (Simon et al. 2009) (Burns et al., 1993). The foraging strategy of the rorquals places greater energetic demands on these whales than the balaenids (see 2 recent papers by Potvin and Werth in PLOS ONE and revise accordingly).

*Propulsive Efficiency vs. Total body length (m)*

In this study, propulsive efficiency directly relates to the amount of work the animal does to propel itself forward. Previous research has shown that propulsive efficiency would remain constant or slightly increase with increasing body size (Citations). However, we found that propulsive efficiency decreases with increasing body size among rorquals (See Fig. 7B). The mechanistic explanation of this finding is that larger individuals have a slightly increased thrust generation but a greatly increased drag coefficient (Figs. 4 and 6), thus resulting in a lower propulsive efficiency, because more energy may be required to overcome drag and achieve equivalent locomotor performance.

Our analyses suggest that size is an important determinant of swimming performance in rorquals . Balaenopteridae exhibit a size range than spans an order of magnitude in body mass, from minke whales to blue whales (Lockyer 1976). 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). Interestingly in parallel with the trend of maximum speed in which intermediate animals exhibited the highest performance with lower maximum speeds for small and large animals, it was found for whales that efficiency, another locomotor performance variable, decreased above and below an optimal size (Hirt et al., 2017). Although the power requirements require to achieve maximum speed appear to be constrained at large body sizes, large rorquals may benefit from a low cost of transport (Gough et al. 2019; Williams, 1999 Phil Trans Roy Soc). Accordingly, 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. Our results are some of the first to quantify the fine-scale hydrodynamics that underlie these energetic differences between routine and energetically expensive swimming modes and include some of the largest absolute body sizes as well as a larger body size range than any previous study on swimming animals.

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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 (Routine) (m s-1)*** | ***Oscillatory Frequency (Routine) (Hz)*** | | ***Swim Speed (Lunge) (m s-1)*** | ***Oscillatory Frequency (Lunge) (Hz)*** | | ***Total Length (m)*** | ***Wetted Surface Area (m2)*** | ***Body Mass (kg)*** | ***Chord Length (m)*** | ***Fluke Area (m2)*** |
| ***Humpback*** | 31 (30) | 2.15 ± 0.066 | 0.24 ± 0.006 | | 2.85 ± 0.100 | 0.34 ± 0.011 | | 11.09 ± 0.33 | 61.50 ± 1.80 | 20537.85 ± 1363.54 | 1.05 ± 0.03 | 3.14 ± 0.18 |
| ***Blue*** | 18 | 2.27 ± 0.063 | 0.19 ± 0.004 | | 3.05 ± 0.056 | 0.24 ± 0.004 | | 22.50 ± 0.32 | 152.50 ± 2.20 | 67301.16 ± 3172.36 | 1.29 ± 0.03 | 4.71 ± 0.18 |
| ***Minke*** | 14 | 2.44 ± 0.053 | 0.40 ± 0.010 | | 2.96 ± 0.117 | 0.49 ± 0.008 | | 7.30 ± 0.34 | 25.54 ± 1.21 | 5528.91 ± 450.57 | 0.55 ± 0.03 | 0.77 ± 0.06 |
| ***Bryde’s*** | 2 | 1.76 ± 0.51 | 0.25 ± 0.005 | | 3.11 ± 0.629 | 0.42 ± 0.01 | | 12.04 ± 2.07 | 51.32 ± 16.39 | 11737.54 ± 5193.87 | 0.81 ± 0.13 | 1.97 ± 0.56 |
| ***Fin*** | 2 | 3.02 ± 0.125 | 0.25 ± 0.015 | | 3.61 ± 0.900 | 0.32 ± 0.018 | | 18.90 ± 0.43 | 109.90 ± 2.50 | 39515.13 ± 2330.65 | 1.07 ± 0.07 | 2.78 ± 0.35 |
| ***Sei*** | 1 | 2.23 | 0.22 | | 2.46 | 0.30 | | 16.62 | 92.71 | 27275.04 | 1.15 | 3.23 |

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 Power (Watts kg-1)*** | ***Drag Coefficient*** | ***Reynolds Number*** | ***Propulsive Efficiency*** |
| ***Humpback*** | 0.30 ± 0.023 | 0.02 ± 0.002 | 2.29 x 107  ±  9.9 x 105 | 0.908 ± 0.003 |
| ***Blue*** | 0.48 ± 0.025 | 0.04 ± 0.006 | 4.89 x 107  ±  1.3 x 106 | 0.860 ± 0.006 |
| ***Minke*** | 0.36 ± 0.028 | 0.01 ± 0.001 | 1.71 x 107  ±  9.9 x 105 | 0.920 ± 0.004 |
| ***Bryde’s*** | 0.50 ± 0.213 | 0.04 ± 0.012 | 2.13 x 107  ±  9.4 x 106 | 0.868 ± 0.022 |
| ***Fin*** | 0.74 ± 0.130 | 0.02 ± 0.007 | 5.46 x 107  ±  1.0 x 106 | 0.889 ± 0.018 |
| ***Sei*** | 0.51 | 0.03 | 3.54 x 107 | 0.876 |

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*** | ***R2*** | ***P – value*** |
| ***Oscillatory Frequency (Hz) vs. Total Length (m)***  ***(Figure 3)*** |  |  |  |
| Routine Effort Swimming | ŷ = -0.478x – 0.135 | 0.88 | <0.001 |
| Lunge-Associated Swimming | ŷ = -0.471x + 0.147 | 0.81 | <0.001 |
| ***Swim Speed (m s-1) vs. Total Length (m)***  ***(Figure 3)*** |  |  |  |
| Routine Effort Swimming | ŷ = 0.081x – 0.605 | 0.56 | 0.415 |
| Lunge-Associated Swimming | ŷ = 0.082x – 0.869 | 0.08 | 0.253 |
| ***Mean Mass-Specific Thrust Power vs. Swim Speed (m s-1)***  **(Figure 4)** |  |  |  |
| Routine Effort Swimming | ŷ = 0.693x – 2.445 | 0.72 | < 0.001 |
| Lunge-Associated Swimming | ŷ = 0.601x – 1.841 | 0.79 | < 0.001 |
|  |  |  |  |
| ***Mean Mass-Specific Thrust Power vs. Total Length (Figure 4)*** |  |  |  |
| Routine Effort Swimming | ŷ = 0.055x – 1.661 | 0.66 | 0.006 |
| Lunge-Associated Swimming | ŷ = 0.062x – 0.939 | 0.71 | 0.013 |
|  |  |  |  |
| ***Drag Coefficient vs. Swim Speed (m s-1)***  ***(Figure 5)*** |  |  |  |
| Routine Effort Swimming | ŷ = -0.603x – 2.452 | 0.63 | 0.001 |
| Lunge-Associated Swimming | ŷ = -0.331x – 2.819 | 0.62 | 0.001 |
| ***Drag Coefficient vs. Total Length (m)***  ***(Figure 5)*** |  |  |  |
| Routine Effort Swimming | ŷ = 0.166x – 6.256 | 0.93 | <0.001 |
| Lunge-Associated Swimming | ŷ = 0.132x – 5.724 | 0.90 | <0.001 |
| ***Propulsive Efficiency vs. Swim Speed (m s-1)***  ***(Figure 6)*** |  |  |  |
| Routine Effort Swimming | ŷ = 0.041x – 0.213 | 0.75 | <0.001 |
| Lunge-Associated Swimming | ŷ = 0.024x – 0.196 | 0.73 | <0.001 |
| ***Propulsive Efficiency vs. Total Length (m)***  ***(Figure 6)*** |  |  |  |
| Routine Effort Swimming | ŷ = -0.005x – 0.046 | 0.72 | 0.325 |
| Lunge-Associated Swimming | ŷ = -0.004x – 0.065 | 0.58 | 0.200 |
|  |  |  |  |
| ***Species-Level Propulsive Efficiency***  ***(Figure 7)*** |  |  |  |
| Odontocetes | ŷ = 0.015 + 0.811 | 0.11 | 0.420 |
| Mysticetes | ŷ = -0.003 + 0.933 | 0.51 | 0.086 |

Table 3. This table contains equations, estimates, R2 values, and p values from generalized linear mixed models for sequential figures 3-7 and 9.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***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* | See Table 1 (Routine Effort Swimming) | See Table 1 | See Table 2 | Current Study |
| ***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 |
| ***Balaenoptera borealis***  *Sei Whale* | See Table 1 (Routine Effort Swimming) | See Table 1 | See Table 2 | Current Study |
| ***Balaenoptera brydei***  *Bryde’s 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.