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 $C_{d,e,go} = 3.4\text{x}10^{-3} \pm 0.0003$, $C_{d,e,gb} = 3.7\text{x}10^{-3} \pm 0.0003$, $C_{d,e,sl} = 3.8\text{x}10^{-3} \pm 0.0004$) were significantly greater than in the nonentangled case ($C_{d,n} = 3.2\text{x}10^{-3} \pm 0.0003$; $P = 0.0156, 0.0312, 0.0078$ 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

(Moore *et al*. 2010, McLellan and Costidis unpublished necropsy report[1]). 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).

<u>Tagging and Behavior</u>

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).

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.

Dive Parameters

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,

$$DAR = \frac{A_a}{DT} = \frac{\sum_{i=2}^{n} \frac{(d_{d,i} + d_{d,i-1})}{2} \times \left(\frac{1}{fs}\right)}{DT} \quad , \qquad (1)$$

where A_a = integrated actual dive area, d_d = tag-derived depth (m) at n intervals during dive, D = maximum depth of dive (m), fs = tag sampling rate (Hz), and T = 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.* 2006*a*), and visually checked these sequences. Based on previously described gliding behaviors in right whales (Nowacek *et al.* 2001, Woodward *et al.* 2006*a*), 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 ($\alpha = 0.05/3 = 0.0167$) 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

$$Re = lU/v \qquad (2)$$

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 (1×10^{-6} m^2 s^{-1} for seawater). Reynolds numbers $>5 \times 10^6$, 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

$$D_f = \frac{1}{2}\rho U^2 A_w C_f, \qquad (3)$$

where ρ 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 $A_w = 0.08M^{0.65}$ (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,

$$C_f = 0.072(Re^{-1/5}). \qquad (4)$$

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,

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

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 γ 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

$$D_w = \frac{1}{2} \rho U^2 S_w C_{D0} \gamma k g \, . \tag{6}$$

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 (% of l) and height of the protuberance (p, m) compared to the length of the body (l, 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 (δ); 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

$$C_{DI,j} = \left(\frac{p_j}{\delta_j}\right)^{(1/3)}, \tag{7}$$

where we calculated boundary layer thickness (δ, 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

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

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):

$$D_I = \sum_{j=1}^{n} D_{I,j} = \sum_{j=1}^{n} \frac{1}{2} \rho U^2 A_{\perp p,j} C_{DI,j} . \tag{9}$$

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:

$$D_T = D_w + a(D_b + D_l) + D_I , \tag{10}$$

where D_b 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 ($D_b + D_l$).

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

$$P_{I,T} = P_L + P_{I,B} = (DU/\eta) + P_{I,B}, \qquad (11)$$

where P_L is locomotory power, and $P_{I,B}$ is power input for standard metabolism, both in W, and η 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 ($3.4M^{0.75}$; where M is body mass in kg), and 3×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_{red}, m s^{-1}) to maintain the same power output in an entangled drag scenario (D_T), is

$$U_{red} = \left[\frac{P_L\, \eta\, U^2}{D_T}\right]^{(1/3)}. \qquad (12)$$

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 γ 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 γ calculated for the mean±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 ($\chi^2 = 26.66$, $P < 0.0001$; 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 ($\chi^2 = 49.87$; $P < 0.0001$; 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 ($\chi^2 = 46.22$; $P < 0.0001$; 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; χ^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; χ^2 = 3220; P <0.0001).

Dive duration (s) differed significantly between phases (χ^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 (χ^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 before (5.00 (2.00) /5 min) and after (5.00 (1.75) /5 min) buoy and gear removal (P = 0.1679).

Proxies for Thrust

Fluke stroke rate increased significantly following sedative injection (Z = -8.417, P <0.0001; Table 3). Fluke stroke rate within dives differed significantly between phases (χ^2 = 18.7179; P = 0.0001; 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; 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 (χ^2 = 5.4288; P = 0.0662). During dive descents, ODBA differed significantly between phases (χ^2 = 8.2055; P = 0.0165), being significantly (10%) lower during Sedation/Entangled than in 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 (χ^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 3.7×10^{-3} to 2.9×10^{-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 $k = 3$ ($C_{d,e,go} = 3.4 \times 10^{-3} \pm 0.0003$, $C_{d,e,gb} = 3.7 \times 10^{-3} \pm 0.0003$, $C_{d,e,sl} = 3.8 \times 10^{-3} \pm 0.0004$) 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×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^{-1}), Midazolam has not been found to cause cardiovascular, respiratory, or airway reflex changes in humans (Reves *et al.* 1985), though a previous study reports increased respiration rates following sedation in right whales (Moore *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 *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 *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 *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 (*ca*. 76 N at 1.3 m s^{-1},(Woodward *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 (Miller *et al.* 2004, Simon *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 (3.7×10^{-3} to 2.8×10^{-3} over a range of speeds) falls well within the range of previously estimated drag coefficients for large whales (5.2×10^{-3} – 1.4×10^{-2}) (Miller *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 (Feldkamp *et al.* 1988). Though fecal glucocorticoid studies have shown markedly elevated stress hormone levels

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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 (7.3×10^9 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.

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Tables

Table 1. List of symbols

Symbol	Units	Definition
δ	m	Boundary layer thickness
γ		Surface drag augmentation factor
η		Propulsive efficiency
ρ	kg m^{-3}	Density of surrounding medium
a		Shielding factor
A_a		Integrated actual dive area
A_w	m^2	Total wetted surface area
$A_{\perp p}$	m^2	Frontal area of protuberance
C_d		Drag coefficient
C_{DI}		Interference drag coefficient
C_{D0}		Profile drag coefficient
C_f		Frictional drag coefficient
C_p		Pressure drag coefficient

d	m	Maximum body width, or diameter
d_d	m	Tag-derived depth (m)
d_x	m	Diameter at a distance l_x from the leading edge
D	m	Maximum depth of dive
D_b	N	Buoy drag
D_f	N	Frictional drag
D_I	N	Interference drag
D_l	N	Line drag
D_T	N	Total drag
D_w	N	Whale body drag
fs	Hz	Tag sampling rate
g		Appendage drag augmentation factor
h	m	Submergence depth, measured from the surface to the center line of the body
k		Profile drag augmentation factor
l	m	Length of body
l_x	m	Distance from the leading edge
M	kg	Body mass
p	m	Protuberance height
P	W	Power
Re		Reynolds number
T	s	Total dive duration
U	m s^{-1}	Velocity (swimming speed)
U_{red}	m s^{-1}	Reduced velocity due to increased drag condition
v	m^{2} s^{-1}	Kinematic viscosity of surrounding medium
x	m	Spacing distance between whale and (first) towed body

Table 2. Timeline of events on 15 January 2011 in Sedation/Entangled, Disentangled and Recovery phases of Eg 3911.

Phase	Dtag Elapsed Time (s)	GPS Time (EST)	Event
Sedation/Entangled	0	10:04:18	Dtag attachment
	1217	10:24:00	Sedation induction
	5048	11:28:00	Possible cut with spring knife

	5348	11:33:00	Cut
	5648	11:38:00	Cut
	6008	11:44:00	Cut
	6188	11:47:00	Cut
	6428	11:51:00	Cut
Disentangled	6667	11:55:00	Buoys slack and removed
	9223	12:36:00	Attachment of LIMPET Tag
	9548	12:43:00	Sedation reversal dart: did not deploy
	9548	12:43:00	Antibiotic dart
	12248	13:28:00	Antibiotic dart unsuccessful attempt
	13808	13:54:00	Antibiotic dart
Recovery	15248	14:18:00	Dart tethers, floats, and 2/4 darts recovered. Vessel *Cabretta* left scene; Vessel *Orion* following at 50-300 m distance.
	22268	16:15:00	Tag off

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.

	Pre-Injection	Post-Injection	*P*
Respiration Rate (/5 min)	5.00 (4.50)	5.00 (1.75)	0.4312
Dive Depth (m)	6.70 (3.07)	6.67 (1.86)	0.6876
Proportional Dive Depth	0.500 (0.229)	0.477 (0.122)	0.2835
Dive Duration (s)	70.40 (15.55)	71.00 (45.80)	0.8511
Time above:below significant depth	7.02:1	2.87:1	< 0.0001
Fluke stroke rate (Hz; flukes/s)	0.277 (0.049)	0.288 (0.058)	< 0.0001
Fluke stroke RMS energy (degrees)	0.0798 (0.0124)	0.1023 (0.0163)	0.002

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})

Tow Point	Configuration	Vessel Speed (m s^{-1})	Drag Force (N)
Surface	Gear Only	0.772	2.9 (2.0)
		1.49	21.6 (3.9)
		2.83	59.8 (4.9)
Surface	Gear and Buoys	0.772	16.7 (2.9)
		1.49	55.9 (12.7)
		2.73	377.6 (36.3)
Surface	Sinkline 160m	0.772	11.8 (2.9)
		0.772	8.8 (3.9)
		0.772	11.8 (3.9)
		1.49	80.4 (2.9)
		2.73	202.0 (23.5)
Bottom	Gear Only	0.772	12.7 (2.9)
		1.49	76.5 (6.9)
		2.52	415.8 (28.4)
		2.73	2.9 (2.0)
Bottom	Gear and Buoys	0.772	36.3 (3.9)
		1.49	77.5 (9.8)
		2.98	80.4 (13.7)
Bottom	Sinkline 160m	0.772	29.4 (3.9)
		1.49	70.6 (6.7)
		2.83	194.2 (24.8)

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).

	Velocity (m s^{-1})	Total Drag (N)	Total Power (W)	Locomotor Power (W)	Percent Total Power Increase	Percent Locomotor Power Increase	Percent Velocity Decrease
Gear Only	0.77	62.1 - 178.4	2920 - 8718	320 - 918	4.1 - 4.6	60.0 - 67.2	14.5 - 15.8
	1.49	223.0 - 603.9	4818 - 13806	2218 - 6006	20.8 - 26.4	65.3 - 83.2	15.4 - 18.3
	2.52	577.4 - 1556.5	12304 - 33957	9704 - 26157	44.0 - 56.5	65.8 - 84.5	15.5 - 18.5
	2.73	656.8 - 1784.3	14538 - 40234	11938 - 32434	58.8 - 46.5	65.0 - 82.2	15.4 - 18.1
	2.83	676.5 -	15361 -	12671 -	55.7 -	62.8 - 75.6	15.0 -

		1881.8	43297	35497	46.3		17.1
Gear and Buoys	0.77	73.9 - 190.2	2980 - 8778	380 - 978	6.8 - 4.8	70.6 - 98.9	20.5 - 16.3
	1.49	260.3 - 641.1	5189 - 14176	2589 - 6376	24.0 - 36.2	75.5 - 113.8	17.1 - 22.4
	2.73	953.9 - 2081.5	19939 - 45635	17339 - 37835	66.2 - 117.9	92.5 - 164.6	19.6 - 27.7
	2.98	1094.7 - 2420.9	24376 - 55957	21776 - 48157	69.1 - 120.9	90.3 - 158.2	19.3 - 27.1
Sinkline	0.77	74.4 - 190.7	2983 - 8780	383 - 981	4.39 - 6.9	71.0 - 100.2	16.7 - 21.4
	1.49	268.7 - 649.5	5272 - 14260	2672 - 6460	24.7 - 38.3	77.8 - 120.7	19.5 - 27.4
	2.73	775.9 - 1903.5	16704 - 42400	14103 - 34600	54.4 - 82.5	76.0 - 115.3	17.2 - 22.6
	2.83	808.2 - 2013.5	17844 - 45780	15244 - 37980	54.6 - 80.1	74.2 - 109.7	16.9 - 21.9

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/Entanglement, (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

Alexander, D. E. 1990. Drag coefficients of swimming animals: effects of using different reference areas. Biological Bulletin 179:186-190.
Andrews, R., R. Pitman and L. Ballance. 2008. Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. Polar Biology 31:1461-1468.
Aoki, K., Y. Y. Watanabe, D. E. Crocker, *et al*. 2011. Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: validation of at-sea metrics of body density. Journal of Experimental Biology 214:2973-2987.
Baumgartner, M. F. and B. R. Mate. 2003. Summertime foraging ecology of North Atlantic right whales. Marine Ecology Progress Series 264:123-135.
Bill, R. G. and W. F. Herrnkind. 1976. Drag reduction by formation movement in spiny lobsters. Science 193:1146-1148.
Blake, R. W. 1983. Fish locomotion. Cambridge University Press, Cambridge, UK.

Cassoff, R. M., K. M. Moore, W. A. McLellan, S. G. Barco, D. S. Rotstein and M. J. Moore. 2011. Lethal entanglement in baleen whales. Diseases of Aquatic Organisms 96:175-185.

Cavatorta, D., V. Starczak, K. E. Prada and M. J. Moore. 2005. A note on the friction of different ropes in right whale (*Eubalaena glacialis*) baleen: an entanglement model. Journal of Cetacean Research and Management 7:39-42.

Clapham, P. J., S. Young and R. J. Brownell. 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mammal Review 29:35-60.

Devore, J. 2008. Probability and statistics for engineering and the sciences. Thomson Higher Education, Belmont, CA.

Dunkin, R. C., W. A. McLellan, J. E. Blum and D. A. Pabst. 2010. The buoyancy of the integument of Atlantic bottlenose dolphins (*Tursiops truncatus*): Effects of growth, reproduction, and nutritional state. Marine Mammal Science 26:573--587.

Fahlman, A. 2008. The pressure to understand the mechanism of lung compression and its effect on lung function. Journal of Applied Physiology 104:907-908.

Fahlman, A., R. Wilson, C. Svärd, D. A. S. Rosen and A. W. Trites. 2008. Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*. Aquatic Biology 2:75-84.

Fedak, M. A., P. Lovell and S. M. Grant. 2001. Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. Marine Mammal Science 17:94-100.

Feldkamp, S. D. 1985. The effects of net entanglement on the drag and power output of a California sea lion, *Zalophus californianus*. Fishery Bulletin 83:692-695.

Feldkamp, S. D., D. P. Costa and G. K. DeKrey. 1988. Energetic and behavioral effects of net entanglement on juvenile northern fur seals, *Callorhinus ursinus*. Fishery Bulletin 87:85-94.

Fish, F. E. 1993. Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). Journal of Experimental Biology 185:179-193.

Fish, F. E. 1995. Kinematics of ducklings swimming in formation: consequences of position. Journal of Experimental Zoology 273:1-11.

Fish, F. E. 1998. Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological correlates with swimming performance. Journal of Experimental Biology 201:2867-2877.

Fish, F. E. and J. J. Rohr. 1999. Review of dolphin hydrodynamics and swimming performance. US Navy SPAWAR Systems Center Technical Report 1801. 193 pp.

Fortune, S. M. E. 2012. North Atlantic right whale growth and energetics. M.Sc., University of British Columbia, Vancouver, B.C. 93 pp.

Gallivan, G. A. 1992. What are the metabolic rates of cetaceans? Physiological Zoology 65:1285-1297.

Geraci, J. R. and V. J. Lounsbury. 2005. Marine mammals ashore: a field guide for strandings. National Aquarium in Baltimore, Baltimore, Maryland.

Hamilton, P. K., A. R. Knowlton and M. K. Marx. 2007. Right whales tell their own stories: the photo-identification catalog. Pages 75-104 *in* S. D. Kraus and R. M. Rolland eds. The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA.

Hamner, W. A., G. S. Stone and B. S. Obst. 1988. Behavior of southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphausia superba*. Fishery Bulletin 86:143-150.

Hertel, H. 1966. Structure, form, movement. Reinhold Publishing, New York, NY.

Hertel, H. 1969. Hydrodynamics of swimming and wave-riding dolphins. Pages 31-63 *in* H. T. Andersen ed. The biology of marine mammals. Academic Press, New York.

Hind, A. T. and W. S. C. Gurney. 1997. The metabolic cost of swimming in marine homeotherms. Journal of Experimental Biology 200:531-542.

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

Hunt, K. E., R. M. Rolland, S. D. Kraus and S. K. Wasser. 2006. Analysis of fecal glucocorticoids in the North Atlantic right whale (*Eubalaena glacialis*). General and Comparative Endocrinology 148:260-272.

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

Johnson, M. and P. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3-12.

Jones, T. T., B. Bostrom, M. Carey, *et al*. 2011. Determining transmitter drag and best-practice attachment procedures for sea turtle biotelemetry. NOAA Technical Memorandum NMFS SWFSC-480:1-58.

Kraus, S. D., J. H. Prescott, A. R. Knowlton and G. E. Stone. 1986. Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. Report of the International Whaling Commission (Special Issue 10):139-144.

Ledwell, W., K. Curren, H. Huntington and C. Hood. 2010. The whale man of Newfoundland and Labrador: Jon Lien 1939-2010. Canadian Field-Naturalist 124:384-398.

Lighthill, M. J. 1971. Large-amplitude elongated-body theory of fish locomotion. Proceedings of the Royal Society of London Series B, Biological Sciences 179:125-138.

Mayo, C. A. and M. K. Marx. 1990. Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. Canadian Journal of Zoology 68:2214-2220.

McGregor, A. E. N. 2010. The cost of locomotion in North Atlantic right whales *Eubalaena glacialis*. PhD, Duke University, Durham, NC 182 pp.

Millar, J. S. and G. J. Hickling. 1990. Fasting endurance and the evolution of mammalian body size. Functional Ecology 4:5-12.

Miller, C. A., P. B. Best, W. L. Perryman, M. F. Baumgartner and M. J. Moore. 2012. Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. Marine Ecology Progress Series 459:135-156.

Miller, P. J. O., M. Johnson, P. Tyack and E. A. Terray. 2004. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. Journal of Experimental Biology 207:1953-1967.

Moore, M., R. Andrews, T. Austin, *et al*. 2012. Rope trauma, sedation, disentanglement, and monitoring-tag associated lesions in a terminally entangled North Atlantic right whale (*Eubalaena glacialis*). Marine Mammal Science:n/a-n/a.

Moore, M. J., A. Bogomolni, R. Bowman, *et al*. 2006. Fatally entangled right whales can die extremely slowly. Pages 1-3 OCEANS 2006.

Moore, M. J., A. R. Knowlton, S. D. Kraus, W. A. McLellan and R. K. Bonde. 2004. Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002). Journal of Cetacean Research and Management 6:199-214.

Moore, M. J. and J. M. van der Hoop. 2012. The Painful Side of Trap and Fixed Net Fisheries: Chronic Entanglement of Large Whales. Journal of Marine Biology 2012:4.

Moore, M. J., M. Walsh, J. Bailey, *et al*. 2010. Sedation at sea of entangled North Atlantic right whales (*Eubalaena glacialis*) to enhance disentanglement. PloS one 5:e9597.

Morin, D. and J. Kenney. 2011. 2010 Large Whale Entanglement Report. National Marine Fisheries Service. 70 pp.

Nowacek, D. P., M. P. Johnson, P. L. Tyack, K. A. Shorter, W. A. McLellan and D. A. Pabst. 2001. Buoyant balaenids: the ups and downs of buoyancy in right whales. Proceedings of the Royal Society of London Series B, Biological Sciences 268:1811-1816.

Parks, S. E., J. D. Warren, K. Stamieszkin, C. A. Mayo and D. Wiley. 2012. Dangerous dining: surface foraging of North Atlantic right whales increases risk of vessel collisions. Biology Letters 8:57-60.

Reves, J. G., R. J. Fragen, H. R. Vinik and D. J. Greenblatt. 1985. Midazolam: pharmacology and uses. Anesthesiology 62:310-324.

Robbins, J. and A. R. Knowlton. 2012. Apparent survival of North Atlantic right whales after entanglement in fishing gear. Final Report for NOAA CA #NA09OAR4320129. 29 pp.

Robbins, J. and S. Landry. 2012. Apparent survival and sub-lethal effects of entanglement on Gulf of Maine humpback whales. Final Report for NOAA CA #NA09OAR4320129. 36 pp.

Semmlow, J. 2012. Signals and systems for bioengineers: a MATLAB-based introduction. Academic Press, Waltham, MA.

Simon, M., M. Johnson, P. Tyack and P. T. Madsen. 2009. Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). Proceedings of the Royal Society of London Series B, Biological Sciences 276:3819-3828.

Sumich, J. L. 1986. Growth in young gray whales (*Eschrichtius robustus*). Marine Mammal Science 2:145-152.

van der Hoop, J. M., M. J. Moore, S. G. Barco, *et al*. 2012. Assessment of management to mitigate anthropogenic effects on large whales. Conservation Biology 27:121-133.

Videler, J. J. and D. Weihs. 1982. Energetic advantages of burst-and-coast swimming of fish at high speeds. Journal of Experimental Biology 97:169-178.

Watson, K. P. and R. A. Granger. 1998. Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). Journal of Experimental Biology 201:2497-2505.

Williams, T. M. 2001. Intermittent swimming by mammals: a strategy for increasing energetic efficiency during diving. American Zoologist 41:166-176.

Williams, T. M., W. A. Friedl and J. E. Haun. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. Journal of Experimental Biology 179:31-46.

Wilson, R. P., C. R. White, F. Quintana, L. G. Halsey, N. Liebsch, G. R. Martin and P. J. Butler. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. Journal of Animal Ecology 75:1081-1090.

Woodward, B. L., J. P. Winn and F. E. Fish. 2006*a*. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. Journal of morphology 267:1284-1294.

Woodward, B. L., J. P. Winn, M. J. Moore and M. L. Peterson. 2006*b*. Development of a towed telemetry tag for tracking the long term movements of right whales at sea. Final Report for NOAA Award # NA04NMF4720400. 18 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.

	Width to Total Body Length Rati							
	10%	20%	30%	40%	50%	60%	70%	80%
Mesomorphic Right Whales (n = 10)	0.149	0.191	0.226	0.22	0.207	0.176	0.126	0.063
Eg3911	0.132	0.175	0.199	0.195	0.156	0.121	0.078	0.051
Eg3911:Mesomorphic ratio	0.887	0.92	0.88	0.887	0.751	0.684	0.617	0.798
Mean Ratio								0.803