**Title:**

*The Physics of Whale Movement: Swimming Performance and Propulsive Efficiency of Free-Swimming Baleen Whales*

**Authors and Affiliations:**

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**Abstract:**

Mysticete (baleen) whales 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. The current study uses data from inertial whale-borne sensors coupled with morphometric measurements from UAV drones to calculate kinematic parameters related to oscillatory swimming for three whale species (minke, humpback, blue) ranging in size from 9-25m. These data have allowed us to produce the first estimates of thrust power, drag coefficient, Reynolds numbers, and propulsive efficiency for swimming baleen whales. Our results show that mass-specific thrust increases with increasing swim speed but is unaffected by body size or tail area. Our data also shows that propulsive efficiency increases with increasing swim speed but decreases with increasing body size, contrary to previous estimates for smaller animals that propulsive efficiency should increase with increasing body size. We also compared our empirically-parameterized estimates to a rigid-body model and found that the drag for a swimming animal is roughly 2-3 times higher than the simple gliding model. The relationships between kinematics, morphometrics, and hydrodynamic performance that we have shown for these massive animals ultimately confirm that oscillatory swimming remains an effective and efficient swimming mode, regardless of body size. Together with previous studies of smaller animals, our results could help us understand why this particular swimming style has proliferated so widely and remained relatively conserved over the evolutionary history of swimming.

**Introduction:**

The re-invasion of aquatic and marine environments by cetacean (whale) ancestors has resulted in a host of unique morphological adaptations that facilitate life in water. Among these is the evolution of a fusiform body shape and flattened control surfaces to move more effectively through the water (Fish, Howle, and Murray, 2008). These morphological adaptations are functionally convergent with similar structures in other swimming animals such as thunniform fish, sharks, sirenians, and the extinct ichthyosaurs (citations needed). The majority of these swimmers use an oscillatory swimming style that involves side-to-side or up-and-down movement of a tail to generate lift and thrust and overcome drag (Frank citations). What makes mysticete (baleen) cetaceans unique among oscillatory swimmers is their enormous body sizes, which they have evolved rapidly in the last five million years (Slater et al 2017 Proc B). Because of their size and the similarity of their body shape and swimming method to other aquatic and marine animals, baleen whales present an ideal system to study how swimming performance variables scale with extreme body size.

The three whale species in our study – the minke whale (*Balaenoptera bonaerensis*; citation), humpback whale (*Megaptera novaeangliae*; citation), and blue whale (*Balaenoptera musculus*; citation) – tend to have similar life histories and behaviors but range from ~9m in length for the minke whale up to ~25 for an adult blue whale (citations). Finer-scale 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 (citations). Scaling studies among baleen whales allow us to dissect how dissimilar body size and morphology interact and affect swimming kinematics and hydrodynamic performance.

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 unstable 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). However, recent technological advances are finally allowing us to study these animals *in situ* using remote sensing biologgers that allow for the measurement of uncontrolled behavior as well as the surrounding ecological context (Johnson, 2011; Goldbogen et al., 2017). Additionally, unmanned aircraft systems (UAS) are especially useful for classifying the demographic and health status of marine mammals (Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016; Johnston, 2019). When used in concert, biologging devices and UAS drones 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, Pearlstine, & Percival, 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 ~75-85% (Fish, 1998), but the upper end of the body size range remain 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 peper). 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). A propulsive efficiency of >80% for these large whales would fill in our knowledge gap for the extreme upper end of body size and support the idea that oscillatory swimming is one of the most energetically efficient swimming modes for animals of any size that are required to swim rapidly or travel long distances .

**Methods:**

*CATS Tags and UAV Technology*

The CATS camera tags (Figure 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 minutes to 26 hours (Cade et al., 2016). For more information on the tags used in this study, see Goldbogen et al. (2017).

Aerial drone photography was used to determine individual animal body size. Total length and maximum diameter were calculated by multiplying the number of pixels by the ground sampling distance (GSD) (Fearnbach et al., 2012).

(1)

(2)

with *L, npix*, *a*, *lfoc*, *Sw*, and *Pw* corresponding to total length of the animal (m), number of pixels, altitude (m), focal length (mm), width of sensor size (mm), and width of the image resolution in pixels, respectively. The width was used for the sensor size and image resolution because the whales were captured full frame widthwise (Gough et al., 2019).

*Morphometric Measurements*

In ImageJ, the scale was set by creating a straight line from the notch in the middle of the fluke to the tip of the nose and entering the total length into known distance. The fluke area was calculated by carefully drawing a polygonal outline of the fluke to measure the area. Chord length was measured by drawing a straight line from the notch in the fluke to the top of the fluke (not the peduncle). These measurements are shown in Figure 2.

*Mathematical Calculations*

We digitized models from Chopra and Kambe (1976) to find the essential parameters needed for our swimming kinematic calculations and to obtain numerical relationships for the reduced frequency (:

(3)

where ω is equal to the radian frequency of the motion (equal to 2π*f*, where *f* is the frequency in Hz), *C* is the wing chord, and *U* is swimming velocity (m s-1). Then we calculated (), the proportional feathering parameter:

(4)

which is the ratio of the maximum angle the wing 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). The coefficient of thrust ( is given by:

(5)

where is equal to the total mean thrust, is the density of seawater, is the fluke area, and is the heaving amplitude. The efficiency ( is given by:

(6)

where is the mean rate of oscillation (Chopra and Kambe, 1976, 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 swimming speed (*U*) in m s-1 and fluking frequency (*f*) in Hz, 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 thrust power output (*PT*) is given by:

(7)

where *ρ* is the density of seawater, *C­T* is the coefficient of thrust, *U* is swimming velocity (m s-1), *Fa* is the planar surface area of the fluke (m2), *h* is amplitude of heave (m), and *C* is the chord length (m). The equation for the dimensionless drag coefficient (*CD*) is given by:

(8)

where *Sa* is equal to the surface area of the body (*m2*). The dimensionless Reynolds number (*Re*) is defined by:

(9)

where *L* is the individual’s total length (m) and *v* is the kinematic viscosity of sea water. Propulsive efficiency was calculated through digitation of images in Chopra and Kambe 1976.

*Normal vs. Maximum Effort Swimming*

The relationship between normal and maximum effort swimming can be analyzed where normal 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 ten seconds 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, normal swimming kinematics and maximum swimming kinematics were sorted from one another to be individually analyzed and compared.

*Comparison to a Simple Rigid-Body Model*

We created a simple rigid-body model comparison for our data using an equation devised by Hoerner (1962; Blevins, 1983) that determines the relationship between drag coefficient and Reynolds number for a simple gliding body of a given shape. Hoerner’s equation for drag force can be found by first solving for the drag coefficient with respect to time (*CD*(*t*)) which is given by:

(10)

where is equal to the correction factor for an undulating body (1 for rigid-body simulations), is the animal’s body length (m), is the swimming speed (m s-1) with respect to time, is the kinematic viscosity, and is the maximum body diameter (m). We can then plug the resultant into the equation for drag force () which is given by:

(11)

where is the mass density of seawater and is the wetted body area which is approximated using body mass (Fish, 1993).

We plotted drag coefficient vs. Reynolds number for the simple Hoerner model predictions with our real, empirical estimates of heaving, full body animals. This permitted us to examine the comparison of drag on a rigid, gliding body with no appendages to the drag on a swimming animal with morphological features and control surfaces present.

*Statistical Analyses*

We investigated intra-and-interspecific relationships between and among the animals (n=63) in the study. We compared hydrodynamic performance variables (thrust power output, drag coefficient, Reynolds number, propulsive efficiency) 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 normal effort swimming speed (m s-1) (Figure 3). Linear fit regressions were performed for X (Figure X), Y (Figure Y), and Z (Figure Z)...etc. GLMMs for propulsive efficiency (Figure 6) depending on normal effort swimming speed (m s-1) and total body length (m) were constructed with identical details and parameters as Figure 3. Finally, we show a plot comparing the propulsive efficiencies of our empirical animals, to captive odontocetes (Fish, 1998), to rainbow trout (citation), tuna, manatee, and a human dolphin kick (citation) (Figure 7).

**Results:**

The species-level means (± se) for each of our measured hydrodynamic variablesand morphometrics are given in Table 1.Figure 3 shows that mean mass-specific thrust is constant at increasing body size and increases linearly as swimming speed increases. sswimmingBoth effort levels show slight visual increases with increasing body size but only normal effort was found to be significant (Table 2). At any given body size, the mean-mass specific thrust increased with the transition from normal 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 2).

Figure 6 shows our empirically-derived data for drag coefficient against Reynolds number for swimming whales as well as the rigid-body model regression using 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 (m s-1) (Fig 7A) and total body length (m) (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 study species against other swimming animals showed that all oscillatory swimmers (mysticete cetaceans, odontocete cetaceans, tuna, manatee, pinnipeds) were highly efficient at ~80% or higher (Figure 8). Other styles of swimming were lower, with subcarangiform undulatory swimmers averaging ~75% and drag-based paddling swimmers averaging ~25%.

***Discussion:***

*Mean mass-specific thrust: Swimming velocity (m s-1) and swimming effort*

We predicted that the blue whale will have the largest mass-specific thrust at normal effort because of its sheer size, and we anticipated that the minke would not need nearly as much mass-specific thrust as the other two species because of its overall smaller, streamlined physique. In Figure 3, we see mass-specific thrust and its relation to swimming velocity, and we found that the mass-specific thrust for normal fluking (at lower velocities of 1-3 m s-1) are very similar for all three species.

We produced Figure 4B in order to explore more into mass-specific thrust and how it is different at different speeds (i.e. normal and maximum effort swimming). We expected and found that the mean-mass specific thrust increases with the transition from normal to maximum effort swimming. Additionally, we saw that the thrust increases more rapidly as you increase body length. We contribute this to larger whales having to produce more power than smaller whales when they work to move or effectively forage at a velocity classified as maximum effort swimming.

Body size becomes less important when we look at the increase in thrust from normal to max effort swimming, suggesting that all of our animals are increasing their thrust output for similar reasons and in similar ways. All of the species included in our study are lunge feeders, meaning they feed by opening their mouth like a parachute and engulfing a large volume of water into an expansible throat pouch (Cade et al., 2016; Cade et al., 2019). Empirical data (Cade et al., 2019) and hydrodynamic models (citation) suggest that animals begin these lunges at high speeds (3.5-5 m s-1) in order to overcome heightened drag and move through the prey patch entirely on momentum (Cade et al., 2016; Cade et al., 2019). Our results give an approximation for how much thrust may be required for animals of different sizes to generate the momentum necessary to complete their feeding lunges effectively. This increase tends to be an approximate doubling of the thrust generated during normal swimming.(Cade et al., 2016; Cade et al., 2019).

However, during maximum effort fluking, we see that M. novaeangliae must provide more mass-specific thrust to reach an equivalent foraging velocity as B. musculus. On the other hand, B. bonaerensis needs the least amount of thrust to achieve a similar maximum effort swimming velocity. We inferred that this relationship has to do with the body shape and the style of each whale species – the streamlined blue and minke whales must have a large enough mass-specific thrust power to offset their body size and shape to gain enough momentum and speed to glide and forage effectively on slow moving prey. In contrast, the humpback must work harder and provide more thrust to propel its shorter, bulkier body frame up to an effective foraging velocity to participate in group feeding on slow or fast moving prey.

*Mean mass-specific thrust: Morphology*

For lift-based oscillatory swimmers, thrust is produced via the combination of lift and drag forces produced by control surfaces such as the flippers and tail flukes (Goldbogen, Fish, and Potvin; 2016). Maximum thrust and high propulsive efficiency is typically achieved with a broad, semi-lunate paddle/fluke area that is attached to the body through a constricted peduncle region (Fish, 2004). We understand that there are morphological variations in rorquals across scale (Woodward et al. 2006; Kahane-Rapport & Goldbogen, 2018). Therefore, we investigated how the mass-specific thrust would calibrate with the scaled relationship of fluke area (Figure S1). We expected that humpback whales will have the largest mass-specific thrust per scaled fluke span because their flukes are much larger than the other species in the study. Interestingly, we found a similar trend with total body length that mass-specific thrust increases only slightly as scaled fluke area increases (Figure 4A). We think the humpback’s large flukes do not need to produce as much thrust power because humpbacks possess other unique control surfaces that allow them to use less thrust to be more maneuverable. Humpback whales are able to feed on krill and small fishes, but social foraging may allow them to forage more efficiently than foraging individually.

Overall, our results show that thrust production on a mass-specific basis is greatest in the largest animals and scales in relation to body size and not necessarily appendage size or shape.

Drag coefficient vs. Reynolds number for empirical and Hoener calculations

In comparison to our tagged animals, the 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 1962; Blevins, 1993). Our goal was to compare the drag coefficients found for our fluking animals to modeled values based upon computational analysis of the R-100 airship all against associated Reynolds numbers. These modeled values suggest that for a minke whale (~9m), the drag coefficients for fluking and non-fluking swimming should be very similar, but that the difference between these coefficients should increase for larger animals, culminating in a three-fold difference for a blue whale (~22m). We have compared our drag coefficients against the CFD analysis in Figure 3 and found that the model holds quite well across the entire rorqual size range. (Hope to get Jean’s input here, too)

*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 4 shows the propulsive efficiencies of the three species in our study. It corresponds to lower velocities or normal effort swimming. 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.

*Total body length (m)*

In this study, propulsive efficiency directly relates to the rate at which energy is taken in by the whale as food and the amount of work it does to propel itself forward. We predicted that *B. musculus* would have the greatest propulsive efficiency because of its streamlined body shape and high fineness ratio, while we predict *B. bonaerensis* has a lower propulsive efficiency due to its similar shape but lower fineness ratio. We think *M. novaeangliae* and its rotund body shape and low fineness ratio would have the lowest propulsive efficiency. However, we see that propulsive efficiency decreases with increasing body size among rorquals (See Figure 5.2). This suggests that the smaller, minke whales expend less energy to reach the same level of performance as the other two species. Blue whales must expend more energy using their relatively small flippers and flukes to make a turn while the humpback can utilize its unique morphology of large flippers and flukes to quickly turn and move more efficiently than the blue whale.

Still need propulsive efficiency comparisons to rainbow trout, tuna, mantee, and human dolphin kick (figure and table).

**Conclusion:**

The present study is one of the first to quantify the swimming performance of baleen whales *in situ.* For Antarctic minke, blue, and humpback whales, we were able to quantify thrust power, drag coefficient, Reynolds number, and propulsive efficiency for each individual flukebeat during tag deployment. We found the size of the fluke - the thrust generation surface - had little impact on mass-specific thrust production across individuals and species. Rather, the total body size most strongly correlates with thrust. In addition, we compared empirical drag coefficient calculations to lab-rooted Hoerner model calculations in an attempt to obtain improved estimates of animal drag which will contribute to the development of numerical methods of calculating drag for specific whale morphologies. We analyzed the relationship between propulsive efficiency and swimming speed; finding that it increases with higher swimming velocities and that all cetaceans follow a similar trend where propulsive efficiency increases with the square root of swimming velocity. We found propulsive efficiency to be inversely related to body size, and lastly, we were able to compare the propulsive efficiencies of different species.

These findings improve our understanding of swimming at the upper extremes of body size, where small losses in efficiency could have far-reaching consequences for the energetics and continued fitness of a species. Altogether, studying a whale’s hydrodynamic performanceis just a small piece in understanding the energetics and evolution of gigantism at sea.

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**Competing Interests:**

We have no competing interests to report.

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**Figures/Legends**

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | ***Hydrodynamic Calculations*** | | | | |  | ***Morphometrics*** | | | |  | |
| ***All Whales*** | ***Number of Individuals*** | ***Mass-Specific Thrust*** | ***Drag Coefficient*** | ***Reynolds Number*** | ***Propulsive Efficiency*** | ***Fluke Area*** | | ***Chord Length*** | ***Total Length*** | | |
| ***Minke*** | 14 | 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 | 0.766 | | 0.552 | 7.30 | | |
| ***Humpback*** | 31 | 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 | 3.140 | | 1.05 | 11.09 | | |
| ***Blue*** | 18 | 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 | 4.708 | | 1.29 | 22.50 | | |
|  |  |  |  |  |  |  | |  |  |  | | | |

Table 1. Metadata related to each species. All animals (n=63) included have been tagged and their morphometrics analyzed with UAV. All values are given as the mean of all tailbeats in a deployment. *Mass-specific thrust* is shown as the log(N/kg), *Drag Coefficient, Reynolds Number,* and *Propulsive Efficiency* are dimensionless. Finally, *Fluke Area* is shown in m s-1 and *Chord Length and Total Length* are shown in m. (Still need to do +- standard error)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **GLMM equation** | **Estimate** | **P - value** | **R2** |
| **Mean Mass-Specific Thrust Power**  **(Figure 1)** |  |  |  |  |
| Speed (m s-1) | y = 0.834x – 2.872 | 0.834 | *< 0.001* | 0.79 |
| Total Length (m) | y = 0.027x – 1.154 | 0.027 | *0.004* | 0.07 |
| 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 2)** |  |  |  |  |
| Normal Effort | y = 0.025x – 0.637 | 0.025 | *0.016* | 0.11 |
| Maximum Effort | y = 0.030x – 1.571 | 0.03 | 0.201 | 0.33 |
|  |  |  |  |  |
| **Drag Coefficient vs. Total Length (m)**  **(Figure 3)** |  |  |  |  |
| Empirical (*in situ* calculations) | y = 0.162x – 6.115 | 0.162 | *<0.001* | 0.88 |
| CFD (lab rooted calculations) | y = -0.007x – 4.940 | -0.007 | 0.131 | 0.99 |
|  |  |  |  |  |
| **Propulsive Efficiency**  **(Figure 4)** |  |  |  |  |
| 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 2. This table contains equations, estimates, R2 values, and p values from generalized linear mixed models for sequential figures 1-4.

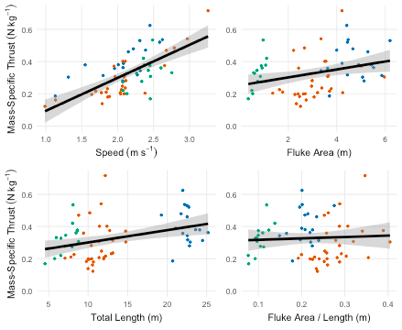


Figure 1. Relationships between log-transformed mean Mass-Specific Thrust (N kg-1) and Swimming Speed (m s-1), Total Length (m), Fluke Area (m2), and Fluke Area divided by Total Length (m). The solid black line denotes the observed regression and grey bars denote the standard error. We calculated the regression for all four plots using a statistics linear model command in RStudio. The green dots represent Antarctic minkes, the orange dots represent humpbacks, and the blue dots represent blue whales.

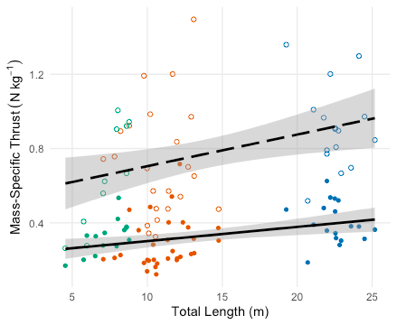


Figure 2. Relationships between log-transformed mean Mass-Specific Thrust (N kg-1) and Total Length (m). We analyzed the relationship between normal effort thrust production (free-stream swimming) and maximum effort thrust production (foraging or breaching). The solid black line and full dots denote the observed regression for normal effort swimming and grey bars denote the standard error. The dotted line and transparent dots denote the observed regression for maximum effort swimming and grey bars denote the standard error. We calculated the regression using a statistics linear model command in RStudio. The green dots represent Antarctic minkes, the orange dots represent humpbacks, and the blue dots represent blue whales.

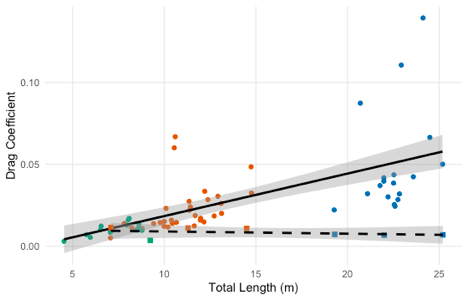
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Figure 3. Relationships between the dimensionless Drag Coefficient and Total Length (m). The solid black line and circle shaped dots denote the observed regression for this study’s empirical drag coefficient calculations for all animals (n=63) and grey bars denote the standard error. The dotted line and square dots denote the observed regression for the lab rooted, CFD drag coefficient calculations for animals (n=7, (one Antarctic minke, three humpbacks, and 3 blues)) and grey bars denote the standard error We calculated the regressions using a statistics linear model command in RStudio. The green dots represent Antarctic minkes, the orange dots represent humpbacks, and the blue dots represent blue whales. Regression, R2, and p values can be found in Table 3st.

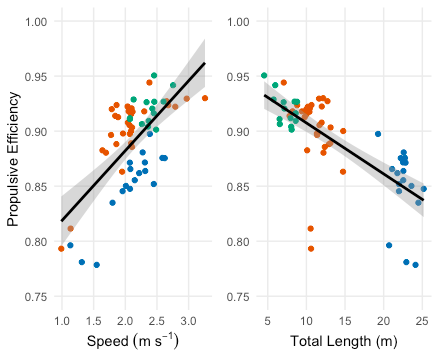
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Figure 4. Relationships between the dimensionless Propulsive Efficiency and Swimming Speed (m s-1) and Total Length (m). The solid black line denotes the observed regression and grey bars denote the standard error. We calculated the regression for the two plots using a statistics linear model command in RStudio. The green dots represent Antarctic minkes, the orange dots represent humpbacks, and the blue dots represent blue whales.