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Hydrodynamic properties of fin whale flippers predict maximum rolling performance

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Abstract

Maneuverability is one of the most important and least understood aspects of animal locomotion. The hydrofoil-like flippers of cetaceans are thought to function as control surfaces that effect maneuvers, but quantitative tests of this hypothesis have been lacking. Here we construct a simple hydrodynamic model to predict the longitudinal-axis roll performance of fin whales, and we test its predictions against kinematic data recorded by on-board movement sensors from 27 free-swimming fin whales. We found that for a given swimming speed and roll excursion, the roll velocity of fin whales calculated from our field data agrees well with that predicted by our hydrodynamic model. Although fluke and body torsion may further influence performance, our results indicate that lift generated by the flippers is sufficient to drive most of the longitudinal-axis rolls used by fin whales for feeding and maneuvering.

Keywords

fin whale, roll, swimming, kinematics, maneuvering

Introduction

Understanding the relationship between morphological design and locomotor performance remains a central challenge in the field biomechanics ([Webb, 1984](#)). Simple physical models and engineering analogues have been used to approximate different aspects of terrestrial ([Biewener, 2003](#)), aerial ([Ellington, 1984](#); [Pennycuick, 1975](#)), and aquatic locomotion ([Alexander, 2005](#); [Daniel, 1984](#)), even though these models do not capture the full complexity of natural systems ([Altshuler et al., 2005](#)). Maneuvers, which by nature are rapid and transient, may also be amenable to simple modeling as a first approximation, and this approach could improve our understanding of the links between morphology and critical life functions such as defending territories, capturing prey, or escaping predators.

Large aquatic animals provide a unique opportunity to study locomotor performance and maneuverability because they can be instrumented, allowing *in situ* body kinematics to be remotely measured ([Goldbogen et al., 2013](#); [Miller, 2004](#); [Watanabe et al., 2015](#)). The performance of this diverse assemblage of organisms is highly influenced by the anatomical geometry of the control surfaces used to generate lift during swimming ([Fish, 2002](#); [Fish, 2004](#); [Fish and Lauder, 2006](#)). In whales and dolphins (Cetacea), these control surfaces include flukes and flippers with geometries and hydrodynamic properties similar to those of engineered wings ([Fish, 2004](#); [Weber et al., 2014](#)). A central paradigm of cetacean locomotion is that posteriorly positioned flukes are oscillated to generate thrust ([Fish et al., 2014](#)), while the anteriorly located flippers create lift used for maneuvers, stability and the maintenance of body trim ([Fish, 2002](#); [Fish et al., 2003b](#); [Weber et al., 2009](#)). Given that their locomotion relies on separate propulsion and control surfaces ([Fish, 2002](#)), and the evidence that their vertebral design may limit flexibility ([Long et al., 1997](#); [Woodward et al., 2006](#)), large cetaceans may behave more like rigid-hulled objects, and their maneuvering performance can be modeled as such.

A roll is a rotation about the longitudinal axis and is a common maneuver exhibited by many flying and swimming animals ([Fish, 2002](#); [Fish et al., 2003a](#); [Fish et al., 2006](#); [Fish et al., 2007](#); [Norberg, 1990](#); [Schilstra and Hateren, 1999](#)). Rolls form the basis for more complex maneuvers, such as banked turns ([Schilstra and Hateren, 1999](#)), and are used as building blocks for intricate maneuvering trajectories. Rolling performance affects many functions including reorientation of the visual field ([Goldbogen et al., 2013](#)), prey capture and feeding ([Fish, 2002](#); [Fish et al., 2007](#)), cleaning ([Limbaugh, 1961](#)), social interactions ([McBride and Kritzler, 1951](#)), and dislodging parasites ([Fish et al., 2006](#); [Weihs et al., 2007](#)). Baleen whales in the family Balaenopteridae, or rorquals, frequently roll during feeding events ([Goldbogen et al., 2006](#); [Kot and Borda, 2014](#)). Rorqual whales can perform 360° barrel rolls, but more often use 90° lateral rolls or 180° inverted rolls for feeding and maneuvering ([Kot and Borda, 2014](#)). It is unknown why rorquals roll during feeding, but given their dependence on high prey density ([Goldbogen et al., 2015](#)), rolling is thought to increase the efficiency of foraging by facilitating prey capture ([Goldbogen et al., 2013](#); [Potvin et al., 2010](#)).

It is hypothesized that rolling maneuvers are primarily controlled by the flippers, but few studies have examined this mechanism. We tested this hypothesis by developing a simple model that incorporates empirically measured hydrodynamic performance of fin whale (*Balaenoptera physalus*) flipper morphology ([Weber et al., 2014](#)) to predict rolling performance. The predictions made from the model were compared to kinematic data measured by multi-sensor tags attached to the body with suction-cups and equipped with inertial movement units.

Materials and Methods

Hydrodynamic model

Using previously published morphological and hydrodynamic measurements of fin whales (Weber et al., 2014), we constructed a simple hydrodynamic model to predict longitudinal axis rotational acceleration (α ; Figs. 1A-C, Table 1):

$$\alpha = \frac{\tau}{I} \quad (1)$$

where I is the moment of inertia and τ is the flipper-generated torque. Given the complex shape of a whale's body we estimated the moment of inertia three ways: as a cylinder, two half ellipsoids joined at the bases, and two cones joined at the bases (Fig. 1B), using the following equations:

$$I_{cylinder} = \frac{1}{2}mR_{body}^2 \quad (2)$$

$$I_{ellipsoid} = \frac{2}{5}mR_{body}^2 \quad (3)$$

$$I_{cones} = \frac{3}{10}mR_{body}^2 \quad (4)$$

where R_{body} is the radius of the body measured at the maximum width, and m is the mass estimated using the equation for northern hemisphere fin whales ([Lockyer, 1976](#)):

$$m = 0.0015L_{body}^{3.46} \quad (5)$$

The torque (τ) is calculated as:

$$\tau = R_{force} \times F_{total} \quad (6)$$

where R_{force} is the radius at which the force is applied (Fig. 1A). Because the center of pressure along the surface of a balaenopterid flipper is not known, we approximated R_{force} as R_{body} plus half the length of the flipper ($L_{flipper}$). The total force applied (F_{total}) is the sum of maximum upwards force (F_{up}) and the maximum downwards force (F_{down}) the flippers can produce on opposite sides of the body (see Fig. 1A; Table 1). These forces were calculated using the lift equation:

$$F = \frac{1}{2} \rho A C_L V^2 \quad (7)$$

where ρ is density, A is the planar area of the flipper, C_L is the coefficient of lift (measured empirically by Weber et al. (2014)), and V is the velocity of the oncoming flow. The maximum torque is achieved when one flipper generates the maximum upwards force ($F_{max,up}$, $C_{L,max}$), and the other flipper generates the maximum downwards force ($F_{max,down}$, $C_{L,min}$; Fig. 1A). Since the forces depend on the velocity of the oncoming flow (V), we calculated the angular acceleration at swimming speeds of 1 m s⁻¹, 2 m s⁻¹, 3 m s⁻¹, and 4 m s⁻¹. This range of speeds is commonly used by foraging fin whales (Goldbogen et al., 2006), but remains well below the reported maximum for the species (10 m s⁻¹, [Bose and Lien, 1989](#)).

Each roll consists of an acceleration phase and deceleration phase. We estimated maximum angular velocity (ω) achieved during acceleration phases of 15°, 45°, 75°, 105°, 135°, and 165° using the following equation:

$$\omega = \sqrt{2\alpha\theta + \omega_i^2} \quad (8)$$

where α is assumed to be constant, θ is the angular deflection during the acceleration phase, and the initial angular velocity (ω_i) is zero ([Halliday et al., 2014](#)).

Because angular velocity is highly influenced by moment of inertia, at a given swimming speed the maximum angular velocity of the species is expected to be close to that of its smallest individuals (see supplementary materials for derivation). The inputs of the model, measured from a small adult fin whale, are reported in Table 1 and detailed predictions can be found in the supplementary materials (Table S1).

Roll velocity measurements

Between 2010 and 2015 we deployed digital acoustic recording tags (DTAGs; $n = 25$, 124 hours and 43 minutes; Johnson and Tyack, 2003) and Customized Animal Tracking Solutions (Queensland, Australia; Oberstdorf, Germany) tags (CATS; $n = 2$, 24 minutes) on fin whales in both the Pacific Ocean (Southern California Bight) and the Atlantic Ocean (Stellwagen Bank). The whales were approached in a rigid-hulled inflatable boat and tagged using a 6 m carbon-fiber pole. The tags were affixed to the dorsal surface of the animal with suction-cups. The tags were equipped with accelerometers (DTAGs: 50, 200, or 500 Hz; CATS: 40 Hz), magnetometers (DTAGs: 50, 200, or 500 Hz; CATS: 40 Hz), and depth sensors (DTAGs 50, 200, or 500 Hz and CATS: 10 Hz). Additionally, the DTAGs included hydrophones (up to 64 kHz) while the CATS tags included onboard video cameras (720 p, 24 frames s^{-1}), and gyroscopes (40 Hz). After a period of time, the tags released from the whale and floated to the sea surface where they were retrieved. All of the procedures were conducted under permits from the U.S. National Marine Fisheries Service Permitting Authority and were approved by the Institutional Animal Care and Use Committees at Stanford University and Oregon State University.

Roll angle about the longitudinal axis of the body was calculated from the accelerometers and smoothed using a low pass Butterworth filter with a cutoff frequency of 0.15 Hz (0.5×0.3 Hz stroke frequency, from Goldbogen et al., 2006). Roll velocity was calculated by taking the derivative of a third order interpolation spline fit to the roll angle. Pitch angles were calculated using the accelerometers and the swimming speed was estimated by calibrating measurements of the background noise recorded by the hydrophones or video camera microphones, against the orientation-corrected depth rate (for pitch angles $>45^\circ$ and depth $>10\text{m}$; Goldbogen et al., 2006; [Simon et al., 2012](#)). A representative sequence of rolls is presented in Fig. 2. To account for differences in tag placement and hydrophone sensitivity we used a separate calibration curve for each deployment. Six deployments were excluded from the analysis because there were few segments with steep pitch angles, or there was not a strong positive correlation between corrected depth rate and flow noise. The calibration curves for the remaining 21 deployments had an average correlation coefficient of 0.63 ± 0.05 s.e.m. Calculations were performed in MATLAB (Mathworks Inc., Natick, MA) and Python (Python Software Foundation) programming languages.

We defined rolls as trajectories where the roll velocity starts and ends at zero, and the angle rolled was $>45^\circ$. This stands in contrast with previous studies that identified rolls as rotational deviation from an upright, cruising posture and were intended to relate rolling behavior to feeding events (Goldbogen et al., 2006; [Goldbogen et al., 2013](#); Stimpert et al., 2007). To minimize the errors due to gimbal lock ([Johnson and Tyack, 2003](#)) we excluded rolls where the maximum pitch angle was $>60^\circ$ and $<-60^\circ$. For each roll event we measured the average swimming speed and the maximum instantaneous roll velocity. We compared the maximum angular velocity of rolls with acceleration phases of different durations (15° , 45° , 75° , 105° , 135° , and $165 \pm 15^\circ$), to the predictions made with the hydrodynamic model.

Results and Discussion

We identified 3199 rolls performed by 27 fin whales. Because our method of estimating swimming speed was only reliable at depths below 10 m, we discarded 1099 rolls. We discarded an additional 426 rolls where the estimate of swimming speed was not reliable. Of the remaining 1674 rolls performed by 21 whales, we identified 1567 rolls where the angular deflection (θ) was $90 \pm 45^\circ$, 86 rolls where the angular deflection was $180 \pm 45^\circ$, 1 roll where the angular deflection was $270 \pm 45^\circ$, and 16 rolls where the angular deflection was $360 \pm 45^\circ$. Additionally, we found 4 rolls where the angular deflection was $>405^\circ$ (Table S2).

The hydrodynamic model was not intended to predict exact roll velocity, and there are several mechanisms by which a whale could perform a slower-than-predicted roll. Whales have methods of modulating lift production by varying the angle of attack and sweep of the flippers ([Cooper et al., 2008](#); [Fish and Battle, 1995](#); [Weber et al., 2014](#)), and this introduces a behavioral component to the measured roll velocities. Additionally, rorqual whales change their shape during engulfment ([Goldbogen et al., 2010](#)), effectively increasing their diameter and mass and theoretically slowing their roll velocity ([Goldbogen et al., 2013](#)). To estimate the success of our model, we report the percentage of rolls that occur at or below the predicted maximum.

The majority of the measured rolls had angular velocities that were slower than the maximum predicted by the hydrodynamic model (Fig. 3). This suggests that the lift generated by the flippers is sufficient to drive the longitudinal-axis rolls used by fin whales for feeding and maneuvering. Of the 1661 rolls with acceleration phases ranging from 0° to 180° in duration, the conical model for moment of inertia predicted 92.8% of the measured roll velocities. This pattern held when the analysis was repeated using the more conservative estimates for moment of inertia (ellipsoid model: 85.4%; cylindrical model: 78.7%) and when

using the 95% confidence intervals for swimming speed (conical model: 58.0% to 99.6%; ellipsoid model: 48.6% to 98.7%; cylindrical model: 41.8% to 96.8%). The true moment of inertia is probably best represented by the conical or ellipsoid model, or an intermediate version. The cylindrical model was the simplest model used, and likely resulted in overly conservative predictions of maximum roll velocity.

Despite its simplicity, our hydrodynamic model predicts the maximum angular velocity across a range of typical fin whale swimming speeds and roll durations. The range of recorded fin whale size and morphology is extensive ([Goldbogen et al., 2010](#)), with the largest individuals reaching lengths of up to 23 m and masses of up to 70,000 kg ([Lockyer, 1976](#)), and a substantial amount of temporal and geographic variation ([Lockyer and Waters, 1986](#)). The individual used for the hydrodynamic model calculations was smaller than average (14.4 m, estimated mass 15,300 kg; [Weber et al., 2014](#)). Because of the whale's smaller proportions and the inverse relationship of body size to maximum roll velocity, the calculations likely represent the upper boundary of adult fin whale rolling performance for a given swimming speed. One of the drawbacks to the tag data was that there was no information about tagged whale size or flipper morphology, and both are factors that would strongly influence the rolling performance calculated with the model. Body mass is directly related to the moment of inertia, whereas flipper area is related to the lift and thus the force necessary to effect the rotation. Although 133 of the 1661 rolls with acceleration phases lasting between 0° and 180° were faster than the maximum predicted by the conical hydrodynamic model, these rolls may have been performed either by smaller whales or whales with relatively large flippers. We did find individual differences in roll performance among whales that could be a result of morphological variation. In spite of the high uncertainty, flow noise measurements remain a common and effective method for estimating swimming speed in whales ([Laplanche et al., 2015](#); [Simon et al., 2012](#)). Although direct

measurement of water flow is now possible through the use of paddle-wheels ([Shepard et al., 2008](#); [Watanabe et al., 2011](#)), these have yet to be widely incorporated in suction-cup attached tags, where the placement of the tag on the animal is more variable. These uncertainties underscore the importance of developing new methods to measure the size, shape, and swimming speed of tagged whales, if this type of hydrodynamic model is to be refined further.

Longitudinal axis rolls are a well-documented and important component of rorqual whale locomotion ([Goldbogen et al., 2006](#); [Goldbogen et al., 2013](#); [Stimpert et al., 2007](#)). Previous studies have suggested that fin whales mostly perform rolls of less than 90° ([Goldbogen et al., 2006](#)). Our data show that fin whales also perform inverted rolls (180°) and barrel rolls (360°). As would be expected by the size differences, fin whale rolls attain higher angular velocities (average across all swimming speeds: $39 \pm 3^\circ \text{ s}^{-1}$ for 16 rolls of $360 \pm 45^\circ$) than those previously measured in rolling blue whales (average: $33 \pm 8^\circ \text{ s}^{-1}$ for 33 rolls of 360°; from [Goldbogen et al., 2013](#)). As onboard tag databases expand to include more species and individuals, there will be an increased opportunity for rigorous comparisons of roll performance across body size and shape. Different rorqual species demonstrate a wide range of body sizes (minke whales to blue whales; [Lockyer, 1976](#)), body shapes (ellipsoid humpback whales vs conical fin whales; [Goldbogen et al., 2010](#)), and flipper morphology (humpback whale flippers vs other species; [Fish and Battle, 1995](#); [Miklosovic et al., 2004](#)), which are all factors that impact maneuverability. A new development in tag design is the incorporation of multiple cameras that will allow for a detailed analysis of flipper and fluke kinematics during roll performance ([Goldbogen et al., 2013](#)). The use of cameras combined with the techniques of our current work will also help to elucidate the function of roll events during lunge feeding by providing simultaneous information regarding flipper orientation, visual cues, prey, and gape ([Goldbogen et al., 2016](#)).

Cetacean flippers evolved from the tetrapod forelimb in whale ancestors as an adaptation for aquatic locomotion ([Fish, 2002](#); [Fish, 2004](#)). Similar to engineered wings, flippers have a fusiform cross-section and a swept-back planform, and this morphological design enables enhanced lift generation relative to drag ([Weber et al., 2009](#)). The highly tapered, high aspect ratio flippers of fin whales yield greater lift-to-drag characteristics and a greater coefficient of lift compared to other large cetaceans that have more paddle-like flippers ([Weber et al., 2014](#)). The results from this study suggest that the flippers are capable of producing the long-axis torque used by fin whales to perform most rolls across a broad range of angular displacements. Although cetaceans may be able to generate additional torque to enhance roll performance through torsion of the flukes ([Fish, 2002](#); [Fish et al., 2006](#)), this ability may be limited in larger cetacean species that have restricted spine and body flexibility ([Long et al., 1997](#); [Woodward, 2006](#)). The extent to which the flippers and flukes work in concert to enhance maneuvering performance in large cetaceans requires further investigation, however, according to this model, the flippers can generate enough torque to effect the measured roll velocities.

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Competing interests

The authors declare no competing interests.

Author contributions

P.S.S. refined the model, analyzed the data, and wrote the manuscript. D.E.C. devised the procedures used to prepare the whale tag data for analysis, calculated swimming speeds, contributed to the data collection, and assisted with the manuscript preparation. F.E.F. and J.P. designed the hydrodynamic model, conceived the study, and assisted with the manuscript preparation. J.A.G. oversaw the whale tag data collection, conceived the study, and assisted with the manuscript preparation. A.S.F. and J.A.G. conceived the camera-movement tag design built by CATS. Tagging and fieldwork operations were performed by A.A., A.S.F., J.A.G. and J.C..

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Table

Table 1: Hydrodynamic model inputs, from Weber et. al. 2014

body length	L_{body}	14.4 m
body diameter	D_{body}	2.63 m
flipper area	A	0.1195 m ²
flipper length	$L_{flipper}$	1.48 m
coefficient of lift, max	$C_{L,max}$	1.45
coefficient of lift, min	$C_{L,min}$	-1.04
density	ρ	1024 kg m ⁻³

Figures

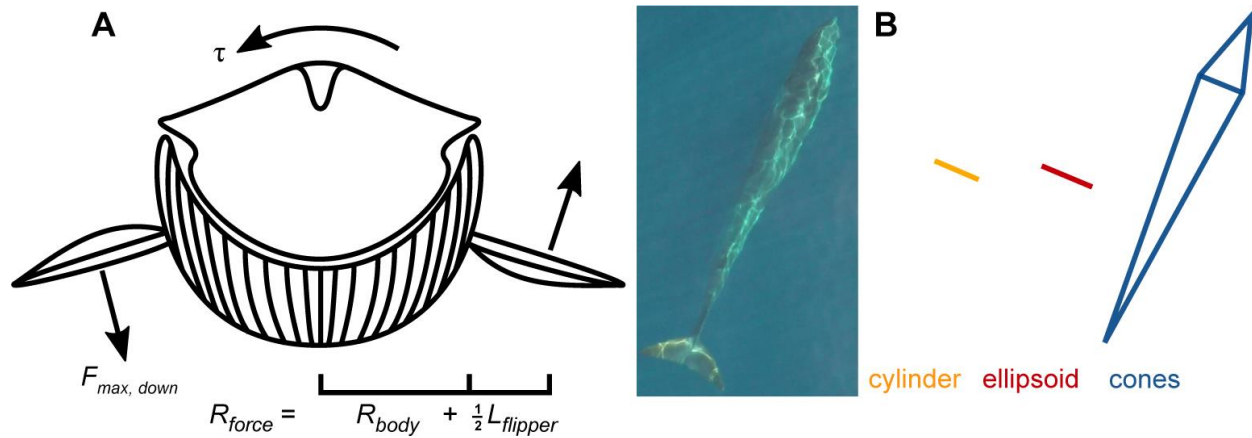


Figure 1. A simple hydrodynamic model to predict roll performance in fin whales. A) The whale was modeled as a rigid body and torque was calculated as cross product between radius and total force produced. The total force was the sum of the maximum upward force produced by one flipper, and the maximum downward force produced by the other flipper. B) An aerial view of a fin whale demonstrates the shape of the body. We used cylindrical, ellipsoid, and conical models to estimate the moment of inertia about the longitudinal axis. The image was taken immediately before the whale performed a 90° roll while lunge feeding (supplementary materials Video S1).

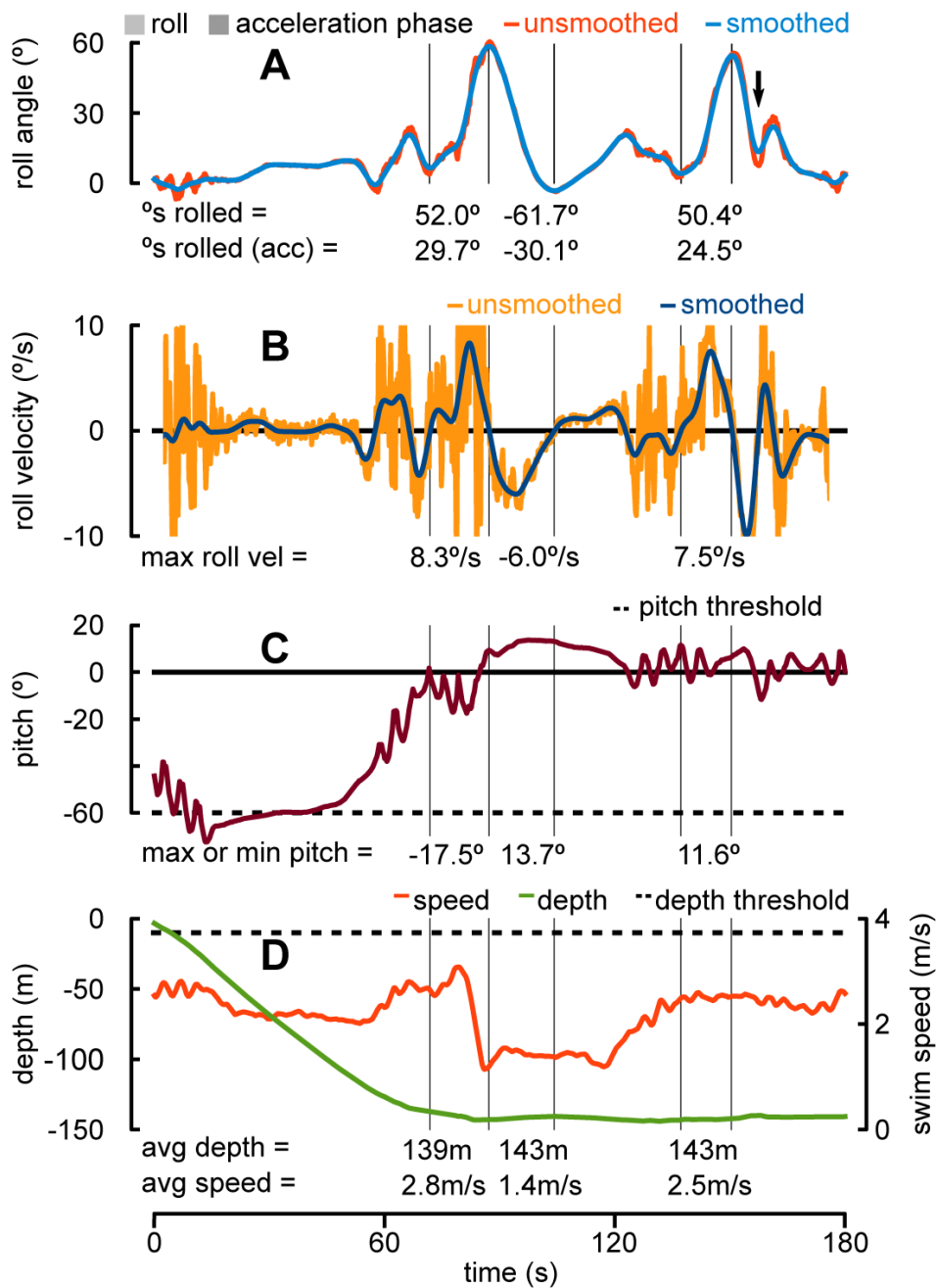


Figure 2. An example of raw data collected from a free swimming fin whale demonstrates the search parameters used for identifying rolls. Three rolls were performed during a 180

second segment (grey bars; roll properties calculated from the graphs are listed underneath each bar). A) Roll angle was calculated from the accelerometer data (red) and was smoothed with a low pass Butterworth filter (blue; cutoff frequency 0.15 Hz). B) Maximum roll velocity was calculated from the smoothed angular velocity (blue; unsmoothed velocity shown in yellow). Smoothed roll velocity was used to determine the acceleration phases of each roll (dark grey bars). C) Only rolls where the pitch was between 60° and -60° were included in the analysis. D) Swimming speed (orange, with 95% confidence intervals shown) was estimated by measuring the level of the background noise recorded by the hydrophones or video camera microphones. This method of calculating swimming speed is only valid when the whale is at depths below 10m (green).

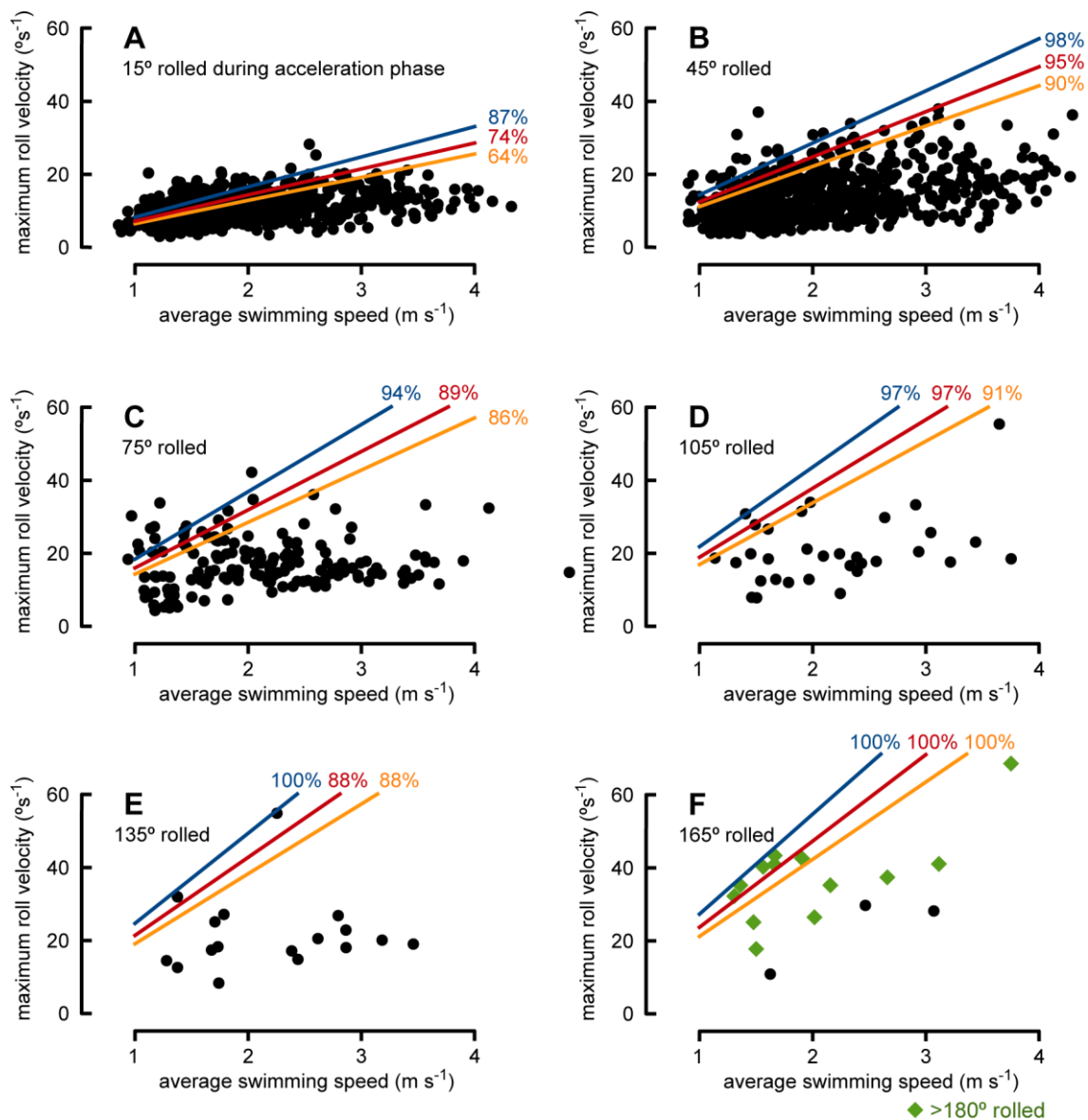


Figure 3. The simple hydrodynamic model predicts maximum roll velocity of free-swimming fin whales. A) 706 rolls with an angular acceleration phase of $15 \pm 15^\circ$ performed by 21 individual fin whales. 87.1% of the measured rolls had a maximum angular velocity that was below the maximum angular velocity predicted by the hydrodynamic model, using the conical

approximation for moment of inertia (blue line). The predictions based on the ellipsoid (red line) and cylindrical (yellow line) models are also shown. Similar graphs are shown for: B) 736 rolls with an angular acceleration phase of $45 \pm 15^\circ$ performed by 21 fin whales; C) 166 rolls with an angular acceleration phase of $75 \pm 15^\circ$ performed by 20 fin whales; D) 32 rolls with an angular acceleration phase of $105 \pm 15^\circ$ performed by 10 fin whales; E) 17 rolls with an angular acceleration phase of $135 \pm 15^\circ$ performed by 9 fin whales; and F) 4 rolls with an angular acceleration phase of $165 \pm 15^\circ$ performed by 3 fin whales. Additionally, 13 rolls with an acceleration phase $>180^\circ$ performed by 8 whales are shown as green diamonds. Altogether, the conical model predicted 92.8% of the measured roll velocities with angular acceleration phases lasting between 0° and 180° .