Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement

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Abstract

Protracted entanglement in fishing gear often leads to emaciation through reduced mobility and foraging ability, and energy budget depletion from the added drag of towing gear for months or years. We examined changes in kinematics of a tagged entangled North Atlantic right whale (Eg 3911), before, during and after disentanglement on 15 Jan 2011. To calculate the additional drag forces and energetic demand associated with various gear configurations, we towed three sets of gear attached to a load-cell tensiometer at multiple speeds. Tag analyses revealed significant increases in dive depth and duration; ascent, descent and fluke stroke rates; and decreases in root mean square fluke amplitude (a proxy for thrust) following disentanglement. Conservative drag coefficients while entangled in all gear configurations (mean±SD $C_{d,e,go} = 3.4\times10^{-3} ± 0.0003$, $C_{d,e,gb} = 3.7\times10^{-3} ± 0.0003$, $C_{d,e,st} = 3.8\times10^{-3} ± 0.0004$) were significantly greater than in the nonentangled case ($C_{d,n} = 3.2\times10^{-3}±0.0003$; $P = 0.0156, 0.0312, 0.0078$ respectively). Increases in total power input (including standard metabolism) over the nonentangled condition ranged 1.6%-120.9% for all gear configurations tested; locomotory power requirements increased 60.0%-164.6%. These results highlight significant alteration to swimming patterns, and the magnitude of energy depletion in a chronically entangled whale.

Keywords: Disentanglement, Dtag, Drag, Energetics, Entanglement, Sedation, Right whale, *Eubalaena glacialis*
**Introduction**

Entanglement in fishing gear is the leading cause of detected mortalities of large whales in the Northwest Atlantic (van der Hoop *et al.* 2012). Upon initial entanglement, a number of outcomes are possible: individuals may die anchored in gear, or may break free, either cleanly or carrying all or a portion of the entangling gear (Clapham *et al.* 1999). Chronic effects of entanglement in free-swimming individuals include systemic infection and debilitation from extensive tissue damage (Cassoff *et al.* 2011). More common in protracted cases is severe emaciation due to the inability to cope with a negative energy budget, driven by the combined effects of reduced mobility and foraging ability, and increased energetic demand imposed by towing accessory gear for months to years (Moore *et al.* 2006, Moore and van der Hoop 2012).

Whereas disentanglement efforts were first developed to release large whales entangled and anchored in fixed fishing gear (Ledwell *et al.* 2010), techniques have been adapted to address the issue in free-swimming individuals (Moore *et al.* 2010). Disentanglement response efforts are coordinated by multiple agencies with the primary goal of removing all entangling gear. During a disentanglement procedure, buoys or floats are often added to trailing gear to increase a whale’s drag through the water and slow its movement (Moore *et al.* 2010). To further reduce boat aversion and allow for close approaches necessary for successful disentanglement, methods have been developed to lightly sedate large whales at sea (Moore *et al.* 2010). No data exist for large whales on the behavioral impacts of sedation and disentanglement or on the energetic cost of entanglement in fishing gear due to drag. Through detailed spatial and behavioral monitoring by means of a biologging tag (Dtag)
(Johnson and Tyack 2003), we examined changes in dive behavior and kinematics of a
tagged entangled North Atlantic right whale (North Atlantic Right Whale Catalog
(Hamilton et al. 2007) No. 3911, hereafter Eg 3911), before, during, and after
disentanglement procedures on 15 Jan 2011. Further, we estimate drag forces experienced
by the whale based on its body proportions, and the additional drag forces and energetic
demand experienced while entangled in various gear configurations.

Methods

Eg 3911, born in 2009 (NARWC Database, 2011), was first sighted entangled and
displaying consequent emaciation on 25 Dec 2010 by an aerial survey team offshore
Ponte Vedra Beach near Jacksonville, FL, USA. The entanglement involved attachment
at a minimum of six sites around the mouth, wraps around both pectoral fins, and
approximately 30 m of line trailing aft of the flukes (Moore et al. 2012) (Fig. 1). We
conducted disentanglement attempts on 29 and 30 Dec 2010, though the whale remained
entangled and was tracked by a satellite telemetry buoy. A third and final multiagency
disentanglement effort took place 15 Jan 2011 near Melbourne, FL, during which we
tagged Eg 3911 with a biologging device (Dtag). Subsequently, we sedated, partially
disentangled to the extent possible, administered antibiotics, and tracked the whale for six
days via satellite with a Low Impact Minimally-Percutaneous External-electronics
Transmitter (LIMPET) (Andrews et al. 2008) (Fig. 2). We observed Eg 3911 dead at sea
by an aerial survey team on 1 Feb 2011, and towed her ashore for necropsy performed on
3 Feb 2011. The ultimate cause of death was pre-mortem shark predation, though the
proximate cause was chronic constrictive deep rope lacerations and severe emaciation
Upon necropsy, we systematically removed, photographed, and described the remaining entangling gear. In total, the entanglement involved approximately 132 m of 1.12 cm diameter floating synthetic line, including six gangions and two fragments of vinyl coated trap mesh. This gear was consistent with that used in fixed trap/pot fisheries, though the target species could not be identified (Morin and Kenney 2011). We used a portion of the entangling gear in the experiments, below.

**Sedation**

To determine appropriate sedative dosages, we calculated a range of weight estimates based on a body length estimate (945 cm) obtained from aerial photographs of Eg 3911 next to a vessel of known dimensions and four length-to-weight methodologies (Supplemental Information). We found Eg 3911 to be 20% thinner than adult female right whales (Miller et al. 2012) (see Supplemental Information for details). To consider this emaciation, we reduced weight estimates by 20%, to ~7,000 kg.

We administered sedative via injection (Moore et al. 2010) of 14 mL (0.1 mg kg\(^{-1}\)) body weight) each of 50 mg mL\(^{-1}\) Butorphanol and Midazolam (ZooPharm Inc., Windsor, CO, USA), and sedative reversal via 7 mL (0.05 mg kg\(^{-1}\)) of 50 mg mL\(^{-1}\) Naloxone and 49 mL of 0.1 mg mL\(^{-1}\) Flumazenil. The reversal needle inserted fully, but on recovery it was discovered that the syringe had malfunctioned and the dose remained in the syringe barrel and was not administered. We also administered two doses of antibiotics (56 mL each; total 17.6 g of 220 mg mL\(^{-1}\) Ceftiofur; Pfizer Inc, Madison, NJ, USA). Injections occurred via a ballistic syringe system (Paxarms, Timaru, New Zealand; (Moore et al.)

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2010); Fig. 3), with the syringe attached to a stainless steel leader tied to 20 m of 80 kg test line spooled at the projector barrel tip, and then tied to a custom float. The float is designed to extract the needle and provide a visual marker for retrieval (Moore et al. 2010).

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118 **Tagging and Behavior**

119 Prior to the disentanglement, we attached a Dtag at 1004 EDT on 15 Jan 2011 via suction cup just above the right dorsal midline, midway between the blowhole and tail (Fig. 3). Deployment lasted 6:11 (h:min).

120 The Dtag is equipped with depth and temperature sensors, 3-axis accelerometers and magnetometers sampling at 50Hz, and a hydrophone sampling at 96kHz (Johnson and Tyack 2003). We down-sampled sensor data to 5Hz, and calibrated accelerometer and magnetometer measurements to account for the orientation of the tag on the whale (Johnson and Tyack 2003). We derived pitch and roll from the accelerometer and heading from the magnetometer measurements.

127 **Dive Parameters**

128 We defined dives as depths >5 m, representing the top 29%-38% of the water column where Eg 3911 was tagged. We estimated bottom depth from bathymetric charts with coordinates of pursuit and disentanglement operations. Tidal range for 15 Jan 2011 was only 30 to 70 cm above chart datum for Cape Canaveral, FL. We calculated proportional depth as the amount of the water column explored relative to available (depth of dive/approximate depth of dive location). We manually detected descent and ascent periods of each dive, reflecting periods of sustained motion to depth and to the
surface, respectively. Dive profiles appeared in randomized order for the manual
determination of descent and ascent periods to reduce potential bias. We calculated
descent and ascent rates as the distance traveled from the surface to the depth at which
the descent period ends (or from depth to surface for ascents), over the duration of that
period.

Wave drag is greatest when the ratio between the submergence depth $h$ of a body
of diameter $d$ is $h/d = 0.5$, and becomes negligible at $h/d = 3$ (Hertel 1969). To determine
the relative amount of time spent swimming in more costly conditions, we compared the
ratio of time spent above vs. below this wave drag limit ($h/d = 0.5$) between phases. We
calculated dive duration (s) from when the animal left the surface (to a depth >5 m) until
returning to <1 m depth.

**Dive Area Ratio (DAR)**

We created a dimensionless, depth- and duration-independent index to compare
dive shapes under entangled and nonentangled conditions. The Dive Area Ratio (DAR),
similar to the Time Allocation at Depth (TAD) Index (Fedak *et al.* 2001), is based on the
concept of a time-depth area, being the area enclosed by a dive profile or the integral of
dive depth over the dive duration. We therefore calculate the DAR as the ratio of the total
dive area (the integral of the dive profile) and the maximum dive area,

$$ DAR = \frac{A_{\text{total}}}{DT} = \sum_{i=2}^{n} \frac{(d_{d,i} + d_{d,i-1})}{2} \times \left( \frac{1}{f_s} \right) $$

\begin{equation}
, \quad (1)
\end{equation}
where $A_a = \text{integrated actual dive area}$, $d_d = \text{tag-derived depth (m) at } n \text{ intervals during}$
dive, $D = \text{maximum depth of dive (m)}$, $f_s = \text{tag sampling rate (Hz)}$, and $T = \text{total dive}$
duration (s).

The DAR differs from the TAD Index in that it does not remove the “necessary travel area” (the area required to descend and ascend to and from maximum depth) from each dive. The time to descend and ascend is of particular interest in this analysis, as changes in drag and buoyancy due to the presence of entangling gear will have the greatest effect in these portions of the dive cycle. The DAR thus provides greater information on the difference in dive shapes over the entire duration of the dive, not only the bottom period between descent and ascent.

Respiration

We determined respiration rate from aerial observer counts of the number of visual respiration cues per 5-minute interval, from 40 min prior to and 3:45 h:min following tag attachment.

Proxies for Thrust

The Dtag captures individual fluke strokes as cyclic oscillations in the deviation of the pitch angle (degrees) from mean orientation. We considered three tag-obtained measures of thrust production: (1) fluke stroke rate, the inverse of the time between peaks in pitch angle averaged over 30 s bins (fluke strokes per second, Hz) (Johnson and Tyack 2003), which is a relative indicator of thrusting intensity; (2) the root mean square (RMS) energy of fluke amplitude, a measure of signal average and variability and is proportional to power (Semmlow 2012), measured only within dives to discount large changes in pitch associated with surfacing events; and (3) glides, characterized by periods where no fluke
oscillation occurs in the pitch rate signal. We identified glides as segments where the absolute value of the Hilbert transform of the pitch rate signal was <0.05 (Woodward et al. 2006a), and visually checked these sequences. Based on previously described gliding behaviors in right whales (Nowacek et al. 2001, Woodward et al. 2006a), we defined the minimum glide duration as 5 s.

**Overall Dynamic Body Acceleration (ODBA)**

Following (Wilson et al. 2006) and (Fahlman et al. 2008), we calculated Overall Dynamic Body Acceleration (ODBA, g) by smoothing accelerometer measurements in three separate axes, with a window size of 3 s. We then subtracted these smoothed data (static acceleration) from the unsmoothed data to estimate the dynamic acceleration in each axis. Finally, we then calculated ODBA as the sum of the absolute value of dynamic acceleration in each axis. We observed peaks and identified outliers in ODBA at each surfacing event, and therefore calculated mean ODBA values within dives, between dives, and during descent and ascent periods of each dive.

**Phase Definitions and Statistical Analyses**

We defined three phases of the sedation and disentanglement of Eg 3911 (Table 2) hereafter referred to as (1) Sedation/Entangled: animal towing gear and attached buoys, and sedative injection; (2) Disentangled: following removal of most of trailing gear and buoys, administration of antibiotics, and attachment of the satellite LIMPET tag (Andrews et al. 2008); and (3) Recovery: retrieval of injection darts, dart tethers and floats (Moore et al. 2010), and the end of active boat approaches.

To determine the behavioral effects of sedation on an entangled whale, we used Wilcoxon rank sum tests to compare dive parameters and respiration rates within the
Sedation/Entangled phase, between the 21 min prior to and the 50 min following sedative injection, but prior to removal of the gear and buoys. We used Three-sample Kruskal-Wallis single factor analysis of variance tests with tied ranks and posthoc Bonferroni-corrected (α = 0.05/3 = 0.0167) Wilcoxon rank sum tests to compare the distributions of various dive parameters between Sedation/Entangled, Disentangled and Recovery phases. To compare the observed vs. expected ratio of time spent above and below the wave drag limit between phases, we used Chi-square contingency tables.

We compared fluke stroke rate, RMS, and the frequency and duration of glides across phases within the single tag deployment to infer changes in thrust intensity and power requirements. As propulsive (thrusting) forces should equal resistive forces (net buoyancy and drag), we expect thrusting intensity (stroke rate, and RMS) to be greater and for fewer and shorter glides to occur in entangled versus nonentangled conditions. We present all dive parameters as median (IQR) unless otherwise stated.

Gear Towing

We conducted a series of tests in Marion Harbor, MA, USA on 13 May 2011 towing three sets of gear off the side of a 7.3 m (24 ft), 25HP motor-propelled Carolina Skiff: (1) 24.93 m of 1.12 cm diameter floating line removed from Eg 3911 in the disentanglement procedure on 15 Jan 2011, ‘gear-only’; (2) this same line with two buoys as attached during disentanglement, ‘gear-and-buoys’; and (3) 160 m of 0.89 cm sinking line for comparison, ‘sinkline’, all detailed below.

To measure drag force, we used an MLP-100 load cell tensiometer (Transducer Techniques, Temecula, CA, USA) between two eyebolts threaded into opposite sides of the cell. One eyebolt suspended the load cell parallel to a vertical spar on the side of the
Skiff. The second eyebolt attached to a leader running through the pulley at the base of the spar, then immediately attached to the gear (i.e., the leader produced drag that was negligible compared to the gear). We held the base of the spar at the surface and at 2 m depth, consistent with the animal’s body depth of 2.20 m.

We modified the drag force signal from the load cell as in Cavatorta et al. (2005) and recorded it through the serial port on a laptop, sampled at 250 ms. We calculated mean (±SD) drag forces from the data record for a given gear configuration (gear-only, gear-and-buoys, or sinkline), anchor point (surface or 2 m depth), and boat speed (0.772 – 2.98 m s\(^{-1}\)). We measured boat speed via a handheld GPS unit and used this speed as a relative indicator of the effect of whale swimming speed. These speeds are biologically relevant, as right whales are known to swim in the range of 0.52 (Mayo and Marx 1990) to 2.05 m s\(^{-1}\) (Baumgartner and Mate 2003) and maximum speeds for balaenids have been recorded between 4 - 4.5 m s\(^{-1}\) (Hamner et al. 1988). Tide was less than 0.5 knot.

The entangling gear removed 15 Jan 2011 (Configuration 1; ‘gear-only’) measured 24.93 m in length, and consisted of parallel arrangements of six line segments for the first 0.7 m, three segments for the next 1.50 m and two segments for the next 2.20 m; the remaining 20.53 m was a single piece of line with one gangion (a large knot connecting a second line) and three figure-eight knots (Fig. 4). The combined length of all line segments was 33.63 m.

To mimic the configuration on the animal, we attached the buoys added during disentanglement (Configuration 2; ‘gear-and-buoys’), an A3 Polyform buoy (42.5 cm diameter) and an NB60 Scanmarin buoy (45.4 cm diameter) to the aft-most figure-eight knots on the removed gear (i.e., Configuration 1). We connected each buoy to its
respective figure-8 knot by an 11.4 cm karabiner and an approximately 1 m long lanyard
of 0.95 cm diameter polysteel. The buoys and karabiners used in the tow deployments
were identical to those used in the disentanglement procedure; however, during the
disentanglement, we attached buoys to the fore-most and aft-most knots. We assume this
difference in the gear configuration does not change the results materially.

As a control, we towed 160 m of 0.89 cm diameter sinkline (Configuration 3; ‘sinkline’) in a single-line configuration with no knots, gangions, or buoys.

Energetic Requirements

We applied the following calculations to determine the forces acting on Eg 3911.

The Reynolds number, $Re$, describes the relative importance of viscous and inertial forces
acting on a body, calculated as

$$ Re = \frac{l U}{v} \tag{2} $$

where $l$ is the length of the body (m), $U$ is the velocity or swimming speed (m s$^{-1}$) and $v$ is
the kinematic viscosity of the surrounding medium (1x10$^{-6}$ m$^2$ s$^{-1}$ for seawater). Reynolds
numbers >5x10$^6$, as calculated here and is the case for other large whales, indicate a
turbulent boundary layer.

Total drag on a body is composed of frictional, pressure, interference, and surface
components. Frictional drag, $D_f$ (N), is given by

$$ D_f = \frac{1}{2} \rho U^2 A_w C_f \tag{3} $$

where $\rho$ is the density of the surrounding medium (here seawater, 1025 kg m$^{-3}$), $A_w$ is the
total wetted surface area (m$^2$; Alexander 1990) calculated from body mass $M$ (kg) as $A_w =
0.08 M^{0.65}$ (Fish 1993). $C_f$ is a frictional drag coefficient, which depends on boundary
layer flow characteristics (e.g., Blake 1983). For a turbulent boundary condition, as calculated above,

\[ C_f = 0.072(Re^{-1/5}) \]  \hspace{1cm} (4)

The pressure drag coefficient, \( C_p \), is relatively constant for \( Re > 10^6 \). By convention, we calculated \( C_p \) as a fraction of \( C_f \) by calculating \( C_{D0} \), the profile drag coefficient,

\[ C_{D0} = C_f + C_p = C_f \left[ 1 + 1.5 \left( \frac{d}{l} \right)^{3/2} \right] + 7 \left( \frac{d}{l} \right)^3 \]  \hspace{1cm} (5)

where \( d \) is the maximum width of the body (or diameter; m) estimated from photographs using width-to-length ratios of the widest point of the body.

We added three drag augmentation factors. (1) Appendages increase interference, frictional, and pressure drag over the theoretical condition due to protrusion from a streamlined body. We used \( g = 1.3 \) to account for \(~30\%\) increases in drag due to flukes and fins (Fish and Rohr 1999). (2) \( k \) accounts for the oscillation of the flukes and body during active swimming, which alters body shape and increases frontal area and \( C_p \) (Fish and Rohr 1999). Further, boundary layer thinning is expected when the amplitude of the propulsive movement is much greater than the maximum body diameter (Lighthill 1971). Thinning of the boundary layer increases skin friction, \( C_f \), over a greater proportion of the body than if the body were rigid, increasing drag by up to a factor of five (Lighthill 1971). Due to uncertainties on the degree to which whale swimming affects anterior oscillation, we employed values of \( k = 1 \) and \( k = 3 \) (F. Fish, pers. comm.\(^2\)).

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The effect of surface, or wave drag on an object varies with submergence depth \( h \), measured from the surface to the center line of the object; m) relative to body diameter, \( d \). Critical relative submergence depth \( h/d \) values have been established experimentally (Hertel 1966, Hertel 1969) and theoretically (Hoerner 1965) describing the relative contribution of wave drag with depth. Wave drag is highest at the surface \( (h/d = 0.5) \) and decreases with submergence, becoming negligible at \( h/d = 3 \) (Hertel 1969). To account for surface drag (Hertel 1966, Fish 1993), we determined the augmentation factor \( \gamma \) for entangled \( (\gamma = 1.6) \) and nonentangled \( (\gamma = 1.0) \) conditions from tag-derived relative submergence depths (1.81 m and 4.25 m respectively).

We then calculated the drag on the body, \( D_w \) (N), as

\[
D_w = \frac{1}{2} \rho U^2 S_w C_{D0} \gamma \kappa g .
\]  

Line lying flush with the body surface produces a surface protuberance that may disrupt fluid flow over the body, affecting body drag. The total drag of the system is not simply the sum of the drag on the body and on the element, but also the interference between the elements (interference drag) (Blake 1983). The magnitude of interference drag varies non-linearly with the position \( (\% \text{ of } l) \) and height of the protuberance \( (p, \text{ m}) \) compared to the length of the body \( (l, \text{ m}) \) (Jacobs 1934, Blake 1983). As protuberance height is increased from \( p = 0 \) to \( p = 0.001l \) (e.g., from 0 to 1.25 cm diameter line) interference drag is comparatively small, on the order of 10\% of the drag of the element. Increases in drag over this height scale are slow due to the protuberance being in the body’s boundary layer \( (\delta) \); however, they should not be considered negligible (Jacobs 1934). For this height scale, the interference drag coefficient of a protuberance \( j \) \( (C_{DI,j}) \) is...
where we calculated boundary layer thickness ($\delta$, m) at the location of protuberance $j$ (distance from leading edge, $l_{x,j}$; m) based on the ratio between the maximum diameter and the diameter at the location of protuberance $j$ ($d_{x,j}$) as

$$\delta_j = \left( \frac{d}{d_{x,j}} \right)^{0.02} l_{x,j}. \quad (8)$$

We then calculated the total interference drag, $D_I$ (N), as the sum of the interference drag associated with all $n$ protuberances on the frontal projection of the body (Hoerner 1965):

$$D_I = \sum_{j=1}^{n} D_{l,j} = \sum_{j=1}^{n} \frac{1}{2} \rho U_j^2 A_{x,p,j} C_{Dl,j}. \quad (9)$$

Bodies in water have a shielding effect that reduces drag on objects floating in their wake (Hoerner 1965). In the wake of the first body, the dynamic pressure is reduced and drag is decreased over the distance of $x/d = 2$, where $x$ is the distance between the two bodies (m). Organisms take advantage of reduced drag in a wake by forming queues (e.g., Fish 1995, Bill and Herrnkind 1976), and the same theory holds for an animal towing accessory gear in its wake. Any object at a distance lesser than $x/d = 2$ should experience a reduction in drag by a factor of approximately 0.75 (Hoerner 1965).

We calculated the total drag, $D_T$ (N), on an entangled whale:

$$D_T = D_w + a(D_h + D_l) + D_I, \quad (10)$$

where $D_h$ is the drag on tethered buoys or other accessory gear, $D_l$ is the drag on the attached line, $D_I$ is the interference drag, and $a$ is the shielding factor, based on the spacing distance, $x$, between the body and the towed gear where if $x/d$ is less than 2, $a = 0.75$, and if $x/d$ is greater than 1, $a = 1$. In this study, we empirically measured ($D_h + D_l$).
We derive the total power input \((P_{I,T}; W)\) required for propulsion at a certain speed under any calculated drag condition (generic \(D\)) as

\[
P_{I,T} = P_L + P_{I,B} = \left(\frac{D U}{\eta}\right) + P_{I,B}, \tag{11}
\]

where \(P_L\) is locomotory power, and \(P_{I,B}\) is power input for standard metabolism, both in \(W\), and \(\eta\) is an efficiency coefficient of 0.15 (Fish 1993, Hind and Gurney 1997). Given the uncertainties in appropriate metabolic rate estimation for cetaceans (Gallivan 1992), we estimated minimum and maximum standard metabolism \((W)\) using Kleiber \((3.4M^{0.75};\)

\[M\] is body mass in kg), and \(3 \times \text{Kleiber.}\)

Facing an increase in drag, an individual can: (1) maintain a characteristic velocity and exponentially increase energy expenditure to overcome added drag; or (2) swim at a reduced speed in order to maintain the same power output as if under normal conditions (Jones et al. 2011). For the latter case, the decrease in velocity \((U_{\text{red}}, \text{m s}^{-1})\) to maintain the same power output in an entangled drag scenario \((D_T)\), is

\[
U_{\text{red}} = \left[\frac{P_L \eta U^2 \gamma^{1/3}}{D_T}\right]. \tag{12}
\]

To determine the additional power demands experienced by Eg 3911 while entangled, we compared \(P_{I,T}\) for the drag conditions of a nonentangled whale, with surface drag factor \(\gamma\) following disentanglement \((i.e., \gamma = 1.0)\), to the conditions of an entangled whale, towing three gear configurations tested in this experiment, with surface drag factor \(\gamma\) calculated for the mean \(\pm \text{SD}\) dive depth prior to disentanglement \((i.e., \gamma = 1.6)\).

**Results**

**Tagging and Behavior**
Dive Parameters

Eg 3911 completed *n* = 152 dives over the 6 h deployment period, to a median (IQR) depth of 11.50 (10.97) m and duration of 98.7 (82.1) s (Fig. 5).

Within the Sedation/Entangled phase, there was no significant difference between the depth or duration of dives completed in the 21 min prior to (*n* = 7) and the 50 min following (*n* = 45) sedative injection (*Z* = 0.402 and 0.188; *P* = 0.6876 and 0.8511 respectively; Table 3).

Dive depth increased significantly with every phase (*χ*² = 26.66, *P* <0.0001; Fig. 6). Median dive depth was significantly (138%) shallower in Sedation/Entangled compared to Disentangled (*Z* = -6.121; *P* <0.0001). Significant increases in dive depth occurred between Disentangled and Recovery (*Z* = 4.607; *P* < 0.0001), though only by 19%. Even when considering increases in approximate regional water column depth with time, proportional dive depth was significantly shallower in Sedation/Entangled (by 95%) compared to following the removal of gear and buoys (*i.e.*, in Disentangled; *Z* = -5.216; *P* <0.0001; Fig. 6). Further, we observed no significant difference in proportional dive depth between Disentangled and Recovery phases (*Z* = -0.679; *P* = 0.497).

Descent rates (m s⁻¹) during dives differed significantly between phases (*χ*² = 49.87; *P* <0.0001; Fig. 6), where descents during Sedation/Entanglement were 57% slower than in Disentangled (*Z* = -6.287; *P* <0.0001). There was no significant difference between the descent rates in Disentangled and Recovery (*Z* = 0.535; *P* = 0.5927).

Ascent rates (m s⁻¹) during dives also differed significantly between phases (*χ*² = 46.22; *P* <0.0001; Fig. 6), with significantly slower ascents (31%) during Sedation/Entanglement compared to in Disentanglement (*Z* = -5.948; *P* <0.0001). Similar
to descent rate, ascent rate did not differ between Disentanglement and Recovery ($Z = 0.090; P = 0.9285$).

For Eg 3911 ($h = 1$ m, $d = 2.20$ m), wave drag is maximal within 0.1 m of the surface, and becomes negligible below $5.58$ m depth ($h = 6.58$ m). The ratio of time spent above vs. below the wave drag limit ($5.58$ m) over the entire deployment was 1.06, meaning Eg 3911 spent almost equal amounts of time above and below the threshold.

However, significantly more time was spent in surface waters where energy requirements are higher before (7.02:1) vs. following sedative injection (2.47:1; $\chi^2 = 141; P < 0.0001$; Table 3), and while entangled (i.e., during Sedation/Entangled; 2.87:1) vs. during Disentangled (0.6656:1) and Recovery phases (0.4405:1; $\chi^2 = 3220; P < 0.0001$).

Dive duration (s) differed significantly between phases ($\chi^2 = 26.67; P < 0.0001$; Fig. 6), where dives during Sedation/Entangled were 56% shorter than in Disentanglement ($Z = -3.151; P < 0.0016$). Dive duration also increased significantly, by 30%, from Disentanglement to Recovery ($Z = 3.4218; P = 0.0006$).

**Dive Shape**

Dive shape, as measured by the DAR, differed significantly between phases ($\chi^2 = 19.1083; P = 0.0001$; Fig. 7), with significantly lower DAR during Sedation/Entangled than in Disentangled or Recovery phases ($Z = -3.1615, 4.3410; P = 0.0016, < 0.0001$ respectively). There was no significant difference in the DAR between Disentangled and Recovery phases ($Z = 0.9443, P = 0.3450$).

**Respiration**

Respiration rate per 5-minute interval did not change following sedative delivery ($P = 0.4312$; Table 3). We detected no significant difference between respiration rate
Fluke stroke rate increased significantly following sedative injection \((Z = -8.417, P < 0.0001; \text{Table 3})\). Fluke stroke rate within dives differed significantly between phases \((\chi^2 = 18.7179; P = 0.0001; \text{Fig. 8})\), being significantly lower during Sedation/Entangled compared to the Disentangled phase \((Z = -3.928; P < 0.0001)\). Fluke stroke rate did not differ in Disentangled and Recovery phases \((Z = -0.0323, P = 0.9742)\).

Following sedative injection, RMS energy within dives increased significantly, by 28% \((Z = -3.0832; P = 0.0020; \text{Table 3})\). RMS energy was 12% lower after gear and buoy removal \((Z = 3.1943; P = 0.0014)\). From Disentangled to Recovery phases, RMS energy within dives significantly decreased \((Z = -2.5960; P = 0.0094)\).

Glide duration did not differ significantly before and after sedative injection \((P = 0.1993)\), or before and after the removal of the gear and buoys \((Z = 0.334; P = 0.9734)\).

While glides occurred in all phases, the portion of the dive cycle in which gliding occurred differed between phases. When entangled \((n = 18)\), 50% of glides occurred during the bottom period, 33% during descent and 17% on ascent. However, following disentanglement \((n = 41)\), 85% of glides were performed during the bottom period, and 15% during ascent. No glides were performed during descent following disentanglement.

**ODBA**

Within dives, ODBA did not differ significantly between phases \((\chi^2 = 5.4288; P = 0.0662)\). During dive descents, ODBA differed significantly between phases \((\chi^2 = 8.2055; P = 0.0165)\), being significantly (10%) lower during Sedation/Entangled than in...
20

the Disentangled phase ($Z = -2.7230; P = 0.0065$; Fig. 8). There was no significant difference between ODBA in dive descents between Disentangled and Recovery phases ($Z = -1.2603; P = 0.2076$). During ascents, ODBA did not differ significantly between phases ($\chi^2 = 2.8613; P = 0.2392$; Fig. 8).

Gear Towing

Mean drag forces (N) of gear removed from Eg 3911 were consistently though not significantly greater at all speeds with buoys attached (Table 4). Sinkline drag forces were intermediate between gear-only and gear-and-buoy configurations (Table 4). Mean drag forces showed no significant difference between surface and 2 m anchor points for gear-only ($P = 0.4595$), gear-and-buoys ($P = 0.4888$) or sinkline ($P = 0.4965$) configurations (Devore 2008).

Energetic Requirements

The mean theoretical drag coefficient of a nonentangled right whale ($C_{d,n}$) of Eg 3911’s dimensions, swimming at 0.75 - 2.9 m $s^{-1}$ ranged from $3.7 \times 10^{-3}$ to $2.9 \times 10^{-3}$ respectively (mean±SD; $C_{d,n} = 3.2 \times 10^{-3} \pm 0.0003$; Fig. 10). The drag coefficient for each entangled gear scenario was calculated by applying Equation 6 ($C_d = D_T/(1/2) \rho U^2 A_w \gamma k g$). Though drag coefficients for Eg 3911 entangled in all gear configurations differed based on the value of $k$ (Fig. 9), the most conservative estimates with $k = 3$ ($C_{d,e,go} = 3.4 \times 10^{-3} \pm 0.0003$, $C_{d,egb} = 3.7 \times 10^{-3} \pm 0.0003$, $C_{d,esl} = 3.8 \times 10^{-3} \pm 0.0004$) were significantly greater than in the nonentangled case (Wilcoxon signed rank, $P = 0.0156$, 0.0312, 0.0078 respectively).

Having made low (Kleiber) and high (3×Kleiber) estimates of BMR, and using two values of $k$ (1 and 3), we present drag and power requirements as the lower ($k = 1$,
BMR = Kleiber) and upper ($k = 3$, BMR = $3 \times$ Kleiber) bounds of the model results. Drag forces on Eg 3911 while not entangled ranged from 37.2 N to 1263 N at 0.75 - 2.9 m s$^{-1}$. The associated total power requirements in the nonentangled condition (Eq. 11) ranged from 2791 W – 16140 W (Fig 10). Locomotory power requirements ranged from 191 – 25021 W.

Drag forces on Eg 3911 entangled in various gear configurations are summarized in Table 5. Across all gear configurations, mean entangled drag values ranged from 62.1 N to 2421 N. Increases in total power input over the normal (nonentangled) condition ranged from 4.1%-58.8% for the gear-only configuration, 4.9%-82.5% for the sinkline configuration, and 4.8%-120.9% for the gear-and-buoy configuration (Fig. 9).

Locomotory power requirements increased on average 70.5% (SD 9.5) for the gear-only configuration, 91.0% (22.5) for the sinkline configuration, and 101.9% (31.9) for the gear-and-buoy configuration (total range 60.0%-164.6%). Alternatively, to maintain the same power output over the range of swimming speeds, an individual entangled in gear-only, sinkline, and gear-and-buoy configurations would need to decrease swimming speed by 16.2% (SD 1.5), 19.2% (3.0), or 20.5% (3.9), respectively (total range 14.5%-27.7%).

**Discussion**

We describe the effect of sedation and near-complete disentanglement of a free-swimming entangled right whale, Eg 3911. Tag data show major changes in locomotion before and after disentanglement. Modeling the drag forces of the removed gear, we show that entangled whales can have significantly increased energetic demand.
Sedative injection had little to no effect on dive parameters or respiration rate. It is likely that in this condition, behavior is dominated by the effect of entangling gear rather than of a light sedative. At the dosage level (0.1 mg kg\textsuperscript{-1}), Midazolam has not been found to cause cardiovascular, respiratory, or airway reflex changes in humans (Reves \textit{et al.} 1985), though a previous study reports increased respiration rates following sedation in right whales (Moore \textit{et al.} 2010).

After sedation, Eg 3911 spent a greater proportion of time below the wave-drag threshold (5.58 m), though showed no difference in maximum dive depth. This increased submergence time may be linked to the lethargy associated with sedation. Moore \textit{et al.} (2010) describe less forceful surfacing events in sedated right whales. However, increased fluke rate and RMS energy post sedation may suggest the drugs had an analgesic effect in reducing entanglement-associated pain, and therefore freeing the animal to locomote more strongly.

The near-complete disentanglement of Eg 3911 resulted in significant increases in dive duration and depth. Similarly, Williams \textit{et al.} (1993) found that increased drag loading in harbor seals led to shortened dive times. As dive duration is considered limited by the total amount and rate of consumption of body oxygen stores, the elevated energetic cost associated with additional entanglement drag likely quickly depletes available oxygen, leading to premature dive termination.

Changes in kinematics and dive parameters indicate the whale altered its behavior immediately following disentanglement. Previous studies suggest that propulsive forces are increased in response to changes in resistive forces, where elephant seals adjust stroke intensity when buoyancy is experimentally altered (Aoki \textit{et al.} 2011). Animals may also
actively alter swimming dynamics or posture to compensate for an added load. As suggested by Watson and Granger (1998), animals facing an increase in drag may either (1) maintain characteristic velocity, exponentially increasing energy expenditure; or (2) reduce swimming speed in an attempt to reduce the cost of locomotion. Fluke stroke rate, which has been shown to correlate with speed in dolphins (Fish 1993) and other cetaceans (Fish 1998), increased significantly following disentanglement. Further, Eg 3911 showed descent and ascent speeds 57% and 31% faster (respectively) after disentanglement, greater than the expected 14.5% – 27.7% as calculated above. While changes in swimming speed were likely due to a combination of factors rather than energy conservation alone (e.g., sedation, pursuit by a vessel), this case suggests that entanglement significantly alters swimming modes.

The greater increase in descent speed (57%) vs. ascent speed (31%) following disentanglement likely highlights the effects of both drag and buoyancy related to the entangling gear and buoys. In order to dive to depth, an individual must overcome resistive buoyant forces. More active swimming is thus required on descent, while ascents can be passive (Nowacek et al. 2001). Such buoyant effects are also evident in dive shape. The overall depth- and duration-normalized dive area (DAR) was significantly lower while entangled. Dive descents to, and ascents from maximum depth were more gradual, and less time was spent in the bottom phase of the dive while the animal was entangled as compared with the behavior following disentanglement.

Given that the added buoys were further from the whale than the water column was deep, the buoys should have never been submerged to provide an upwards buoyant force that Eg 3911 could take advantage of to conserve energy in diving (Nowacek et al.)
2001). Glides occurred in all phases of the dive cycle, indicating that passive swimming
was not timed to take advantage of changes in buoyancy by gliding on ascent while
entangled. The emaciated condition of Eg 3911 may have led to negative buoyancy, as
has been found in emaciated bottlenose dolphins (Dunkin et al. 2010), and dive depths
were much shallower than the predicted depth of lung collapse in cetaceans (30 – 235 m)
(Fahlman 2008). It is thus likely that glides were employed to conserve energy (Videler
and Weihs 1982, Williams 2001) rather than to optimize the benefits of buoyancy.

ODBA has shown to be a reliable estimator for activity and metabolic rate in free-
swimming animals (Fahlman et al. 2008). It was thus expected that ODBA be greater
under the entangled condition; however, ODBA was often lower while entangled,
compared to after disentanglement. We suggest that restraint by the drag and buoyancy of
the gear may have reduced Eg 3911’s ability to make large dynamic movements.
Accelerometer measurements determine only the movement of the animal (i.e., net
movement) and those forces associated, but not the forces required to move against any
materials that may be restraining movement (i.e., total exertion). Consider a running
parachute: the runner expends considerably more energy with the parachute, though their
motion is more limited and is slower than without the apparatus. The application of
ODBA to free-swimming and restrained cases likely requires separate metabolic
calibrations for each condition, which are not available for entangled large whales at this
time.

Together, the effects of added buoyancy, added drag, and reduced swimming
speed due to towing accessory gear pose many threats to entangled whales. If buoyancy
overwhelms an animal’s ability to descend to the depth of its preferred prey, its foraging
ability may be significantly compromised, accelerating the transition to a negative energy balance. Increased time spent in surface waters results in greater overall drag, due to surface effects (Hoerner 1965, Hertel 1969), and places individuals at greater ship strike risk (Nowacek et al. 2001, Parks et al. 2012). Reduced swimming speed will lead to increases in travel time, potentially delaying an entangled individual’s arrival to feeding or breeding grounds in the case of migratory species (Watson and Granger 1998, Jones et al. 2011).

Most significant, however, is the energy drain associated with added drag. The drag experienced by an animal is significantly affected by the size of the animal relative to the entangling gear, and its configuration, position of attachment, placement in the animal’s wake, and surface area (Feldkamp 1985). The addition of buoys to entangling gear during disentanglement procedures to increase surface area, buoyancy, and turbulence does significantly increase drag forces; however, this method has been used successfully to disentangle whales that have survived to breed (Robbins and Knowlton 2012, Robbins and Landry 2012). Therefore, we suggest that current practice be continued in adding buoys only for short-term operations, such as a single disentanglement attempt. The benefits of partial or full gear-removal likely outweigh the short-term energetic impact buoy-addition may incur.

Since not all entanglements can be resolved during a single attempt, a 36 cm diameter satellite/VHF telemetry buoy is the current method of tracking entangled individuals for later re-sighting and disentanglement. In eight cases, these buoys have also provided sufficient drag to allow whales to remove some or all remaining gear (S.
Landry pers. comm.\(^3\). Since the current telemetry buoy does create drag force (\textit{ca.} 76 N at 1.3 m s\(^{-1}\),\(^{(Woodward \textit{et al.} 2006b)}\)) entanglement responders should continue to make every effort to: use telemetry on a case-by-case basis, strategically place the telemetry buoy to minimize impacts, remove as much of the original trailing gear to minimize additional drag force and reduce the duration of buoy placement. Longer-duration, lower drag telemetry buoy designs should continue to be developed for tracking entangled individuals for later disentanglement.

To reduce locomotory costs, marine mammals have adapted low drag coefficients. Drag has been estimated from Dtag records (\textit{Miller \textit{et al.} 2004, Simon \textit{et al.} 2009, McGregor 2010}), though this method requires a measure of speed, which cannot be obtained from this tagging event due to boat noise and low pitch angles. Still, the theoretical coefficient we estimated for Eg 3911 (3.7x10\(^{-3}\) to 2.8x10\(^{-3}\) over a range of speeds) falls well within the range of previously estimated drag coefficients for large whales (5.2x10\(^{-3}\) – 1.4x10\(^{-2}\)) (\textit{Miller \textit{et al.} 2004, McGregor 2010}). Significant increases (2.3%-69.2%) in the drag coefficient occur in the entangled scenario, leading to 60.0%-164.6% increases in locomotory power output.

These energetic requirements are only related to propulsion in an entanglement scenario and do not consider increased thermoregulation to compensate for loss of body fat, or stress-related changes in metabolic rate, which have increased up to 16.25% in entangled northern fur seals despite increased resting time (\textit{Feldkamp \textit{et al.} 1988}). Though fecal glucocorticoid studies have shown markedly elevated stress hormone levels

\(^3\) Scott Landry, Provincetown Center for Coastal Studies Marine Animal Entanglement Response, 5 Holway Ave, Provincetown MA 02657 USA
in a severely entangled right whale (Hunt et al. 2006), the relationships between entanglement stress and metabolic rate are too complex to be considered here.

High energetic requirements and negative energy balance are not uncommon in large whales. Right whales routinely enter a phase of energy deficit during the fasting cycle associated with annual migrations between high-latitude foraging habitats and low-latitude calving areas. Sufficient endurance to survive the fasting phase and subsequently recoup losses in the following foraging season are likely adaptations, though prolonged periods of an imbalance of greater magnitude may impact an individual’s energy reserve to a point beyond which recovery is not possible (Millar and Hickling 1990). The magnitude of power output due to drag of entangling gear almost certainly would make such long distance (~2,900 km, from the Gulf of Maine to Florida (Kraus et al. 1986)) fasting migrations much more energetically costly for an entangled whale.

A simple calculation can illustrate both the effects of increased drag, and of reduced swimming speed (Watson and Granger 1998, Jones et al. 2011). Using our most conservative estimate, a nonentangled right whale swimming 2,900 km, at an average speed of 1.5 m s\(^{-1}\) could complete a one-way migration in 22 d, expending 7.3x10^9 J of energy. Entangled in the gear-only configuration, an individual could migrate at the same speed, arriving on time and expending 9.3x10^9 J of energy (a 27% increase) or could swim at a reduced speed to arrive 5 d late, expending 9.6x10^9 J (a 31% increase). If this same calculation is made with a more energetically costly entanglement scenario (e.g., gear-and-buoys), the entangled individual could arrive on-time, expending 1.0x10^10 J (a 37% increase), or 5 days late expending essentially the same 1.0x10^10 J. Under both entanglement and speed maintenance or reduction scenarios, the energy store budgeted
for a nonentangled one-way migration (7.3x10⁹ J) would be exhausted between 71%-78% of the distance to the destination.

These results provide the first visualization of significant alteration to swimming patterns associated with entanglement. Understanding the major behavioral and energetic implications of towing accessory gear is crucial in considering the sub-lethal effects of persistent entanglement in a critically endangered population.

Acknowledgements

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Tables

Table 1. List of symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Units</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>δ</td>
<td>m</td>
<td>Boundary layer thickness</td>
</tr>
<tr>
<td>γ</td>
<td></td>
<td>Surface drag augmentation factor</td>
</tr>
<tr>
<td>η</td>
<td></td>
<td>Propulsive efficiency</td>
</tr>
<tr>
<td>ρ</td>
<td>kg m⁻³</td>
<td>Density of surrounding medium</td>
</tr>
<tr>
<td>a</td>
<td></td>
<td>Shielding factor</td>
</tr>
<tr>
<td>A_a</td>
<td></td>
<td>Integrated actual dive area</td>
</tr>
<tr>
<td>A_w</td>
<td>m²</td>
<td>Total wetted surface area</td>
</tr>
<tr>
<td>A_p</td>
<td>m²</td>
<td>Frontal area of protuberance</td>
</tr>
<tr>
<td>C_d</td>
<td></td>
<td>Drag coefficient</td>
</tr>
<tr>
<td>C_DI</td>
<td></td>
<td>Interference drag coefficient</td>
</tr>
<tr>
<td>C_D0</td>
<td></td>
<td>Profile drag coefficient</td>
</tr>
<tr>
<td>C_f</td>
<td></td>
<td>Frictional drag coefficient</td>
</tr>
<tr>
<td>C_p</td>
<td></td>
<td>Pressure drag coefficient</td>
</tr>
</tbody>
</table>
### Table 2. Timeline of events on 15 January 2011 in Sedation/Entangled, Disentangled and Recovery phases of Eg 3911.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Dtag Elapsed Time (s)</th>
<th>GPS Time (EST)</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sedation/Entangled</td>
<td>0</td>
<td>10:04:18</td>
<td>Dtag attachment</td>
</tr>
<tr>
<td></td>
<td>1217</td>
<td>10:24:00</td>
<td>Sedation induction</td>
</tr>
<tr>
<td></td>
<td>5048</td>
<td>11:28:00</td>
<td>Possible cut with spring knife</td>
</tr>
</tbody>
</table>
Disentangled

<table>
<thead>
<tr>
<th>Time</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>11:33:00</td>
<td>Cut</td>
</tr>
<tr>
<td>11:38:00</td>
<td>Cut</td>
</tr>
<tr>
<td>11:44:00</td>
<td>Cut</td>
</tr>
<tr>
<td>11:47:00</td>
<td>Cut</td>
</tr>
<tr>
<td>11:51:00</td>
<td>Cut</td>
</tr>
<tr>
<td>11:55:00</td>
<td>Buoys slack and removed</td>
</tr>
<tr>
<td>12:36:00</td>
<td>Attachment of LIMPET Tag</td>
</tr>
<tr>
<td>12:43:00</td>
<td>Sedation reversal dart: did not deploy</td>
</tr>
<tr>
<td>12:43:00</td>
<td>Antibiotic dart</td>
</tr>
<tr>
<td>13:28:00</td>
<td>Antibiotic dart unsuccessful attempt</td>
</tr>
<tr>
<td>13:54:00</td>
<td>Antibiotic dart</td>
</tr>
<tr>
<td>14:18:00</td>
<td>Dart tethers, floats, and 2/4 darts recovered. Vessel <em>Cabretta</em> left scene; Vessel <em>Orion</em> following at 50-300 m distance.</td>
</tr>
<tr>
<td>16:15:00</td>
<td>Tag off</td>
</tr>
</tbody>
</table>

**Table 3.** Median (IQR) respiration rate (/5 min), dive depth (m), proportional dive depth, dive duration (s) and surface interval (s), time spent above:below the significant wave drag depth, fluke stroke rate (Hz) and fluke stroke root-mean-square (RMS) energy (degrees) before and following sedation injection, but prior to gear and buoy removal. Significance values (P) from Wilcoxon rank sum tests are presented.

<table>
<thead>
<tr>
<th></th>
<th>Pre-Injection</th>
<th>Post-Injection</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration Rate (/5 min)</td>
<td>5.00 (4.50)</td>
<td>5.00 (1.75)</td>
<td>0.4312</td>
</tr>
<tr>
<td>Dive Depth (m)</td>
<td>6.70 (3.07)</td>
<td>6.67 (1.86)</td>
<td>0.6876</td>
</tr>
<tr>
<td>Proportional Dive Depth</td>
<td>0.500 (0.229)</td>
<td>0.477 (0.122)</td>
<td>0.2835</td>
</tr>
<tr>
<td>Dive Duration (s)</td>
<td>70.40 (15.55)</td>
<td>71.00 (45.80)</td>
<td>0.8511</td>
</tr>
<tr>
<td>Time above:below significant depth</td>
<td>7:02:1</td>
<td>2.87:1</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Fluke stroke rate (Hz; flukes/s)</td>
<td>0.277 (0.049)</td>
<td>0.288 (0.058)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Fluke stroke RMS energy (degrees)</td>
<td>0.0798 (0.0124)</td>
<td>0.1023 (0.0163)</td>
<td>0.002</td>
</tr>
</tbody>
</table>
Table 4. Mean (SD) drag forces (N and kg) exerted by (1) 33.63m of fishing gear and (2) gear and buoy configurations removed from Eg 3911, and (3) 160m of sinkline at surface and bottom (2m) towpoints at various boat speeds (m s⁻¹)

<table>
<thead>
<tr>
<th>Tow Point</th>
<th>Configuration</th>
<th>Vessel Speed (m s⁻¹)</th>
<th>Drag Force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>Gear Only</td>
<td>0.772</td>
<td>2.9 (2.0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>21.6 (3.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.83</td>
<td>59.8 (4.9)</td>
</tr>
<tr>
<td>Surface</td>
<td>Gear and Buoys</td>
<td>0.772</td>
<td>16.7 (2.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>55.9 (12.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.73</td>
<td>377.6 (36.3)</td>
</tr>
<tr>
<td>Surface</td>
<td>Sinkline 160m</td>
<td>0.772</td>
<td>11.8 (2.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.772</td>
<td>8.8 (3.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.772</td>
<td>11.8 (3.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>80.4 (2.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.73</td>
<td>202.0 (23.5)</td>
</tr>
<tr>
<td>Bottom</td>
<td>Gear Only</td>
<td>0.772</td>
<td>12.7 (2.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>76.5 (6.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.52</td>
<td>415.8 (28.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.73</td>
<td>2.9 (2.0)</td>
</tr>
<tr>
<td>Bottom</td>
<td>Gear and Buoys</td>
<td>0.772</td>
<td>36.3 (3.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>77.5 (9.8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.98</td>
<td>80.4 (13.7)</td>
</tr>
<tr>
<td>Bottom</td>
<td>Sinkline 160m</td>
<td>0.772</td>
<td>29.4 (3.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49</td>
<td>70.6 (6.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.83</td>
<td>194.2 (24.8)</td>
</tr>
</tbody>
</table>

Table 5. Total drag forces (N) on, and power output (W) required by, Eg 3911 swimming entangled in various configurations (Gear Only, Gear and Buoys, and Sinkline) of fishing gear, and the percentage increase in power, or percent decrease in swimming velocity due to increased drag over the normal (nonentangled) condition. Ranges represent the lower and upper bounds of values of k (profile drag augmentation factor) and metabolic rate (see text).

<table>
<thead>
<tr>
<th>Velocity (m s⁻¹)</th>
<th>Total Drag (N)</th>
<th>Total Power (W)</th>
<th>Locomotor Power (W)</th>
<th>Percent Total Power Increase</th>
<th>Percent Locomotor Power Increase</th>
<th>Percent Velocity Decrease</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gear Only</td>
<td>0.77</td>
<td>62.1 - 178.4</td>
<td>2920 - 8718</td>
<td>320 - 918</td>
<td>4.1 - 4.6</td>
<td>60.0 - 67.2</td>
</tr>
<tr>
<td></td>
<td>1.49</td>
<td>223.0 - 603.9</td>
<td>4818 - 13806</td>
<td>2218 - 6006</td>
<td>20.8 - 26.4</td>
<td>65.3 - 83.2</td>
</tr>
<tr>
<td></td>
<td>2.52</td>
<td>577.4 - 1556.5</td>
<td>12304 - 33957</td>
<td>9704 - 26157</td>
<td>44.0 - 56.5</td>
<td>65.8 - 84.5</td>
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**Figure Titles**

**Figure 1.** Aerial photograph of right whale Eg 3911 on 30 Dec 2010, showing complex entanglement in the head and pectoral fins. Photo under NOAA Fisheries Permit #594-1759

**Figure 2.** Satellite telemetry track of right whale Eg 3911 (black) swimming entangled from 25 Dec 2010 to 15 Jan 2011, and following disentanglement (red; 15 Jan 2011 to 21 Jan 2011) performed from vessels *Cabretta* (blue) and *Orion* (green). Colored circles represent track starting points. The white circle represents Eg 3911’s track at the beginning of the disentanglement effort on 15 Jan.

**Figure 3.** Location of attachment of a suction-cup attached Dtag on right whale Eg 3911 a: Aerial view, with the Dtag visible on right flank, circled in black. b: Lateral view of right flank with the Dtag just above waterline. Three partially extruded darts are shown caudal to the tag. The darts have all folded at the skin surface through water drag. Photos under NOAA Permit 932-1905-00/MA-009526.

**Figure 4.** Fishing gear removed from right whale Eg 3911 on 15 Jan 2011. The total length of the configuration is approximately 24.93 m, with a combined line length of 33.63 m. A tape measure (left) is drawn to 1 m for spatial reference.

**Figure 5.** Dive profile of right whale Eg 3911 over the course of a 6:11 (hr:min) Dtag attachment. Estimated bottom depth (m; horizontal black line) and event markers are plotted for reference.
Figure 6. Boxplots of dive parameters of right whale Eg 3911 separated into phases (1) Sedation/Entangled, (2) Disentangled, and (3) Recovery in the DTAG record of right whale Eg 3911. Brackets denote significant differences between two phases. Asterisks indicate outliers.

Figure 7. Representative dive profiles (black solid line), maximum dive areas (black dashed line), and the calculated Dive Area Ratio (DAR), for phases of (a) Sedation/Entangled, (b) Disentangled, and (c) Recovery in the Dtag record of right whale Eg 3911. The distribution of the DAR for each phase is shown in (d), with brackets to denote significant differences between two phases. See text for phase definition and details.

Figure 8. Boxplots of fluke stroke rate, Root Mean Square (RMS) fluke amplitude, and Overall Dynamic Body Acceleration (ODBA) on dive descent and ascent, separated into phases (1) Sedation/Entangled, (2) Disentangled, and (3) Recovery in the DTAG record of right whale Eg 3911. Brackets denote significant differences between two phases. Asterisks indicate outliers.

Figure 9. Drag coefficient of right whale Eg 3911 at various swimming velocities in the nonentangled condition (line), and while entangled in gear-only (squares), gear-and-buoys (triangles) and sinkline (circles) configurations using minimum (closed symbol) and maximum (open symbol) parameter estimates.

Figure 10. Minimum (open symbol, dashed line) and maximum (closed symbol, solid line) estimates of total power input (W) of right whale Eg 3911 while nonentangled (lines) and entangled in gear-only (squares), gear-and-buoys (triangles) and sinkline (circles) configurations.

Literature Cited


Hoerner, S. F. 1965. Fluid dynamic drag. Published by Author, Midland Park, NJ.


Jacobs, E. N. 1934. Airfoil section characteristics as affected by protuberances 16 pp.


Supplemental Information

We used four methods to estimate body weight from length. (1) Age-weight and length-weight functions (Moore et al. 2004) approximated the weight of a two year old or 950 cm right whale to 6,717 and 6,396 kg respectively, though the paucity of the data at these age values suggests a more plausible range of 8,000 – 10,000 kg. (2) An additional age-dependent length-weight function (Fortune 2012) estimated 10,551 kg. (3) To address the degree of emaciation of the individual and its effect on the above weight estimates, we estimated width-to-total body length ratios at intervals of 10% of the body length from the tip of the rostrum and compared to width-to-length ratios measured using vertical aerial photogrammetry of 10 adult female right whales (Miller et al. 2012) (Table S1). This comparison suggests Eg 3911 was on average 20% thinner than other adult female right whales, allowing for a weight estimation of between 6,400 – 8,440 kg. (4) We reduced other scaling factors for gray whales (Sumich 1986) and generic cetaceans (Geraci and Lounsbury 2005) by 20% to account for emaciation to obtain estimates of 7,048 kg and 7,200 kg respectively.
**Table S1.** Width-to-total body length ratios at intervals of 10% of the body for 10 mesomorphic right whales and Eg 3911.

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